Effects of habitat loss on populations of the eastern green lizard *Lacerta viridis* at the core and periphery of its distribution range

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Ana María Prieto-Ramírez
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1. Gutachter: Prof. Dr. Wolfgang Wägele
2. Gutachter: Prof. Dr. Bernhard Misof

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Abstract

Habitat loss is the main threat to biodiversity. Modified landscapes resulting from habitat loss are characterized by a reduced amount and patchy distribution of habitat, and by changes in landscape composition and landscape configuration (spatial relations between landscape elements). Populations inhabiting such landscapes face reduced connectivity and gene flow, population decline, higher vulnerability to stochastic processes, and eventually, extinction. Ecological specialization is one of the main traits predicting vulnerability of species to habitat loss. It has been mainly studied at the species level, with insights at the intraspecific level being barely addressed in the habitat loss literature. The Kühnelt principle of regional stenoecy states that the range of colonizable habitats and suitable conditions is wider at the core of the distribution range of species compared to the periphery. Then, populations living at the core are habitat generalist, and those in the periphery habitat specialist. This implies that peripheral populations would have a higher sensibility to habitat loss compared to populations at the core, and also that different conservation measures are necessary to protect the species in each region. The study of occupancy patterns of habitat patches across modified landscapes is one of the most useful tools to study effects of habitat loss on the persistence of populations, and can be applied to test differential sensitivity to habitat loss among populations of the same species in different regions. On the other hand, because this approach depends on the extinction of populations to find patterns and effects, in order to identify vulnerable population before they irreversibly decline, morphological and physiological parameters representative of the status of individuals have also been proposed to be used as early warning indicators of populations' stress. In this project I combined extensive fieldwork with advanced methods in landscape ecology and statistics to study populations of the eastern green lizard *Lacerta viridis* located at the core (Bulgaria) and at the northern periphery of its distribution range (Germany, Czech Republic). *L. viridis* is protected under the EU Habitats Directive and is threatened to extinction in Germany and Czech Republic. The objectives of this research are to test the Kühnelt principle, evaluate if predictions of specialization at the species level regarding effects of habitat loss on occupancy patterns are also met at the intraspecific level, and evaluate the suitability of morphological and physiological parameters as early indicators of populations stress. My results show that peripheral populations of *L. viridis* are specialist in comparison to core ones, have a smaller niche size and select microhabitats based on different environmental parameters regions (Chapter 3). Specialization predictions of vulnerability to habitat loss were also met at the intraspecific level. In the periphery, in comparison to the core, populations depended more on habitat quality, the effects of individual landscape composition predictors were stronger and overall habitat loss had an impact at smaller scales. Moreover, regions differed in the parameters of landscape structure that affected occupancy patterns the most (Chapter 4). Finally, I identified two parameters of individual status -body condition and fluctuating asymmetry- that are suitable to be used as early indicators of stress for populations of *L. viridis* inhabiting modified landscapes (Chapter 5). This dissertation is a contribution to the knowledge of the ecology of *L. viridis* and to the improvement of conservation measures to protect the species across its range. This work also broadens the knowledge about intraspecific regional differences in ecological traits of species and the application of traits at the intraspecific level to predict geographically-dependent populations' sensibility to habitat loss.

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1. General Introduction

1.1. Habitat loss as main threat to biodiversity

The Anthropocene has imposed unprecedented negative pressures on global biodiversity during the last two centuries (Ceballos et al. 2015), and these pressures have become stronger during the last decades with rates of biodiversity loss expected to continue increasingly during the 21th century (Pereira et al. 2010). Among the overall effects of anthropogenic pressures on biodiversity are the expected increment in species extinction rates (Novacek and Cleland 2001; Brook et al. 2008), changes in species distribution and abundance (Gaston and Fuller 2008; Dirzo et al. 2014; Palmer et al. 2015) and changes in communities structure (De Coster et al. 2015; Hamer 2016).

Habitat destruction due to land cover and land use changes is currently the most intense pressure threatening global biodiversity, followed by overexploitation and climate change (Maxwell 2016). More than 75 % of the global terrestrial environment has been altered by humans (Watson et al. 2016), principally due to the expansion and intensification of agriculture (Ellis et al. 2010), and 86% of extant terrestrial vertebrate species evaluated and classified as vulnerable, endangered or critically endangered by the IUCN are affected by habitat destruction (IUCN 2020). The rate of habitat loss has rapidly increased since the 1990's (Watson et al. 2016) and future scenarios of habitat destruction predict habitat conversion to keep increasing (Oakleaf et al. 2015), even under the most optimistic socio-economic scenario directed to reduce CO2 emissions (Chaudhary and Mooers 2018). Thus, changes in land cover and land use are expected to keep being the strongest driver of biodiversity loss by 2100 (Sala et al. 2000, Ellis et al. 2010), causing an increment in the number of endangered species and in the extinction risk of already threatened ones (Powers and Jetz 2019 Gonçalves-Souza et al. 2020), reducing phylogenetic diversity (Chaudhary and Mooers 2018), and intensifying abundance decline of local populations and changes in community structure (Newbold 2015; Wilson et al. 2016).

Moreover, habitat loss acts in synergy with other drivers (Brook et al. 2008) and its interaction with climate change is of especial concern due to the strong projected intensifying effects among both drivers, which can put at risk species adaptive capacity to climate change (Segan et al. 2016; Mantyka-Pringle et al. 2012). Habitat loss can cause the destruction of habitat refugia in localized suitable climatic areas (Dobrowski 2011) or imperil species' dispersal capacity to reach them, blocking one of the most important adaptive responses of species to climate change, that is the expansion or shift of the distribution range (Opdam and Wascher 2004). Additionally, habitat loss can block other in-situ adaptive responses to climate change like phenotypic plasticity (Urban et al. 2014) and microevolutionary processes (Karell et al. 2011) due to its negative effects on genetic and phenotypic diversity as a result of population decline. Effects of habitat loss are also expected to be increased by climate change either because suitable environmental conditions are not met anymore in the vegetation covers that represented habitat, thus increasing the distances individuals have to traverse before finding a suitable habitat area (Williams et al. 2007; Mantyka-Pringle et al. 2012), or because adverse environmental conditions can reduce individual fitness (Kingsolver et al. 2013) and cause stochasticity in population dynamics increasing population extinction risks (Verboom et al. 2010).

Thus, the existent and projected enormous negative effects of habitat loss, alone or in synergy with other drivers, demands the understanding of all the spectrum of mechanisms through which this driver affects ecological processes at different levels of biological organization.

1.2. Habitat loss as an ecological process

Habitat loss is a type of landscape modification occurring across spatial and temporal scales, through which areas that represent habitat are transformed and converted into other land covers usually associated with an anthropogenic use, like croplands or urban areas. The loss of native vegetation around the world is certainly a problem with catastrophic consequences for biodiversity (Watson et al. 2016), and it is for this reason that several authors equate ‘habitat’ to ‘native vegetation’ (Andrén 1994). Also, binary conceptual models based on Island biogeography theory (IBT, MacArthur and Wilson 1967), which make a distinction between habitat and non-habitat land covers, assume that a specific terrestrial biotope or vegetation cover type represents habitat for all native species. Although this classification can be correctly applied in some cases (Santos et al. 2008; Holland and Bennet 2010), in other cases this binary approach is incorrect. In the strict sense, habitat refers to the resources and conditions that allow the survival and reproduction of a given species (Hall et al. 1997). As habitat is a species-specific concept, it is important to acknowledge habitat loss as a species dependent process (Fischer and Lindenmayer 2007; Betts et al. 2014), in which specific land covers might represent habitat for some species but not for others.

As habitat loss is a landscape modification type, this means that as an ecological process it occurs at the landscape level, with ‘landscape’ understood as a spatially explicit heterogeneous mosaic composed of different ecosystems and land cover types (Wiens et al. 1993; Turner et al. 2001). Thus, although habitat loss is a global phenomenon and its effects on biodiversity can be measured at regional and global levels, calculations at these levels are done through landscapes and networks of landscapes that constitute regions, because the ecological processes that govern the early patterns of species decline, which in a later stage define species extinction risks at regional and global scales, occur at the landscape level (Opdam and Washer 2004; Newbold et al. 2015). The extent of the landscape, however, varies depending on the ecological process and/or species under study.

The extirpation of habitat leads to two interrelated spatially explicit patterns: the emergence of portions of habitat patches and the transformation of the landscape structure. In a landscape with disconnected portions of habitat, patches are isolated from each other and have individual characteristics in terms of size, shape and habitat quality. By its side, changes in landscape structure are represented by changes in composition and configuration of the elements in the landscape. Landscape composition refers to the diversity and relative amount of each element in the landscape -land cover/use classes-, and landscape configuration to the spatial arrangement of these elements (With 2019). Thus, after the destruction of part of the habitat in the landscape, the configuration of the habitat is transformed resulting in patches embedded into a matrix of land covers that do not represent habitat.

The high interdependency of variables describing landscape spatial patterns and local patch conditions resulting from habitat loss, makes this ecological process a very complex one. A local patch characteristic like patch size is related to overall habitat amount in the landscape, because as habitat loss progresses, patches become smaller (Fahrig 2003). Reduced patch quality is influenced by the surrounding conditions defined by the composition of the landscape directly adjacent to patches, which can lead to changes in local environmental conditions, promote biological interactions that reduce resources within the patch (Pafilis et al. 2013) and cause edge effects due to the contrast between habitat and non-habitat land covers (Hatfield et al. 2020). Also isolation, which is a characteristic of each individual patch, is defined by the configuration of habitat in the landscape and can correlate with overall amount of habitat, as reduced habitat in the landscape increases distances among patches (Fahrig 2003). To capture this complexity, the study of effects of habitat loss requires a holistic approach that covers the local and landscape parameters that can affect a specific ecological process, in order to be able to test for interdependencies among variables and identify those that account for a specified effect.

Furthermore, habitat loss can occur parallel to other habitat modification types, like habitat fragmentation, but not necessarily (Villard and Metzger 2014). Habitat fragmentation per sé is the subdivision of habitat into fragments (patches) and increases with increasing number of patches in the landscape (Fahrig 2003), and as such is a characteristic of the landscape. Processes of habitat fragmentation take always place in parallel to habitat loss, and evidence has shown this occurs at high and medium levels of habitat amount in the landscape (Villard and Metzger 2014; Melo et al. 2017). However, habitat loss does not always result in an increased number of patches in the landscape, because as habitat destruction progresses, the number of patches is reduced.

Changes in landscape structure, the resulting habitat configuration and the individual characteristics of patches lead to several detrimental processes for populations. To study and understand these processes, several theoretical approaches have been proposed. Among them are the two key foundational theoretical frameworks of landscape ecology, the Island Biogeography Theory (IBT, MacArthur and Wilson 1967) and the Metapopulation Dynamics Model (MDM, Hanski et al. 1998), which assume binary landscapes where patches are surrounded by an inhospitable homogeneous matrix, and in the case of the MDM connected through corridors. These two models predict that small patches will maintain smaller populations and isolation will decrease migration rates among them, resulting in increasing extinction probability with decreasing patch size and increasing isolation. Small population size, reduced migration rates and, in consequence, lower gene flow among populations can cause loss of genetic variability (Haila 2002; Tallmon et al. 2002) and promote mating among close relatives (Charlesworth and Willis 2009), which increases the risk of inbreeding depression and extinction (Henle et al. 2004a).

Although the IBT and the MDM have been very useful to understand some ecological processes that lead to the extirpation of single populations within patches or of metapopulations in the landscape (Opdam 1991; Hanski and Ovaskainen 2000; Laurance 2008), the assumption that the matrix is homogeneous hinders its applicability to most landscapes. The patch-mosaic model (Forman et al. 1995) goes beyond the patch size and isolation perspective, and states that patches are embedded in a heterogeneous matrix, thus accounting for the characteristics of the landscape structure as defined by land covers other than habitat. Through the application of this conceptual approach it has been possible to test effects of the matrix composition and of the spatial relations between non-habitat land covers and patches (configuration), and to better identify important ecological functions of landscapes that further determine the abundance and persistence of populations. For instance, landscape permeability to dispersal is a (species specific) function of the landscape defined by the land covers that compose the matrix and their spatial relations. It influences the levels of isolation, given patches might not only be distant from each other but also separated by land covers that individuals cannot cross and far from structures that could serve as corridors or stepping stones (Evans et al. 2017). Also, the overall habitat amount in the landscape determines resources availability in the landscape, which has direct effects on local populations and on patterns of distribution and abundance of populations, independently of habitat configuration (Melo et al 2017; Gardiner et al. 2018; Watling et al. 2020). Moreover, the amount of other land covers in the landscape can also have direct effects in the persistence of local populations irrespective of the configuration of the habitat (Ryberg and Fitzgerald 2016), and their spatial relations with habitat patches can influence the levels of edge effect that populations within patches experience (Prevedello and Vieira 2009; Hatfield et al. 2020).

The link between habitat loss and spatial patterns of species distribution resulting from the persistence and/or extinction of local populations is a key issue in conservation biology. Therefore, it is very important to identify the characteristics of the landscape structure and/or patches that increase the extinction probability of local populations, and to prevent extant populations from disappearing (Gu and Verboom 2003). However, effects at the individual level are also of special importance to track and identify negative effects of habitat loss that are not yet apparent at the population level. For instance, modified landscape structure and patch conditions may have impacts on morphological and physiological traits of individuals that can be used as early warning indicators to identify those populations that might be at risk of severe decline. Among the main traits used as indicators are fluctuating asymmetry, which are random deviations from perfect symmetry in symmetrical morphological traits (Palmer and Strobeck 1986) and body condition, both of which have been extensively linked to effects of habitat loss (Marchand et al. 2003; Amo et al. 2007a,b; Janin et al. 2011; Benitez et al. 2018). These indicators inform about the health and fitness state of single individuals, and can be associated with specific ecological mechanisms, like competition, shortage of resources or inbreeding (Leamy and Klingenberg 2005; Bucher et al. 2011; Beasley et al. 2013), taking place before populations actually decline.

1.3. Sensitivity of species to habitat loss

In the efforts for understanding the complexity and the effects of habitat loss, one of the main goals of conservation biology is to identify the species that might be more vulnerable to the destruction of their habitats. For this, several morphological, life-history and ecological traits of species have been proposed as predictors of species sensitivity to habitat loss and fragmentation. Among the traits with more empirical support are population size, population variability, rarity and habitat specialization (Henle et al. 2004b; Keinath et al. 2017). Species with small population size, with lower capacity to maintain stable populations after disturbance, with narrow distribution range and/or specialists have a higher risk to become extinct due to habitat loss. Other traits that have been evaluated include dispersal ability, area requirements, reproductive potential, trophic position, body size, sociality and relative position in the geographic range (Henle et al. 2004b; Quesnelle et al. 2014; Chichorro et al. 2019). Species with lower dispersal abilities, high area requirements, low reproductive potential, high trophic position, large body size, complex social or gregarious behaviors and/or located at the edges of their geographic range are expected to have a higher sensitivity to habitat loss.

However, evidence for most traits is mixed mainly due to indirect relations with extinction proneness and interactions among traits. For instance large species might be more sensitive due to small population sizes, lower abundances and higher area requirements, but less sensitive due to expected lower population size fluctuations, higher longevity - which would mean better recover chances in the long term (storage effect), and because of expected higher mobility (Quesnelle et al. 2014). Dispersal ability predicts lower risk, but if it is due to large home range it means that area requirements are higher, and then fewer individuals can be supported after habitat destruction, leading to small population size and increasing extinction risk. Also, species with high dispersal power would be more exposed to mortality risks while moving through a hostile matrix (Fahrig 2007). Social or gregarious species are predicted to have higher area requirements and therefore a higher risk, but if it is linked with high mobility, then social species are less sensitive than solitary ones (Jauker et al. 2013).

Although all these interactions make it very difficult to identify appropriate traits that better indicate sensitivity of species to habitat loss, specialization is still one of the traits most directly linked to extinction proneness (Ewers and Didham 2006; Fisher and Lindenmayer 2007; Keinath et al. 2017). Even after accounting for the fact that traits have synergistic effects, which is species and landscape dependent, habitat specialization appears to be one of the high ranked indicators of sensitivity (Hatfield et al. 2018). Evidence of higher sensibility of specialist species to threatening processes of habitat loss has been reported for insects (Krauss et al. 2003; Koh et al. 2004; Powney et al. 2015), birds (Devictor et al. 2008; Gillies and St. Clair 2008), mammals (Püttker et al. 2013; Pardini et al. 2017), amphibians (Almeida-Gomes et al. 2016) and reptiles (Walkup et al. 2017).

Specialist species are characterized by having narrow niche breadths, which predict that they are able to survive only in a limited range of habitats and conditions (Devictor et al. 2010). When their habitat is destroyed, specialist species are unable or comparatively less capable of using land covers in the matrix to exploit resources and to move through (Komonen et al. 2004), which makes them more sensitive to the loss of their habitat at the landscape scale compared to generalist species (Swihart et al. 2006). With lower chances to move through the landscape, immigration rates among populations decrease (Püttker et al. 2013), and without the rescue effect of immigration, local populations become more dependent on local patch size, which increases the risk to suffer severe population decline as patches are cut off (Krauss et al. 2003; Pardini et al. 2017). Further, the degradation of habitat conditions within patches can reduce the quality of the resources individuals can utilize, sharpening the risk of population decline (Ye et al. 2013). Hence, the sensibility of specialist species can be characterized by their higher vulnerability across spatial scales (Vergara and Armest, 2009) and by the combined effects with two other traits, lower mobility capacity and small population size. These two traits might not be characteristics of the species when inhabiting non-modified landscapes, but can be emergent properties derived from species intrinsic lower capacity to respond to habitat loss (Miguet et al. 2016).

1.3.1 Intraspecific differences in sensitivity to habitat loss

Although species traits are important to predict effects of habitat loss and identify more sensitive species, more concern has been raised about the fact that traits cannot always be extrapolated across distribution ranges of species and the importance to consider site specific responses (Thornton et al. 2010; Hatfield et al. 2018). Ecological traits of species like population abundance have been shown to change across the distribution range of species, with populations often being less abundant towards range edges (Brown 1996). In a similar way, the degree of ecological specialization can change across the distribution range of species. The Kühnelt principle of regional stenoecy (Kühnelt 1965) states that in the case of species with broad distribution ranges, due to a narrower range of available suitable habitats and conditions in the periphery compared to the core, populations living at the periphery are comparably more stenoecious or specialized than populations at the core. This suggests that at a local scale, the characteristics of the species at their range edge might fit those of specialist species, exploiting narrow ecological niches, and having restricted and more discontinuous distributions (Brown 1996).

In some species, niche breadth has been shown to be narrower towards the periphery of the distribution range (Thomas et al. 1999; Lappalainen and Soininen 2006), creating a pattern at the intraspecific level that is not evident at the species level, and that consists of the interaction of two traits known to predict vulnerability to habitat loss: specialization and position within the distribution range. Intraspecific differences in the interaction among traits imply that there are also differences in the sensitivity to habitat loss among populations of the same species. The link between species traits and differential response and sensitivity to habitat loss has been partially demonstrated in other studies performed at the regional level across species. Komonen et al. (2004) showed that among butterfly species in Finland, those for which the study region represented the northern edge of their distribution ranges, had narrower niche breadths and lower mobility capacity compared to species that were further from their range edge. Also, in an agricultural landscape in Indiana, USA, Swihart et al. (2003, 2006) found that mammals, amphibian and turtle species that were located at their northern range edge had not only a narrower niche breadth, but also higher sensitivity to reduced habitat amount and landscape diversity, resulting in lower occupancy rates compared with species that were further from their range edge.

Accounting for differential sensitivity to habitat loss of peripheral populations, should necessarily lead to the application of different conservation measures for populations at the edge of the range compared with those applied at the core. Peripheral populations are usually genetically and morphologically divergent from core population, and therefore are of important value for the genetic diversity of species, as well as for the potential evolutionary processes that define species range limits or speciation (Lesica and Allendorf 1995; Sexton et al. 2009). Moreover, in the regions where peripheral populations occur, the species might be of conservation priority because it is rare relative to other species in the region (Thakur et al. 2018).

1.3.2. Sensitivity of reptile species

Reptiles are rapidly declining at global (Gibbons et al. 2000) and local scales (Sinervo 2010), and as for most vertebrate taxa, habitat loss represents their main threat (Gibbons et al. 2000; Böhm et al. 2013). As ectotherms, reptiles rely on abiotic conditions, especially temperature, to maintain optimal physiological performance (Meek 1995). Thus, given landscape modification has an impact not only on the structural landscape but also on abiotic conditions (Saunders et al. 1991), reptiles might be more vulnerable than other taxa to habitat loss. Besides their sensitivity to changes in environmental condition, reptiles' sensitivity is in general higher due to their comparatively lower dispersal ability and relative small home ranges (Kearney et al. 2009). Empiric evidence has shown that reptiles are more sensitive than other taxa to reduced patch size (Keinath et al. 2017) and among vertebrate ectotherms, reptiles can be more sensitive to changes in local conditions within patches than amphibians (Larson 2014).

The sensitivity of reptiles to temperature is a key characteristic shaping many ecological processes and also responses to anthropogenic impacts. For instance, thermal niche alone has been found to predict sensitivity of reptiles to deforestation (Frishkoff et al. 2015) and heat tolerance was found to explain sensitivity to habitat modification (Nowakowski et al. 2018). Also, thermoregulatory behavior, which is one of the main strategies of reptiles to disconnect body temperature from environmental temperature by basking or staying in cool spots, and which involves daily and seasonal activity patters of individuals (Meek 1995), is highly dependent on vegetation structure present in the habitat, which increases sensitivity of reptiles to habitat degradation within remnant patches (Kearney et al. 2009). Moreover, it is well known that reptiles are highly threatened by climate change (Le Galliard et al. 2012; Winter et al. 2016), and that the synergistic effects between climate change and habitat loss makes their sensitivity more acute (Foufopoulos et al. 2011, Gadsden et al. 2012). Reptiles are predicted to survive climate change trough three main mechanisms, development of thermal tolerance, change in thermoregulatory behavior and range shifts (Sinervo et al. 2010). The first option implies changes in physiological thermoregulatory mechanisms, either through plasticity or genetic adaptation (Urban et al. 2014; Caldwell et al. 2015). As for the other two options, these strongly rely on habitat availability and quality. With increasing temperatures reptiles will depend on shaded spots provided by vegetation to thermoregulate (Kearney et al. 2009; Grimm-Seyfarth et al. 2017), and on habitat availability across regions to successfully shift their distribution ranges following their climatic niches (Ballesteros-Barrera et al. 2007; Gadsden et al. 2012; Mizsei et al. 2020).

In spite of higher sensitivity to both, habitat loss and climate change, reptiles are not as protected as other vertebrate taxa (Roll et al. 2017), and are much less studied (Böhm et al. 2013), which, together with the ecological context that makes them highly vulnerable to landscape modification, forces to invest resources and research to understand the ecological effects of habitat loss on reptile species. This is especially necessary for lizards, which are the only reptile taxa for which habitat loss is the main threat besides climate change (Fitzgerald et al. 2018).

2. Aims and Scope

The main aim of this thesis is to investigate effects of habitat loss on the eastern green lizard *Lacerta viridis* by performing in depth insights in two directions (Figure 2.1). First, in the possible differential sensitivity to habitat loss between populations located at the core and at the periphery of the distribution range of species due to possible intraspecific differences in the degree of habitat specialization; and second, in the effects of habitat loss on ecological processes occurring at different stages of the population decline process.

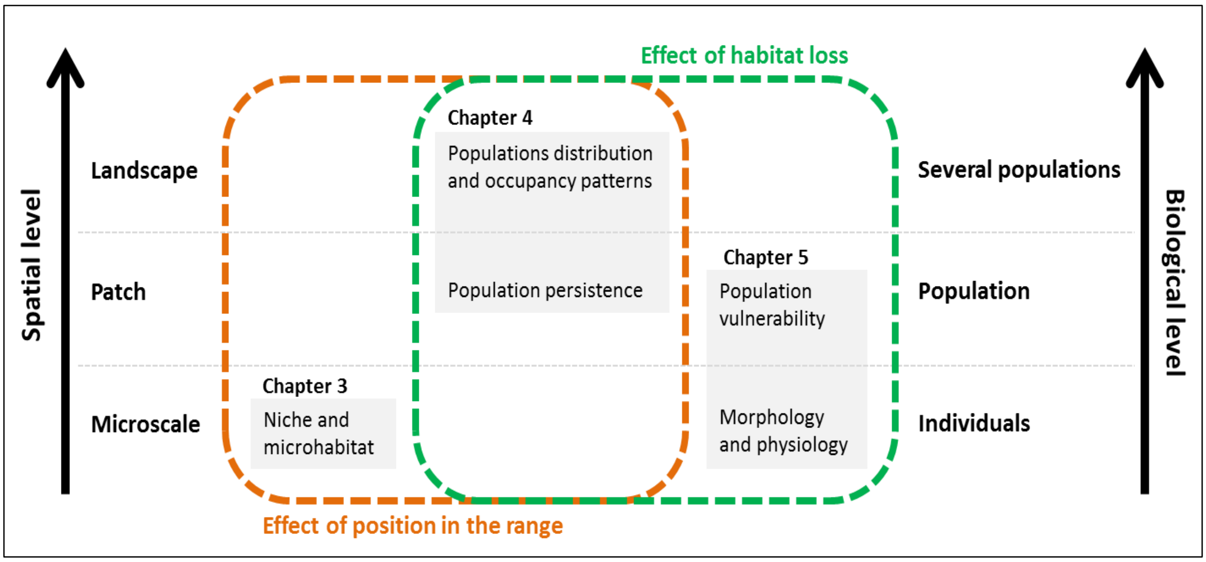

Figure 2.1. Thematic scheme of this dissertation.

To achieve this aim I studied populations of *L. viridis* (Figure 2.2) located at the core of its distribution range, in Bulgaria, and at the northern periphery of its range in Passau, Germany and Prague, Czech Republic. In each region I evaluated ecological processes and patterns occurring at different spatial and biological levels (Figure 2.1.) *L. viridis* is a species with a broad distribution range covering Asia Minor, Eastern Europe and the Balkan Peninsula (Nettmann and Rykena 1984; Kwet 2005). It is regarded as a generalist species, using a wide range of suitable habitats. However, there is enough qualitative information available (eg. Nettmann and Rykena 1984; Strödicke 1995; Laube and Leppelsack 2007; Mollov, 2011) showing a narrower range of habitats used by the species in the northern periphery compared to regions located in the core, thus indicating possible intraspecific differences in specialization degree among regions.

Figure 2.2. Pair of *Lacerta viridis* during the mating season in the surroundings of Plovdiv, Bulgaria.

The habitat of *L. viridis* is known to be fragmented across the distribution range of the species (Elbing et al. 1997) and it is protected by the European Habitats Directive (2007) under Annex IV. In the northern part of its range, the species is at high risk of extinction and therefore included in the red lists of Germany and Czech Republic (Beutler and Rudolph 2003; Zavadil and Moravec 2003). *L. viridis* is a species with a low tendency to disperse, mainly during natal dispersal and for shorter distances compared to other green lizards (Elbing 2000; Schneeweiss 2001). As low dispersal has been linked with high sensitivity of species to habitat loss (Henle et al. 2004b; Chichorro et al. 2019), this characteristic of the species highlights the importance of studying the conditions under which local populations are threatened, as well as the possible indicators that can be used in order to identify vulnerable populations on time before local extinctions occur.

Given the different climatological conditions in different parts of the distribution range of *L. viridis,* there is a high geographical variability in the phenology of the species (Figure 2.3), with annual activity patterns differing among regions (Nettmann and Rykena 1984; Fischer and Rehák 2010). This variability allows for a study design in which different regions in the distribution range of the species can be visited in the same year. Hence, I was able to carry out field seasons that included data gathering in the core as well as in the northern peripheral regions, at the time of the year when activity is higher in each region, which is around the mating season (Nettmann and Rykena 1984).

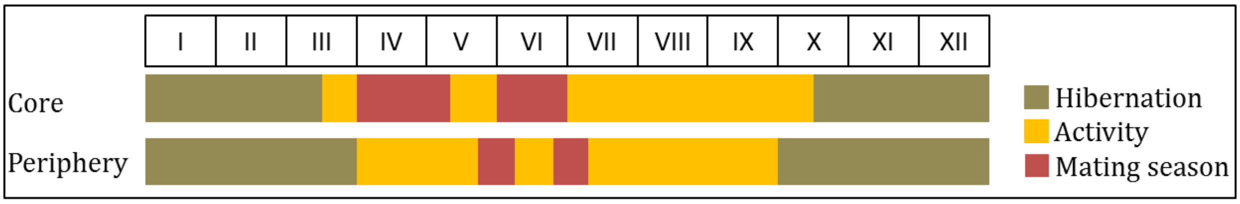

Figure 2.3. Some aspects of the phenology of *Lacerta viridis* at the core and at the northern periphery of its distribution range.

The specific objectives of my work are defined under three hypotheses.

Hypothesis I: Geographical differences in degree of specialization (Chapter 3)

The first objective of this thesis is to quantify differences in niche size and microhabitat use and selection among regions. Following the Kühnelt's principle of regional stenoecy (Kühnelt 1965), I hypothesize that populations in the northern periphery will have a higher specialization degree relative to populations in the core, reflected by a smaller realized niche and by the stringent selection of fewer microhabitat types.

Hypothesis II: Differential sensitivity to habitat loss (Chapter 4)

The second objective is to test effects of habitat loss on the distribution of populations in landscapes located at the core and at northern periphery of the distribution range. For this, I evaluate effects of patch characteristics and landscape structure parameters at different spatial scales on the occupancy probability of populations in each region to find out which are the most important parameters affecting occupancy patterns and at which scale(s) in each region. In this intraspecific comparison, I expect to find the same patterns of the effects of habitat loss reported at the species level in relation to specialization. Thus, I hypothesize that northern, more specialized, peripheral populations are affected by habitat loss at smaller spatial scales and are more sensitive to isolation, patch area and habitat quality, in comparison to core populations.

Hypothesis III: Early warning indicators (Chapter 5)

The third objective of this dissertation is to evaluate the suitability of individuals' morphological and physiological parameters to be used as warning indicators of negative effects of habitat loss before persistence of populations be threatened. To do this, I test effects of habitat loss on the body condition, fluctuating asymmetry (FA) and ectoparasite load of individuals of *L. viridis* inhabiting core populations. I linked population-level response of these three possible indicators with patch and landscape structure characteristics. I hypothesize that these morphological and physiological parameters are sensible to effects of habitat loss, and therefore, suitable as early warning indicators of population vulnerability. Also, I predict that isolation, reduced patch area, reduced habitat amount in the landscape and decreased habitat quality will have negative effects on body condition and positive effects on FA and ectoparasite load.

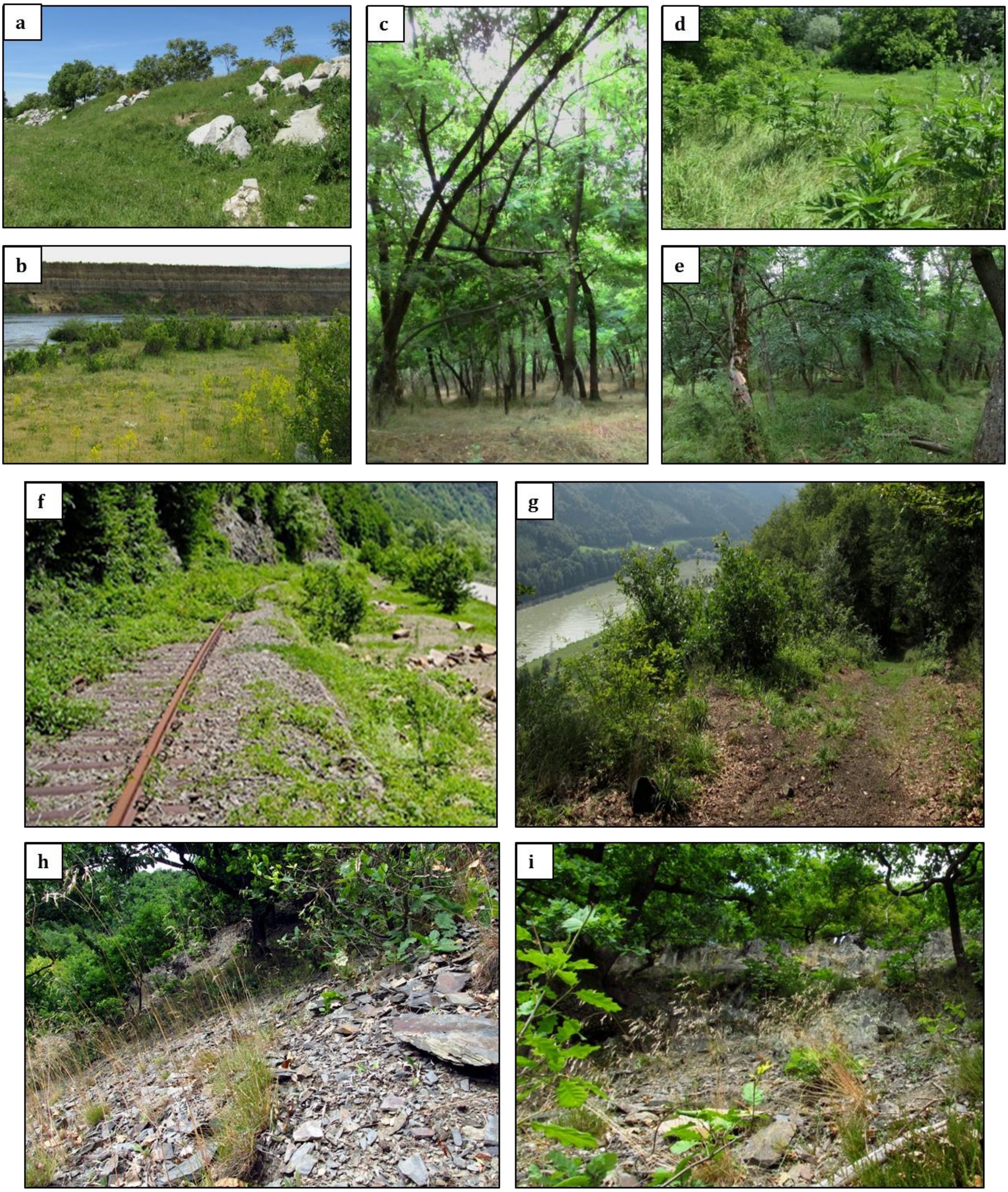

Figure 2.4. Personal observation of the habitat types used by *L. viridis* in the core (a – e) and in two northern peripheral regions, Passau, Germany (f – g) and Prague, Czech Republic (h – i). Photo credits: a-e and g-i by AMPR; f by Ulrich Schulte.

3. Realized niche and microhabitat selection of *Lacerta viridis* at the core and northern periphery of its distribution range

Adult male of the eastern green lizard *Lacerta viridis* in Passau, Germany. Photo credits: AMPR

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3.1. Abstract

The available range of habitats and suitable abiotic conditions like temperature and radiation tends to be narrower toward the periphery of the distribution range of species. Peripheral populations of generalist species could then be more specialized and have a smaller and differentiated realized niche (habitat niche in our study) compared to populations at the core. Likewise, patterns of microhabitat selection can differ between periphery and core. In our study, we compared niche size and microhabitat selection among core (Bulgaria) and northern peripheral (Germany, Czech Republic) populations of *Lacerta viridis* and estimated niche differentiation among regions. We collected data on vegetation structure and abiotic parameters at the microhabitat scale in each region. In order to compare niche size among regions and estimate niche differentiation, we built multidimensional niche hypervolumes. We applied generalized linear mixed models and model averaging, accounting for spatial autocorrelation when necessary, to analyze microhabitat differences among regions and microhabitat selection in each region. Peripheral populations were more specialized, having a smaller niche than core ones, and their niche differed from that in the core (Sørensen overlap in all comparisons <0.3). Microhabitats at the periphery had lower radiation and soil compaction and less structured vegetation. Microhabitat selection at the core depended solely on abiotic parameters, while at the periphery it was defined by only vegetation structure (Czech Republic) or a combination of both, vegetation structure, and abiotic factors (Germany). Thus, peripheral populations seem to compensate for overall harsher climatic conditions by responding to different parameters the microhabitat compared to core populations. We suggest specific conservation measures for *L. viridis* in each studied region and point out the general implications of a higher specialization degree of peripheral populations in relation to climate change and habitat fragmentation.

3.2. Introduction

Availability of resources and environmental conditions change along the distribution range of species, with especially marked differences along the gradients of broadly distributed species (Gaston 2009; Kirkpatrick and Barton 1997). These patterns can lead to ecological differences between populations of the same species living either at the core or at the periphery of its distribution range (Brown et al. 1996). The Kühnelt principle (Kühnelt 1965) states that the range of colonizable habitats is wider at the core where environmental conditions are optimal, whereas at the periphery conditions are suboptimal and fewer microhabitats are suitable for the species. Therefore, populations at the core should be habitat generalists ("euryoecious"), while populations at the periphery of the species' range can, in comparison, be more specialists ("stenoecious") (Böhme and Rödder 2014). Under the Hutchinson's concept of ecological niche (Hutchinson 1957), this suggests that populations living at the periphery of the distribution range will have a smaller locally realized niche breadth compared to generalist core populations. Studies quantifying these differences in animal populations are scarce, but evidence of smaller niche breadth at the periphery compared to the core has been found in a few taxa. For instance, the niche breadth and availability of resources of three invertebrate species, the butterfly *Plebejus argus*, the ant *Myrmica sabuleti*, and the grasshopper *Chorthippus vagans*, were found to decrease toward the northern colder edge of their distribution range (Thomas et al. 1999). In vertebrate species, Lappalainen and Soininen (2006) found that the niche breadth of fresh water percid and cyprinid fishes was narrower toward the northern edge of the distribution range, and Yurkowski et al. (2016) demonstrated that niche breadth at the population level decreased with increasing latitude in ringed seals (*Pusa hispida*) and beluga whales (*Delphinapterus leucas*).

Additional to differences in niche breadth, niche differentiation can also be found when comparing core and peripheral populations. Studies investigating niche differentiation in animal species are focused on evolutionary niche divergence among populations across the species' distribution range (Ahmadzadeh et al. 2013; Cadena and Loiselle 2007), with the niche of relict populations being usually found to be differentiated from that of more central populations (Lozano-Jaramillo et al. 2014). Many approaches exist for such studies, such as occupancy models with climatic, land cover, or other environmental variables as covariates (Araújo and Peterson 2012; Chefaoui et al. 2005; Hirzel and Le Lay 2008), and models that use presence/pseudoabsence data (Morales et al. 2015). These studies are generally done at a macroscale of large regions (often including the whole distribution of a species) and using a coarse spatial resolution of 1 km^2 or more (Pearson and Dawson 2003). Such studies are unable to assess the effects of environmental factors that have a much finer spatial variability. There is a lack of studies on animal species testing niche differentiation by using field data at such microhabitat scale that allows deeper insights into intraspecific niche differences between peripheral and core populations, and into the microhabitat selection patterns shaping these differences.

Elucidating such differences is important for understanding ecological processes like range shifts under global change, as well as for promoting effective conservation measures for edge populations of threatened species (Lesica and Allendorf 1995; Peterman et al. 2013).

Given their sensitivity to environmental changes and thermal dependency, reptiles are of particular interest to study niche and microhabitat selection in regions with different ranges of available habitats and climatological regimes (Buckley 2010; Cunningham et al. 2016). Moreover, for some taxa like lacertid lizards, there is enough qualitative information about niche differences between core and peripheral populations, like the known differences in the diversity of habitats occupied in core regions of the distribution range compared with the northern periphery (Korsós 1982; Olsson 1988). *Lacerta viridis*, for example, is a common species in the Balkan Peninsula in Eastern Europe and Asia Minor (Elbing 2001) and has its northern distribution range located in Germany and in the Bohemian region of the Czech Republic. In core regions, the species is found in habitats ranging from slopes with rock covering, bushlands, and road edges to mixed forest and pine plantations, including several semi-natural and urban habitats (Heltai et al. 2015; Covaciu- Marcov et al. 2009; Popgeorgiev and Mollov 2005). In Germany and Czech Republic, where thermal conditions and other limiting factors like daily hours of sunshine (Frör 1986; Laube and Leppelsack 2007) do not provide many suitable habitats for the species, it is scarce and mostly found in open areas and river valleys (Böhme and Moravec 2011; Böhme et al. 2007a). However, despite substantial descriptive evidence suggesting a narrower range of habitats used by northern edge populations, there are no quantitative studies that explicitly quantify and compare the niche between core and peripheral populations, nor any study comparing the factors that determine microhabitat selection in different regions.

In the present study, we compare the specialization degree with respect to realized niche, and microhabitat selection of populations of *L. viridis* living either at the core (Bulgaria) or at the northern periphery (Germany and Czech Republic) of the species' distribution range (Figure 3.1). The studied populations in the Czech Republic are relict populations, which are not part of the continuous distribution of the species, and in Germany and the Czech Republic, the species is critically endangered and highly protected according to the EU Habitats Directive and national conservation regulations. On the other hand, in Bulgaria, *L. viridis* is the most common lizard species (Beutler and Rudolph 2003; Zavadil and Moravec 2003). We expected to find (a) smaller realized niches in northern edge populations compared to the core, with a niche differentiation present in populations located around Prague (relicts) but not in those in Passau (which are part of the continuous distribution range); (b) higher preference of *L. viridis* in the periphery for specific vegetation structures at the microhabitat scale, like low and open vegetation, as compensation for overall suboptimal climatic conditions; and (c) higher influence of vegetation structure in the microhabitat selection in the northern periphery, where the availability of suitable habitats for the species is a limiting factor, while in the core, where the available range of habitats is broader, abiotic parameters will have a higher influence in the microhabitat selection.

3.3 Materials and Methods

3.3.1. Study regions and site selection

The study region at the core of the species' distribution was located in the Thracian Plain of Bulgaria, in the surroundings of Plovdiv (Figure 3.1a). Bulgaria is the historical and current range core of the species (Popgeorgiev and Mollov 2005),and in the Thracian Plain are represented most of the habitats in which *L. viridis* is present in central regions, from road edges and open shrublands to mesophilic forest. The study regions at the species' northern periphery were located near Passau (Bavaria, Germany) and in the surroundings of Prague (Bohemia, Czech Republic). From now on, we will use the term periphery to refer to the study regions located in the northern periphery. In Passau (Figure 3.1b), populations are found along the Danube Valley in rocky outcrops in the oak and hornbeam forest and on the southern exposed cliffs, but mostly along an abandoned railroad that runs parallel to the river. Populations of *L. viridis* in the surroundings of Prague (Figure 3.1c) are relict populations located in open stony areas of the oak forest and on the slopes of the Vltava valley, as well as those of other valleys perpendicular to the Vltava River. The extent of the areas where the study was carried out in each region was 325 km2, 288 km2, and 522 km2 in Plovdiv, Passau, and Prague, respectively. Based on information available about places where the species has been found and on information about the habitat of *L. viridis* reported in the literature, we identified potential suitable sites into these areas by using satellite maps. Each site represented a portion of habitat potentially holding a population and separated from other sites/populations by structures in the landscape (e.g., agriculture, highways) that do not represent habitat. In order to reduce the effects of probable local processes present in each region, we increased as much as possible the number of sites, by visiting all potentially suitable sites present in the study area in each region. In total, we visited 40, 27 and 33 sites in Plovdiv, Passau, and Prague, respectively. Also, to avoid bias in the habitat types visited in each region, at the periphery, we also visited sites with similar vegetation structure to those where *L. viridis* was found in the core (e.g., mixed forest). In Plovdiv, the area of the sites was 0.1–3.91 km^2 and the distance between sites was 5–6,100 m; in Passau, sites had an area of 0.23–4.51 km^2 and were apart from one another 10–800 m; in Prague, sites were 0.3–2.28 km^2 large and the range of distances between was 5–2,171 m.

3.3.2. Field survey and data collection

Field surveys took place in Plovdiv and Passau in 2014 and in Prague in 2015. In order to make the surveys comparable among regions, they were carried out in each region starting with the onset of the reproduction season: early April in Plovdiv and early to mid-May in the two peripheral regions. Sampling lasted till late May in Plovdiv (core) and till

June and July in Passau and Prague. This shift in sampling made average maximum air temperatures per sampling month similar among sites: 18.5 and 23.4°C in Plovdiv, 23.1 and 24.8°C in Passau, and 22.5 and 24.6°C in Prague.

Data were gathered around a total of 363 points, from which 152 were in the core (presence: 102; absence: 50), 117 in the periphery-Pa (33; 84), and 94 in the periphery-Pr (29; 65). In the core region, lizards were found in a variety of habitats from shrublands to mixed forest, in riverbeds as well as far away from any water body. In Passau, the presence of the lizards is restricted to the lower part of the narrow Danube valley, where the habitat is represented by stony areas with low vegetation. Finally, in Prague, lizards were mainly found in the open rocky slopes of the Vltava valley and the valleys of tributary rivers.

We used an occupancy survey design to incorporate detection probability. Following study designs proposed by Mackenzie and Royle (2005) and based on estimates of detection probability for similar species (Janssen and Zuiderwijk 2006; Sewell et al. 2012), the number of visits per site was set to two, one in the morning (9:00–12:00 a.m.) and one in the afternoon (14:00–19:00 p.m.) in accordance with the species' daily activity pattern (Korsós 1983). The second visit in each population was carried out either on the same day or one day later. Only in two populations in Plovdiv (core) and two in Prague visits were separated by 7 days. Each visit lasted one hour, and sites were surveyed by means of line transects. Walking speed was standardized at 20 m/min. Thus, one hour visit corresponded to 1,200 m, which were divided into transects of variable lengths (50–400 m). Transects were systematically placed in order to represent the area of the site and all different habitat types present at it. With the use of maps and based on the relative coverage of each habitat type into each site, we calculated the length of each transect and the number of transects that had to be placed in each habitat type. The entire length of each transect was placed only in one habitat type and did not crossed to another. The number of transects surveyed per site ranged from 3 to 12. To avoid double counting of observed lizards among transects, the minimum distance between transects was 100 m. A width of 2.5 m at each side of the transect was set to carefully inspect visually for *L. viridis*. A metal stake was placed on the specific point where each lizard was seen and coordinates were taken. In a 25 m^2 plot around this point (presence plots), data on vegetation structure and abiotic parameters were recorded. Percentage of vegetation coverage was visually estimated for the following categories: herbs with a height lower than 30cm (Herbs 1), between 40 and 80cm (Herbs2) and higher than 90 cm (herbs3); woody plants < 2 m and woody plants > 2 m; dry leaves, rocks and fallen trunks (rocks_trunks), bare soil, way (road edges, dirt tracks, walking paths), and coverage of branches (Branches). Vegetation height was measured with a retractable measure tape. Abiotic parameters included air temperature at 1.5 m height, 10 cm height and ground surface, soil compaction, soil composition, slope, and aspect. Temperature and soil compaction were measured at

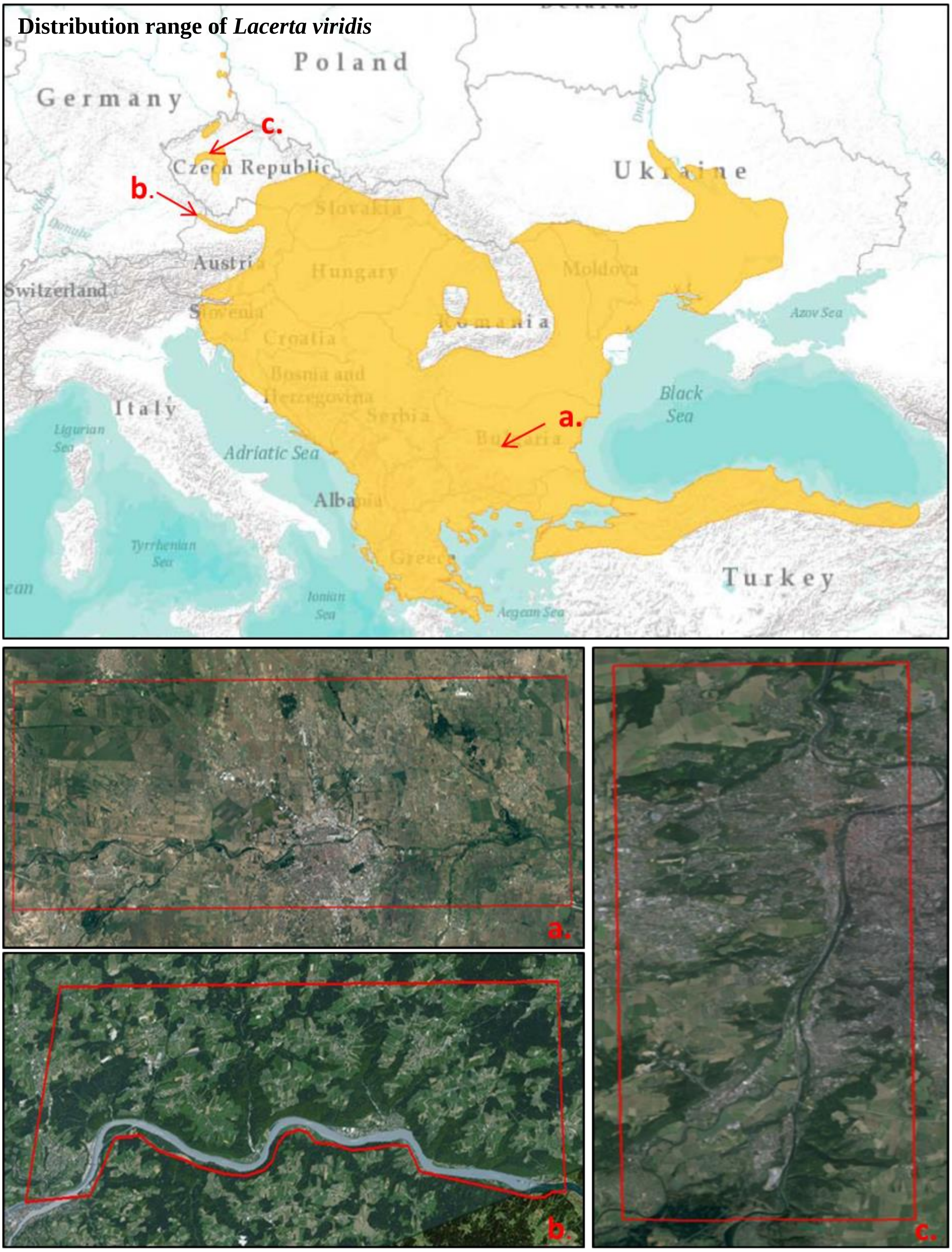

Figure 3.1. Distribution range of *Lacerta viridis* (IUCN, 2009) and study sites in the core located in Plovdiv, Bulgaria (a), and in two peripheral regions corresponding to Passau, Germany (b) and Prague, Czech Republic (c).

three random points (different for each parameter) within each plot and then averaged for the analysis. Soil compaction was measured with a manual penetrometer, and soil composition was qualitatively classified into humus, organic, clay, gravel, or sand. Temperature was measured with a precision digital thermometer (Greisinger GTH 175/PT), exposition was taken with a GPS (Garmin 62S) and slope with a compass (Global system DS 50G).

In order to analyze microhabitat preference of the species, the same data were collected in 25 m^2 plots around random points along each transect, where the lizard was not seen at the time of the survey. These random plots are specific locations that the lizard might use at other time and where it might not be permanently absent, but in order to simplify terminology, from now on we will call them absent plots. Random points were chosen by blindly selecting points along each transect in the GPS. Data gathering in each presence/absence plot took approximately 15 min, which were not accounted for as sampling time, and in consequence one hour of surveying lizards represented 2–4 hr of data sampling. Therefore, due to time constrains, data were gathered around a maximum of three “presence” points per transect per visit in the case more than three lizards were encountered, and a minimum of one random “absence” point per transect. If a lizard was encountered in an already surveyed plot during the second visit, data were not included in the analysis to avoid pseudo-replication.

Additionally, to variables measured in the field, we estimated radiation at each data point and at the specific time range of the study in each region with the “Potential incoming solar radiation” tool of the software SAGA. For this purpose, elevation maps with 30 m resolution were obtained from the USGS database. Aspect was transformed into two variables: cosine values, representing the South-North component (S-N aspect), and sine values, representing the West-East component (W-E aspect). S-N aspect values increase from south to north, and W-E aspect values increase from west to east.

3.3.3. Data preparation and variable selection

The following procedure was performed for the data set including all regions (see section *Comparison of microhabitats among regions*), and separately for the individual dataset of each region (see section *Microhabitat selection in each region*).Vegetation structure data were ARCSIN transformed, tested for correlation with Spearman rank correlation, and assessed for collinearity by estimating the variance inflation factor (VIF). Variables with correlation > 0.6 or VIF > 3 were excluded from analysis (Zuur et al. 2010). In the dataset, including all regions, no correlation or collinearity was found and all variables were retained (Supporting Information Appendix S1, Table S1.1). In Plovdiv, the variable Herbs 2 had a high collinearity (VIF = 17) and was excluded from the analysis of microhabitat selection (see analysis description below). In the other two regions, neither correlation nor collinearity was found (Supporting Information Appendix S1, Table S1.2–S1.4). Therefore, all variables were retained. Continuous abiotic variables were log-transformed and tested for correlation with the Pearson correlation test and also for collinearity with VIF. Variables with correlation >0.6 or VIF > 3 were excluded. Air temperature, temperature at 10 cm height, and temperature at soil surface were correlated ($r > 0.9$) in all study regions; hence for further analysis, only the temperature at the soil surface was used, as lizards' bodies are directly in contact with it, and its influence on microhabitats may be the strongest. No correlation or collinearity was found in other variables (Supporting Information Appendix S1, Table S1.1–S1.4). Correlations between each abiotic continuous variable and the factor soil composition were tested using linear regression. In Plovdiv, soil composition was correlated with soil compaction ($F4,136 = 3.75$, $p < 0.01$) and radiation ($F4,136 = 10.08$, $p < 0.001$) and therefore removed from the analysis. In Passau and Prague, soil composition was correlated with soil compaction ($F2,98 = 3.14$, $p = 0.047$; $F3,73 = 4.45$, $p = 0,038$). To select between soil compaction and soil composition, we tested the effect of each of the two variables on the presence/absence of the lizard in each region and retained the variable with the strongest effect (Poulin et al. 2008). In all regions, soil composition was least correlated with presence/absence of *L. viridis*, and therefore, for further analysis this variable was removed.

3.3.4. Statistical analysis

Niche size and specialization

To compare realized niches among regions, multidimensional niche hypervolumes were derived with the package "Hypervolume" from R software (Blonder, 2015). All calculations were performed separately for vegetation structure and abiotic parameters in each region. Data were scaled and centered, and principal component analysis (PCA) with the R package "ade4" (Dray et al. 2015) was applied to the whole dataset including all points of all regions. This reduction in dimensionality was necessary as the niche hypervolume analysis requires orthogonal axes. Principal components with eigenvalues > 1 were used to construct the hypervolumes of the realized niches in each study region (see Table 3.1 for variable loadings). Six principal components were selected for vegetation structure (77.05% of total variance) and three for abiotic parameters (62.89% of total variance). We used a fixed bandwidth of 0.5 with 1,000 Monte Carlo samples per data point to calculate the volumes. Hypervolume units are standard deviations (SD). Besides the size of each hypervolume, we also estimated the intersection and the union, and for testing niche differentiation, we estimated the Sørensen overlap index for each comparison, which measures the similarity among two samples with values varying from 0 for low overlap to 1 for complete overlap (Blonder et al. 2014).

Table 3.1. Loadings of each variable in the principal components with eigenvalues > 1 selected to build the niche hypervolumes for vegetation structure and abiotic parameters.

	Principal Components					
	PC1	PC2	PC3	PC4	PC5	PC6
Vegetation structure						
Herbs < 30cm	0.19	0.73	-0.37	-0.08	0.09	0.12
Herbs 40-80 cm	-0.43	-0.32	0.16	-0.24	0.48	0.06
Herbs > 90cm	-0.38	-0.07	-0.28	0.16	-0.38	-0.49
Woody plants < 2m	0.10	0.17	0.64	0.30	-0.14	0.38
Woody plants > 2m	0.20	0.01	0.17	-0.51	0.26	-0.15
Dry leaves	0.50	-0.46	-0.11	0.05	-0.14	0.07
Rocks_trunks	-0.08	-0.25	-0.35	0.46	0.12	0.43
Bare soil	0.17	0.07	0.37	0.41	0.09	-0.58
Way	-0.11	-0.06	0.15	-0.40	-0.70	0.17
Branches	0.53	-0.24	-0.17	-0.12	-0.01	-0.13
Abiotic parameters						
Temperature	-0.34	-0.09	0.72			
Soil compaction	0.37	0.35	0.53			
N-S exposition	0.05	-0.81	0.13			
W-E exposition	-0.25	0.06	-0.43			
Slope	-0.56	0.41	0.06			
Radiation	0.60	0.20	-0.06			

Comparison of microhabitats among regions

For comparing microhabitats among regions, a multinomial logistic regression was run using the “multinom” function of the “nnet” R package (Ripley and Venables 2016), with “region” as response variable. Analysis was first done separately for vegetation structure and abiotic parameters. After fitting a global model with all variables of either vegetation structure or abiotic parameters, all possible models with a reduced number of parameters were generated with the “dredge” function of the “MuMIn” R package (Bartón 2015). Model comparison was based on Akaike’s information criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). All models with ΔAICc<2 relative to the best model were selected, and parameters were estimated by averaging across these models with the “model.avg” function of “MuMIn” package. Relative variable importance (RVI) was calculated by summing the Akaike weights of each variable across the selected models. Variables with RVI > 0.6 were considered important (Kennedy et al. 2013). Important variables of both sets of variables, vegetation structure and abiotic parameters, were then combined in a third global model. Again, all possible models were generated and those with ΔAICc < 2 were averaged. We selected the approach of analyzing vegetation structure and abiotic parameters separately, and then combine most important variables of both averaged models in order to avoid overfitting of the global model, which is a common risk in mixed models that tends to overweight the variables averaged through the best models (Grueber et al. 2011)

Microhabitat selection in each region

We applied generalized linear mixed models GLMM, with plot presence/absence as response variable, site occupancy (i.e., the presence or absence of the lizard in each visited site) as random factor and variables of vegetation structure or abiotic parameters as fixed factors. Analyses were initially done separately for vegetation structure and abiotic parameters. For each region, a full model containing all variables, either of vegetation structure or of abiotic parameters, was fitted using the "glmer" function of the "lme4" R package (Bates, et al. 2016) with a logit link function and binomial error distribution. We tested for spatial autocorrelation of residuals (SACR) and when present, we applied principle coordinates of neighbor matrices (PCNM) (See "Detection and correction of spatial autocorrelation"). We then proceeded as described in *Comparison of microhabitats among regions* to generate all possible models, averaged through those with ΔAICc < 2 and combine the most important variables of both the vegetation structure and abiotic parameters averaged models. We checked again for VIF and for SACR, and the process of model averaging was repeated to obtain the final model that includes the most important variables among vegetation structure and abiotic factors. For each final model, we report conditional R2 corresponding to the variance explained by fixed factors and random term together, and marginal R2 representing the variance explained by fixed factors only (Nakagawa and Schielzeth 2013).

Detection and correction of spatial autocorrelation

All global models (vegetation structure, abiotic parameters, or combinations thereof) of microhabitat selection in each region were tested for spatial autocorrelation of model residuals (SACR) by estimating Moran's I index, calculating Moran's I-based correlograms and computing autocorrelation of residuals. Correction for SACR was done by means of principal coordinates of neighbor matrices (PCNM). PCNM are a type of Moran's eigenvector maps and consist of calculating spatial eigenvectors based on a matrix of truncated distances. The obtained PCNM vectors can then be added into the model as fixed terms to account for SACR (Borcard and Legendre 2002) (Supporting Information Appendix S2).

3.4. Results

3.4.1. Niche size and specialization

The realized niche of vegetation structure was largest in the core, followed by the periphery-Pa and the periphery-Pr (Table 3.2, Figure 3.3a). The realized niche of vegetation structure was found to differ in both peripheral regions from the niche in the core with the same degree of differentiation (Sørensen overlap = 0.1). Percentages of intersected niche volume ranged between 21.93%–23.18% for the peripheries and 6.5%–7.36% for the core. Between peripheral regions, there was also differentiation (Sørensen overlap = 0.08) and low percentages of overlapped niche volumes (8.24% for periphery-Pa and 8.80% for periphery-Pr).

Table 3.2. Comparison among realized niche size in Plovdiv (Pl), Passau (Pa) and Prague (Pr).

Comparison	Volume1	Volume2	Intersection	Union	Sørensen overlap
Vegetation structure					
Pl - Pa	90.89	28.85	6.69	113.05	0.11
Pl - Pr	90.89	27.03	5.93	111.98	0.10
Pa - Pr	28.85	27.03	2.38	53.50	0.08
Abiotic parameters					
Pl - Pa	32.89	20.97	10.16	47.70	0.37
Pl - Pr	32.89	23.24	4.29	51.84	0.15
Pa - Pr	20.97	23.24	6.32	37.89	0.28

The realized niche based on abiotic parameters was also largest in the core, but in this case, it was followed by that in the periphery-Pr and the smallest abiotic niche was in the periphery- Pa (Table 3.2, Figure 3.3b). In both peripheral regions, it differed from that in the core, with the lowest overlap found between the Periphery-Pr and the core (Sørensen overlap = 0.15), with 18.45% of the niche in periphery-Pr intersecting with 13.04% of the niche in the core. Between periphery-Pa and core (Sørensen overlap = 0.37) intersected volumes were 48.45% and 30.89%, respectively. The comparison between peripheries also showed niche differentiation (Sørensen overlap = 0.28), and 30.13% of the niche of Periphery-Pa overlapped with 27.19% of the niche in Periphery-Pr.

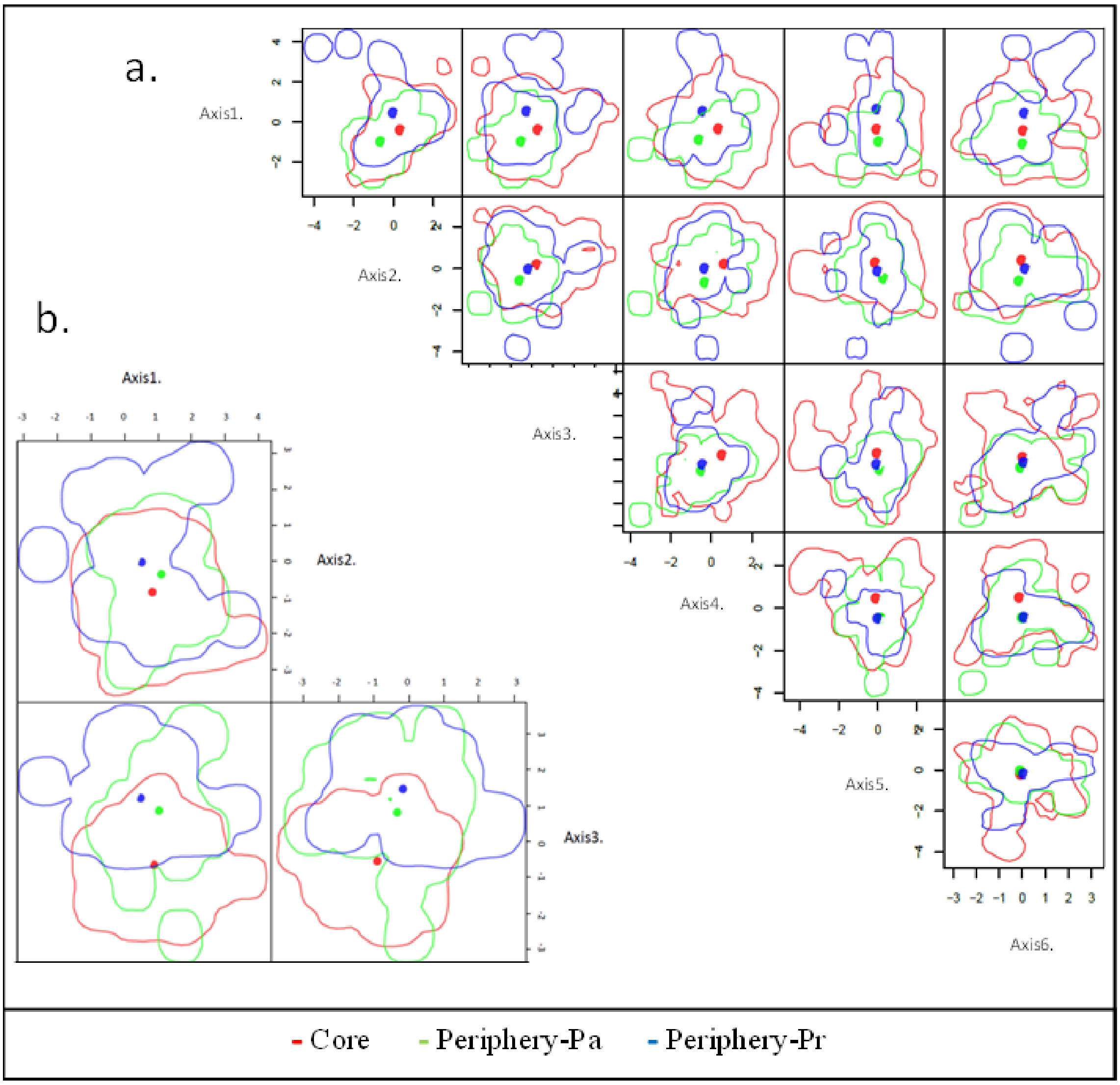

Figure 3.3. Two dimension (2D) representation of the multidimensional niche hypervolumes of realized niches for vegetation structure (a, 6 dimensions) and abiotic parameters (b, 3 dimensions) in the core of the distribution range of *L. viridis* (core, red), in the periphery in Passau (periphery-Pa, green) and in the periphery in Prague (periphery-Pr, blue). Dimensionality of each niche hypervolume corresponds to the number of principal components with eigenvalue >1.

3.4.2. Comparison of microhabitats among regions

With the multinomial logistic regression (Table 3.3), we found that the most important variables differentiating microhabitats used among regions were radiation, soil compaction, Herbs1, Herbs2, Herbs3, woody plants<2 m, woody plants>2 m, and Way (RVI = 1). In both peripheral regions, radiation and soil compaction were lower compared to the core region. Also, herbs and woody plants had a lower proportion in microhabitats used in peripheral regions compared to the core region. When comparing between peripheral regions microhabitats used in periphery-Pr had an even lower radiation and proportion of herbs and woody plants>2 m, but higher soil compaction and woody plants<2 m.

Most of the populations in Prague were found on rocky slopes of the valley, with sparse vegetation and scarce trees. Given the rocky substrate of slopes inhabited by *L. viridis* in Prague, the soil compaction was higher in Prague compared to Passau (Supporting Information Appendix S3, Table S3.1 for model selection and model averaging separately for vegetation structure and abiotic parameters).

3.4.3. Microhabitat selection in each region

Results of model averaging of the GLMMs based on abiotic and vegetation parameters as potential predictors are shown in Table 3.4. Microhabitat selection in the core region was affected only by abiotic parameters. The most important variables found were radiation, slope, soil compaction (RVI = 1), and S-N aspect (RVI = 0.74), with radiation having a positive effect on the presence/absence of *L. viridis*, and slope, soil compaction, and S-N aspect having a negative effect. A high proportion of the variance was explained by our model, with the larger part being explained by the random intercept (conditional R2 = 0.93; marginal R2 = 0.20). The inclusion of random intercepts can enormously improve the explanatory capacity of models, and a high conditional R2 value is a very common output in GLMM that intend to find the best set of variables to explain the data (Nakagawa and Schielzeth 2013) (Supporting Information Appendix S4, Table S4.1 for model selection and model averaging separately for vegetation structure and abiotic parameters).

The most important variables affecting microhabitat selection in the periphery-Pa were a combination of vegetation structure and abiotic parameters: Branches, S-N aspect, W-E aspect, and temperature (RVI = 1). *Lacerta viridis* in the periphery-Pa avoided locations with high coverage of branches and selected places with an eastern and southern aspect where temperatures are higher. The model explained most of the variance, with fixed factors explaining almost half of it (conditional R2 = 0.99; marginal R2-marginal = 0.43) (Supporting Information Appendix S4, Table S4.2 for model selection and model averaging separately for vegetation structure and abiotic parameters).

Microhabitat selection in the periphery-Pr was affected only by vegetation structure variables. *Lacerta viridis* in the periphery-Pr selected places with low structure principally composed by low vegetation (RVI Herbs2, Herbs1 = 1). Most of the variance in the model was explained by fixed factors (conditional R2 = 0.61; marginal R2- marginal = 0.60) with a very small proportion being explained by the random intercept (Supporting Information Appendix S4, Table S4.3 for model selection and model averaging separately for vegetation structure and abiotic parameters).

Table 3.3. Parameter estimates with 95% confidence interval (LCL and UCL) from averaged models of the multinomial logistic regression for the comparison among realized niches in Plovdiv (Pl), Passau (Pa), and Prague (Pr).

		Pl vs Pa			Pl vs Pr			Pa vs Pr		
	RVI	Estimate (SE)	LCL	UCL	Estimate(SE)	LCL	UCL	Estimate (SE)	LCL	UCL
Intercept		14.15 (4.24)	-12.90	26.80	16.56 (4.59)	-23.26	31.80	2.4 (2.60)	-18.15	12.74
Radiation	1	-0.61 (0.14)	-0.96	-0.33	-0.66 (0.15)	-1.01	-0.35	-0.04 (0.09)	-0.21	0.14
Soil compaction	1	-5.57 (1.77)	-10.20	-2.01	-5.40 (1.85)	-10.45	-1.85	0.16 (1.17)	-2.42	2.33
Way	1	-16.09 (5.79)	-28.07	-5.05	-15.28 (6.54)	-27.95	-3.09	0.81 (5.05)	-8.57	10.65
Woody plants<2m	1	-38.38 (12.93)	-67.98	-12.76	-26.11 (11.94)	-51.32	0.34	12.35 (9.47)	-4.68	34.45
Woody plants>2m	1	-13.81 (6.65)	-28.48	-0.88	-27.78 (9.43)	-46.30	-8.34	-13.96 (7.75)	-27.73	2.41
Herbs 1	1	-7.71 (2.52)	-13.43	-2.13	-8.46 (2.48)	-14.42	-2.75	-0.74 (1.85)	-4.54	2.93
Herbs 3	1	-0.22 (2.36)	-5.27	4592	-9.90 (4.29)	-17.94	-1.11	-9.68 (4.11)	-17.23	-1.15
Herbs 2	1	-6.38 (2.91)	-12.90	-0.67	-12.83 (3.28)	-20.00	-6.30	-6.44 (2.14)	-10.64	-2.08
Temperature	0.51	5.77 (7.85)	-3.44	26.28	9.21 (10.86)	1.91	34.53	3.45 (5.22)	-4.07	17.73
Slope	0.47	0.36 (0.58)	-0.51	2.04	0.78 (0.99)	0.10	3.21	0.42 (0.6)	-0.25	2.03

Note: Estimates and confidence intervals correspond to Pa and Pr in comparison to Pl, and to Pr in comparison with Pa. Most important variables are those with relative variable importance RVI > 0.6.

Table 3.4. Microhabitat selection of green lizards in the core (Plovdiv) and in the periphery (Passau, Prague). Table shows the most important variables (relative variable importance RVI > 0.6) among vegetation structure and abiotic factors resulting from model averaging of selected models (ΔAIC < 2)

Variable	Estimate	SE	RVI
Plovdiv			
Intercept	15.3877	7.415	
Radiation	0.5275	0.2727	1
Slope	-3.8056	2.3085	1
Soil compaction	-5.7846	1.4432	1
S-N aspect	-3.6429	2.9139	0.74
Temperature	-1.406	3.5887	0.24
W-E aspect	0.1214	0.6582	0.14
Passau			
Intercept	-1.03e03	6.02e-03	
Branches	-2.91e02	2.89e01	1
S-N aspect	-5.44e01	6.02e03	1
pcnm1	4.48e02	6.02e-03	1
pcnm44	-2.13e+02	4.14e02	1
W-E aspect	4.97e01	6.02e-03	1
Temperature	6.54e02	6.02e-03	1
pcnm6	-4.91e02	6.02e-03	0.9
pcnm9	-60.13	395.32	0.21
pcnm22	-22.36	1341.55	0.12
Way	7.664	22.18	0.11
Herbs 3	1.24	96.80	0.11
Bare soil	-6.25	18.25	0.10
pcnm16	-0.39	146.65	0.10
Prague			
Intercept	-4.27	5.08	
pcnm1	-72.84	96.15	1
Herbs 1	4.88	3.79	1
Herbs 2	85.42	54.62	1
Slope	27.15	364.24	0.57
Way	72.81	1027.02	0.57
Herbs 3	-792.12	14232.53	0.43
Branches	12.87	378.09	0.22
Bare soil	55.08	1421.35	0.22

Note: In the core, none of the vegetation parameters was retained in the global model. PCNM: Principal coordinates of neighbor matrices correcting for spatial autocorrelation

3.5 Discussion

We hypothesized that the microhabitat niche is smaller at the periphery of the distribution of our study species, *L. viridis*, compared to the core and that there should be a higher preference for specific vegetation structures at the microhabitat scale at the periphery. We further hypothesized that in the core, where availability of suitable habitats does not represent a limiting factor, abiotic parameters will determine microhabitat selection. All hypotheses were met in line with Kühnelt's principle (Kühnelt 1965), which states that the range of colonizable habitats is wider at the core where environmental conditions are optimal, whereas at the periphery conditions are suboptimal and fewer microhabitats are suitable for the species. The niche of vegetation structure and abiotic parameters was smaller in the periphery and was differentiated from the niche in the core. In the periphery, *L. viridis* compensated for the overall lower suitability of environmental conditions by selecting microhabitats with specific vegetation structures that allow it to take advantage of sufficiently suitable conditions. As expected, only abiotic parameters determined microhabitat selection at the core, whereas at the periphery in Prague, only variables of the vegetation structure influenced microhabitat selection. However, in the periphery in Passau, a combination of abiotic and vegetation structure parameters determined microhabitat selection.

Smaller niche size and niche differentiation in the periphery can be the result of either different thermoregulatory behavior, phenotypic plasticity or local adaptation (genotypic changes) to conditions that lay near the limits of suitability. On the one hand, thermoregulatory behavior can allow individuals at the northern (and upper altitudinal) periphery to meet their thermal requirements by stringent selection of optimal habitats, which therefore often determines the peripheral limits of the distribution of ectotherms (Henle et al. 2010; Huang et al. 2014). In the core region, thermal condition should be more benign, thus allowing ectotherms to reach their thermal requirements in a larger number of different habitats. This is the basic idea behind Kühnelt's principle of regional stenoecy (Kühnelt 1965) and has been shown qualitatively in various lizard species (Böhme and Rödder 2014). Furthermore, thermoregulatory behavior might avoid selective pressures to act upon physiological traits and is sometimes regarded as the most plausible mechanism to explain patterns of niche differentiation when data relies on realized niche (Araújo et al. 2013; Bogert 1949; Grigg and Buckley 2013; Huey et al. 2003).

On the other hand, thermoregulatory behavior in lizards is more often found to be determinant near the hot extremes of species' niches, where individuals avoid heat by retreating into burrows or staying under shadow, compared to near the colder limits of the niche (Muñoz et al. 2014). Moreover, for peripheral populations that are not connected with the distribution range of the species (relict populations), in which immigration from more central populations cannot contribute to population persistence, pressure for adaptation is stronger and therefore phenotypic plasticity and local adaptation (genotypical changes) can be more plausible mechanisms shaping smaller niche size and niche differentiation (Blanquart et al. 2013; Chevin et al. 2010; García-Ramos and Kirkpatrick 1997). Under this scenario, the selective pressure of environmental conditions can result in adjustments of the thermal physiology, like changes in heat and cooling rates, and critical thermal limits, with the range of selected body temperatures (SBT) at the periphery being different and narrower in comparison with core (Brattstrom 1968; Castilla et al. 1999; Henle et al. 2010; Huey 1982). For instance, the STB of the common lizard *Lacerta vivipara* differs between locations, with populations in southern latitudes having a higher STB compared with those located at higher latitudes (Patterson and Davies 1978; Van Damme et al. 1986). The lack of connectedness with the continuous distribution range is indeed the case of the populations in Prague, which are regarded as relicts, have overall small size, and are genetically differentiated from other peripheral (but not relict) populations (Böhme and Moravec 2011). Additionally, there is evidence in several ectotherm taxa that the expression of the potential phenotypic plasticity of a species is higher near its lower thermal limit, which for several taxa have a strong relation with high latitudes (Chown and Terblanche 2006; Overgaard et al. 2011).

One possible selective pressure acting upon populations in colder northern peripheral regions can be radiation. Contrary to expectation, radiation had a positive effect on the presence of the lizards in the core area but no effect in the peripheral areas. As a consequence, this variable strongly differentiated microhabitats among regions, being lower in both peripheral regions in comparison with the core. Most importantly, the niches of *L. viridis* in peripheral regions were characterized by lower vegetation height than the niche in the core, where higher temperatures can compensate for increased shading by higher vegetation. Thermal conditions and other limiting factors like daily hours of sunshine (Frör 1986; Laube and Leppelsack 2007) presumably do not allow such a compensation at the periphery.

In Passau and Plovdiv, selected microhabitats additionally seem to reflect the response to abiotic parameters shaped also by topography. In Plovdiv, the effects of slope and S-N aspect were six to ten orders of magnitude stronger than the effect of radiation and were negative. This can be explained by the absence of the lizard in the two rocky hills included among the sites we visited in Plovdiv. In the Passau region, the Danube valley is narrow and is characterized by rocky cliffs, above which the habitat changes dramatically into dense mixed forest and oak forest with high coverage of branches. Despite higher radiation values above the cliffs in comparison with the valley ($z = -3.501$, $p < 0.01$) and the relative abundance of forest edges and clearings with potentially suitable vegetation structures, *L. viridis* seems unable to cope with unfavorable microclimatic conditions in the forest to colonize those areas. Similar observations were made for the Taiwanese lizards *Takydromus hsuehshanensis* (Huang et al. 2014). On the other hand, the rocky open valley has a southeastern aspect, with higher temperatures and suitable microclimate for *L. viridis* (Nettmann and Rykena 1984). Then, in Passau, it can be more difficult for *L. viridis* to compensate for overall climatic conditions (e.g., lower radiation) by just selecting suitable vegetation structures, because topography confines lizards mostly to the lower part of the valley and they lack accessibility to alternative localities with suitable microclimate.

In all three regions studied other lizard species are also present, *Lacerta agilis* in Passau and Prague, and *Lacerta trilineata* and *Podarcis tauricus* in Plovdiv. Although interspecific interactions, like competition, can have an influence in the niche and microhabitat selection of species, we think that in the regions of our study the possible effect of these interactions, if present, will be very low. Theory predicts that in peripheral populations in higher (colder) latitudes individuals are more limited by climatic conditions, while biotic interactions like predation and competition are more important at low latitudinal peripheries (Cahill et al. 2014; Holt and Barfield 2009; Price and Kirkpatrick 2009). In Passau and Prague, *Lacerta agilis* occupies much more humid and covered environments than those inhabited by *L. viridis*, which at this part of its distribution range, as our results showed, tends to occupy drier opener places. Evenmore, in Passau, each species occupies completely different habitats and does not occur synoptically (Waitzmann and Sandmaier, 1990). Nevertheless, an influence of the interaction of both species on the niche of *L. viridis* can be expected in southern regions, where the habitat of both species overlaps (Korsós 1982), due to the trend of *L. viridis* to inhabit more covered areas toward lower latitudinal regions. However, even in this region, analyses at a finer scale have demonstrated significant niche segregation (Babocsay 1997; Heltai et al. 2015) that allows the coexistence of both species in the same habitat.

In the core region, the habitats used by *Lacerta trilineata*, *Podarcis tauricus*, and *L. viridis* have an overlap in the driest and least covered portion of the niche of *L. viridis* (Mollov, 2011), which corresponds to the most covered and humid habitats inhabited by the other two species. Therefore, an effect of the interaction with other species on the microhabitat selection of *L. viridis* in this region might be possible but only in a reduced portion of its niche and would have shifted the niche toward the conditions in the periphery if the niche would be indeed suppressed. Analyses at the microhabitat scale in another core region, Hungry also suggest coexistence through niche segregation (Babocsay 1997). Moreover, the differentiation of habitats between *L. trilineata* and *P. tauricus*, and *L. viridis* becomes stronger toward the southern parts of the distribution range of *L. viridis*, like in Greece, where *L. viridis* occupies even more covered habitats (Strijbosch 2001).

3.5.1. Implications for conservation

Our findings have several implications for the management and conservation of core versus peripheral populations of species. Management measures applied for the protection of peripheral populations of *L. viridis* should address the high specialization degree of the species in these regions, their microhabitat selection and their need to compensate for less suitable climatic conditions. In Prague and in Passau, maintenance of low vegetation in sites where the species already occurs is important for the species' viability, as it will allow individuals to compensate for low radiation. In Passau, management measures are already installed in the lower parts of the valley (below the cliff; O. Assmann, pers. comm.). However, we suggest that similar measures should be considered in the upper border of the cliff, in order to increase the potentially suitable area for the species. Also, corridors, for example, along forest tracks or powerlines could facilitate connections between suitable habitats below and above the cliffs. We are not aware that measures for maintaining open vegetation are applied around Prague and would recommend considering them for the long-term viability of *L. viridis*.

In Plovdiv (Bulgaria), where our core study area was located, it is the diversity of habitats and their vegetation structures that matters most for the species. In the core, abiotic conditions suitable for *L. viridis* are met in a wide range of habitat types, including those with high vegetation and branches coverage. Landscape heterogeneity is altogether known to be important for the viability of many species (Brachet et al. 1999), and in the case of the populations of *L. viridis* in the core it is the presence of habitats with different vegetation structures that could represent the highest benefits. This can be considered, for instance, in Natura 2000 planning or in agri-environmental measures employed so that they also protect scrubland habitats in the region.

In two of the studied regions, Plovdiv and Prague, the species' habitat was severely fragmented. Recently, Henle et al. (2016) found that peripheral populations of a related lizard species, *Lacerta agilis*, had a higher specialization degree, lower genetic diversity, and were more sensitive to habitat fragmentation compared to those located in the center. A similar pattern of lower genetic diversity and higher sensitivity to fragmentation caused by the narrower niche is likely to occur also in northern peripheral populations of *L. viridis*. Thus, besides protection of high quality habitats, reestablishing connectivity is an important complementary conservation need.

3.5.2. Limitations and outlook

As in many ecological studies dealing with the quantification of spatial ecological patterns, the risk of local processes influencing the geographical correlation with the parameter under study is always present, and in our study, the inclusion of more regions would have allowed a broader generalization of our results. However, we tried as much as possible to counteract this risk by taking data in less plots per site but increasing the number of sites per region. Most importantly, we defined the spatial scale to which the patterns of niche size are related (Chase and Myers 2011). To do so, we selected regions that had to fulfill two preconditions closely related to processes that occur at a biogeographical scale: (a) to have contrasting ranges of habitat availability representative of different parts of the distribution range (broad in the core and narrow in the northern peripheries) and (b) to have clearly different climatic regimes. Both premises were fulfilled by all three regions in our study. Local processes due to the particularities of each location, like the topography in Passau and Plovdiv, or the disconnectedness in Prague, are of course still present, but their effects might probably be more related with mechanisms (e.g., local adaptation) acting at a rather local scale, than with differences in niche size and microhabitat selection per sé, which might more strongly respond to a spatial gradient of habitat availability and climatic regimes at a larger spatial scale.

Although our study only includes high latitudinal peripheries of the species' range and the core and lacks data from other locations along the distribution range of the species, we consider this a valuable input given the many empirical gaps in studying species' range limits, namely, a detailed analysis of the factors affecting species at the core versus periphery (Sexton et al. 2009). As a next step, it is important to investigate whether limitations in other regions also lead to changes in niche and microhabitat selection compared to the core. The peripheral regions in our study one a relict (Prague) and the other at the tip of a narrow extension of the distribution range of the species (Passau) might not fully represent the northern periphery. In other northern edges, located at the border of the contiguous distribution range, habitat availability might not be broader and climatic conditions might be as limiting as in Passau and Prague, but the persistence of populations might depend more on immigration than on adaptation to specific conditions. Hence, niche would still be smaller compared to the core but probably less differentiated. On the other hand, in low latitudinal regions, interactions with other lizards' species might have a more important role in restricting the niche than it does in northern peripheries (Cahill et al. 2014).However, the study of the niche and microhabitat selection of several species must be carefully addressed at the proper spatial scales in order to correctly quantify possible overlaps or segregation among species (Heltai et al. 2015), and its effects in the intraspecific comparison of the niche of populations at peripheries with the core.

Other regions not included in our study that could also represent cold range edges are those located at high altitudes. High altitudinal populations of *L. viridis* are located in the central and southern parts of the species' range, in the Balkan Peninsula from southern Rumania to northern Anatolia (Pafilis and Maragou 2013; Schmidtler 1986; Uhrin et al. 2016). Although these regions are characterized either as subtropical or transitional subtropical-temperate climatic zones (Nojarov 2017), it is possible that climatic conditions at high altitudes, as well as an expected narrower range of habitats available, have the same effect on the niche size of *L. viridis* as the conditions in temperate peripheries. This can be especially possible in the Carpathians in south Rumania, where there is a more continental climatic regime with less oceanic and subtropical influence, and where some mountainous populations of *L. viridis* have been reported (Strugariu 2009). As these regions are surrounded by the contiguous distribution range of the species, and therefore, might strongly depend on immigration, compared with the peripheral regions that we visited, niche differentiation might be lower.

Finally, a higher specialization degree is already known to be linked with a higher sensitivity to habitat fragmentation and climate change at the species level (Henle et al.

2004b; Lancaster2015; Vergara and Armesto, 2009). In the same way, peripheral populations may be more specialized than core populations and be stronger affected by these two processes (Cahill et al. 2014; Hampe and Petit 2005; Henle et al. 2016). Therefore, the identification of differences in niche and microhabitat selection at fine scales in various locations across the distribution range of single species would significantly improve predictions of species distributions under different scenarios of climate change and habitat fragmentation. This would be enormously valuable to prioritize the application of conservation measures at the population level and at regional and local scales.

3.6 Acknowledgments

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3.7. Supporting Information

Appendix S1. Correlations and variance inflation factor (VIF).

Appendix S2. Correction of spatial autocorrelation of residuals (SACR).

Appendix S3. Individual models of vegetation structure and abiotic parameters for the comparison of microhabitats among regions.

Appendix S4. Individual models of vegetation structure and abiotic parameters for the analysis of microhabitat selection in each region.

4. Differential effects of habitat loss between core and northern peripheral populations of *Lacerta viridis*

Adult female of the eastern green lizard *Lacerta viridis* in Prague, Czech Republic. Photo credits: AMPR

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4.1. Abstract

The effects of habitat loss on the distribution of populations are often linked with species specialization degree. Specialist species can be more affected by changes in landscape structure and local patch characteristics compared to generalist species. Moreover, the spatial scale at which different land covers (eg. habitat, cropland, urban areas) affect specialist species can be smaller. Specialization is usually assumed as a constant trait along the distribution range of species. However, for several taxa, there is evidence of higher specialization degree in peripheral populations compared with populations in the core. Hence, peripheral populations should have a higher sensitivity to habitat loss, and strongest effects should be found at a smaller spatial scale. To test these expectations, we implemented a patch-landscape approach at different spatial scales, and compared effects of landscape structure and patch characteristics on occupancy probability among northern peripheral, more specialized populations (Czech Republic) and core populations (Bulgaria) of the eastern green lizard *Lacerta viridis*. We found that landscape structure and patch characteristics affect differently the occupancy probability of *L. viridis* in each region. Strongest effects of habitat loss were found at a spatial scale of 150m around patches in the periphery, but at a scale of 500m in the core. In the periphery occupancy probability of populations was principally affected by landscape composition, and the effect of habitat quality was stronger compared to core populations. In the core, persistence of populations was mainly explained by characteristics of the spatial configuration of habitat patches. We discuss possible ecological mechanisms behind the relationship between sensitivity to habitat loss, populations' specialization degree and position in the distribution range, and suggest conservation measures for *L. viridis*.

4.2 Introduction

Anthropogenic land-use changes lead to the loss of natural and semi-natural habitats, resulting in reduced overall amount of habitat available, fragmentation into smaller patches and increasing isolation among these patches due to land-use intensification forming a matrix of inhospitable land. These processes alter landscape composition and configuration: as patch area decreases, patch isolation increases, and spatial relations between landscape elements (e.g. habitat, non-habitat areas, and topographic features like rivers) are altered. The ecological consequences for species, at the landscape scale, include reduced functional connectivity and reduced viability (Fahrig 2003), leading to declining trends in abundance and distribution.

The effects of modified landscape structure on the distribution of natural populations have been widely studied and linked with species-specific traits (Blanchet et al. 2010; Jauker et al. 2013; Swihart et al. 2003). In particular, habitat specialization is one of the main traits shaping species' response to habitat loss (Davies et al. 2004; Henle et al., 2004b). Specialist species are known to be more sensitive to changes in patch size (Keinath et al. 2017; Krauss et al. 2003), isolation (Devictor et al. 2008; Hoehn et al 2007; Soga and Koike 2013), habitat quality (Ye et al. 2013), and overall amount of habitat in the landscape (Carrara et al. 2015; Püttker et al. 2013), whereas generalist species can typically better cope with reduced patch size and overall reduce in the amount of habitat (Vergara and Armesto 2009).

Differential responses to habitat loss between generalist and specialist species have also been linked to the 'scale of effect' of different parameters. We define the 'scale of effect' as the extent of area at which the strongest effect of a given factor on an ecological response is found (Jackson and Fahrig 2012). It has become a central topic in ecology in the past years, with particular focus onto the question how landscape composition influences species' distribution. The scale of effect of habitat amount on species' distribution has been shown to be smaller for specialist than for generalist species across different taxa such as butterflies (Cozzi et al. 2008), birds (Carrara et al. 2015; Vergara and Armesto 2009) and rodents (Morris 1996). Similarly, the scale of effect of other landscape composition variables is usually expected to be smaller for specialist species (Miguet et al. 2016).

Studies on the effects of habitat loss that consider species' specialization usually assume species to be characterized by the same trait along their distribution range. However, the degree of specialization can change across the distribution range of a given species, resulting in intraspecific differences among populations. The Kühnelt principle (Kühnelt 1965) states that the range of colonizable habitats is wider at the core of the distribution range where environmental conditions are optimal, whereas at the periphery conditions are suboptimal and fewer microhabitats are suitable for the species. Therefore, populations at the core should be habitat generalists ("euryoecious"), while populations at the periphery of the species' range can be, in comparison, more specialized ("stenoecious") (Böhme and Rödder 2014). Accordingly, it has been found in lizards (Olsson 1988; Prieto-Ramírez et al. 2018), birds (Blanco-Fontao et al. 20105) and insects (Svensson 1992) that individuals in peripheral populations have narrower realized niches than those living in the core of the distribution range. However, in spite of existing evidence, most studies on habitat loss carried out at broad scales, involving the total or partial extent of the distribution range of a species, have overlooked this variability, and therefore, the possible differential effects on distribution patterns. Consequently, conservation measures applied at local scales – especially in the periphery – might not be adequate enough to protect threatened populations if the measures were derived from analyses of habitat loss effects in other parts of the distribution range.

Here we investigated the effects of habitat loss and fragmentation on the occupancy patterns of core and northern peripheral populations of the eastern green lizard *Lacerta viridis*. Recently, it has been found that northern peripheral populations of *L. viridis* (Germany, Czech Republic) have a higher specialization degree compared to core populations (Bulgaria) (Prieto-Ramírez et al. 2018). In the periphery, populations have narrower niches and can only persist in habitats with comparably lower vegetation structure that allow them to compensate for suboptimal overall climatic conditions (e.g. lower radiation). In the core, populations have a broader range of available habitats and use microhabitats with higher vegetation structure. The higher specialization degree of *L. viridis* populations in the northern periphery suggests that these populations might also have a higher sensitivity to habitat loss and fragmentation compared to generalist populations living in the core of the distribution range.

In this study, we implemented a patch-landscape approach to evaluate the occupancy patterns of populations of *L. viridis* in Bulgaria (core) and in the Czech Republic (periphery). Our main objectives were to find out which are the most relevant spatial scales affecting patch occupancy in each region and which parameters of the landscape structure and patch characteristics have the strongest effect. We expected to find at the intraspecific level the same patterns of the effects of habitat loss reported at the species level. We hypothesized that: 1) the relevant scale(s) at which occupancy is best explained should be smaller at the periphery compared to the core; 2) the proportion of different land-cover types has a smaller scale of effect at the periphery compared to the core; and 3) peripheral populations are more sensitive to isolation, area and reduced habitat quality compared to core generalist population.

4.3 Materials and Methods

4.3.1. Study areas

The study regions were located in the northern periphery and in the core of the distribution range of *L. viridis* (Figure 4.1). The study region at the species' periphery was located in the surroundings of Prague (Bohemia, Czech Republic), where populations are located in open stony areas within open oak forest and along the cliffs of the Vltava valley, as well as those of other valleys perpendicular to the Vltava river valley (Pr; Figure 4.1b). The core region was located in the Thracian Plain of Bulgaria, in the surroundings of Plovdiv (Core; Figure 4.1c). The region is an alluvial plain dominated by the banks of the Maritsa River and its tributary rivers. Here *L. viridis* inhabits diverse natural and semi-natural habitats, from road edges and open shrubland to mesophilic forest (Mollov 2011). In both study regions habitat of *L. viridis* has been lost due to agricultural expansion and intensification, as well as by (semi)urban development. We selected landscapes in both regions with similar configuration and composition characteristics that could ensure enough levels of comparability. Both landscapes had low percentages of habitat (11.2% in the core and 13.1% in the periphery) and similar habitat configuration in terms of ranges of patch area and isolation (Appendix S1).

4.3.2. Field survey

Field surveys were carried out in Plovdiv in 2014 and in Prague in 2015. *L. viridis* is active from beginning of April to beginning of October in Bulgaria, and from mid-May to beginning of September in the Czech Republic. Therefore, in order to make surveys comparable, data collection was carried out earlier in the core than in the periphery: From beginning of April to late May in the core, and from mid-May to late July in the periphery. The difference in sampling times made average maximum air temperatures per sampling month relatively similar among regions (Core: 18.5–23.4°C ; periphery: 22.5–24.6°C).

Based on literature about the habitat requirements of *L. viridis*, and available information about places where the species has been found in each region (pers.com: Plovdiv: Tzankov, N; Prague: Moravic, J; Chamlar, J.), we identified patches of habitat to be surveyed in each region using satellite maps available in Google earth. We visited 42 patches in the core and 33 in the periphery (see Appendix S2 for locations). All polygons corresponding to the edges of the surveyed patches in both regions were manually digitalized using ArcMap (ESRI 2015).

Occupancy surveys and analysis were designed following the protocol proposed by Mackenzie and Royle (2005), prescribing a specific number of visits depending on the probability of detection of the species. Based on estimates of detection probability

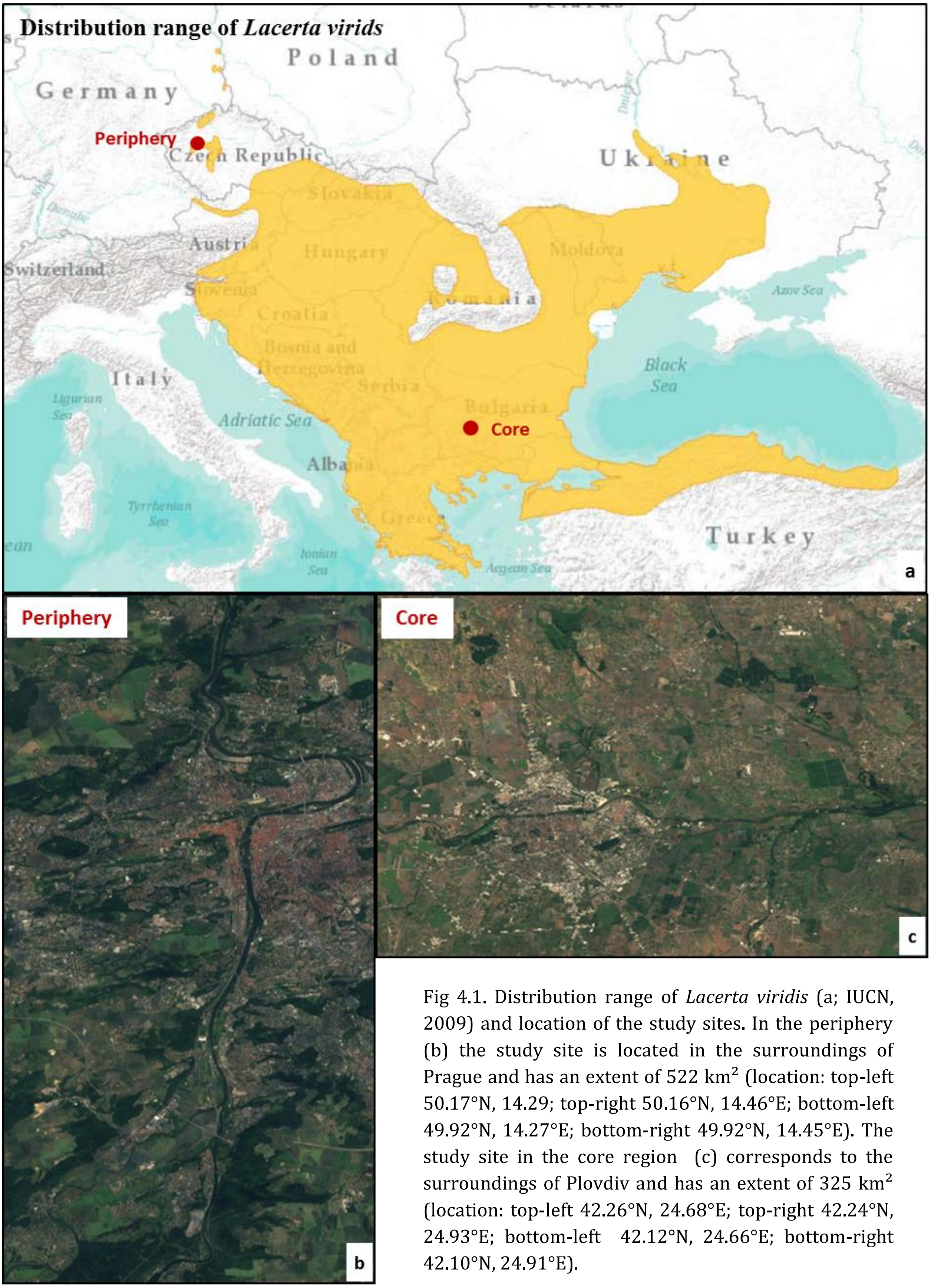

Fig 4.1. Distribution range of *Lacerta viridis* (a; IUCN, 2009) and location of the study sites. In the periphery (b) the study site is located in the surroundings of Prague and has an extent of 522 km^2 (location: top-left 50.17°N, 14.29; top-right 50.16°N, 14.46°E; bottom-left 49.92°N, 14.27°E; bottom-right 49.92°N, 14.45°E). The study site in the core region (c) corresponds to the surroundings of Plovdiv and has an extent of 325 km^2 (location: top-left 42.26°N, 24.68°E; top-right 42.24°N, 24.93°E; bottom-left 42.12°N, 24.66°E; bottom-right 42.10°N, 24.91°E).

for similar species (Janssen and Zuiderwijk 2006; Sewell 2012), the number of surveys per patch was set to two, one in the morning (9:00–12:00 a.m.) and one in the afternoon (14:00–19:00 p.m.) of the same day or one day later, in accordance with the species' daily activity pattern (Korsós 1983).

Surveys lasted one hour each, walking along predetermined line transects. With a standard walking speed of 20 m/min, which is slow enough to search and detect lizards. A one hour survey corresponds to a total length of 1200m, which were subsequently divided into transects. As most patches had a heterogeneous composition, the number and length of transects varied depending on the number of different habitat types into each patch and the proportion of area of the patch covered by each habitat type. Nevertheless, all transects in a patch always summed up 1200 m to assure one hour visit. Satellite imagery was used to define the relative coverage of each habitat type within each patch. Transect lengths varied between 50–400 m. Transects were located at least 100 m of each other, and the total length of each transect was placed in only one habitat type. The number of transects surveyed per patch ranged from three to 12. During transect walking, a width of 2.5 m was scanned at each side of the transect to visually search for *L. viridis*. As surveys were based on visual identification of lizards, and no collection of biological material or handling of animals was required, no permits were necessary for carrying out this study.

4.3.3. Land cover classification

To calculate landscape composition variables around each patch (see section "Calculating patch variables and landscape structures" below), we generated land-cover maps for the two study sites. Land cover classes in each region are described in Table 4.1. Based on reported literature, we define habitat types as the different vegetation structures used *by L. viridis* in each region. Relevant habitat types in the core were: woodland, shrubland, rocky outcrop vegetation (rocky_veg), grassland, transitional vegetation (trans_veg) and open ground and river beds (bare soil). Habitat types in the periphery were: open woodland (openwood), shrubland, rocky outcrop vegetation, dry grassland (dry_grass) and transitional vegetation. Natural or semi-natural areas that are non-habitat in the periphery were dense woodland (densewood) and humid grassland (humid_grass). In both regions, urban areas (urban), and crops and pastures (crop_pas) were defined as other non-habitat land-cover classes (Appendix S3).

To obtain the land cover classified map in the core, a supervised Mahalanobis Distance classification of cloud free, atmospherically and topographically corrected Rapid Eye satellite imagery (acquired on May 8th, 2014; 5m resolution), in combination with information derived from the Copernicus Land Monitoring Service (incl. Urban Atlas 2012, Imperviousness Degree – IMD 2012 and Tree Cover Density – TCD 2012; 20m resolution) was performed. Training (polygon) data for the target classes were generated based on land cover information collected during the field survey and complemented by data digitized based on the RapidEye imagery. Post-processing included a majority analysis (except for the class urban) with a kernel size of 3x3 to remove isolated cropland pixels mapped within (semi-)natural vegetation cover. The final map had an overall accuracy of 91.1%. All processing and analyses were performed in ArcGIS 10.6 (ESRI 2018) and ENVI 5.0 (EVI 2012).

Table 4.1. Land cover classes conforming the classified maps of both core and periphery regions.

Land cover class	Variable name	Description	Region	Habitat
Bare soil	Bare_soil	Open ground corresponding to not paved ways in the interior of patches and sandy, not vegetated river beds	Core, Periphery	Yes
Rocky outcrop vegetation	Rocky_veg	Rock outcrops and its associated grasses and herbs	Periphery	Yes
Grassland	Grass	Dry and mesic grasslands	Core	Yes
Dry grassland	Dry_grass	Broad leaved dry grassland, termophilus herbs, ecotones at the edge of forest and shrubs	Periphery	Yes
Humid grassland	Humid_grass	Perennial grasses in wetlands, wet meadows, moor grasses and river bed grasslands and herbs	Periphery	No
Shrubland	Shrubland	Shrubs and scrubs areas	Core, Periphery	Yes
Transitional vegetation	Trans_veg	Transitional woodlands with cover density <30%	Core, Periphery	Yes
Woodland	Woodland	Woodland with crown cover density >30%	Core	Yes
Open woodland	Openwood	Woodland with crown cover density between 30% – 75%	Periphery	Yes
Dense woodland	Densewood	Woodland with crown cover density between 75% and 100%	Periphery	No
Crops and Pastures	Crop_pas	Areas used for agricultural activities, either cultivation or pasture purposes	Core, Periphery	No
Urban areas	Urban	Continuous and discontinuous urban fabric, road networks	Core, Periphery	No

Classification of land cover classes in the periphery was achieved by reclassifying the most recent vegetation community and land-use map (IPR 2010) available from the Prague Institute for Planning and Development (Institut plánování a rozvoje hl. m. Prahy, IPR). This is a vector map with 5m resolution with 66 classes: 10 corresponding to different urban land uses, two to agriculture and pastures, and 52 representing different vegetation communities. In a first step we reclassified the vegetation communities that correspond to dry_grass, humid_grass, shrubland, rocky_veg and woodland. In a second step, woodland was reclassified as openwood, densewood and trans_veg based on tree cover density (TCD) data available from CORINE. Areas in the northern and southern edges of the study site were unfortunately not covered by the IPR maps. Therefore, for these areas we produced a land cover map based on the Urban Atlas 2012 and TCD information, and when necessary, manually digitalized the different classes by using orthophotos available from the IPR webpage.

4.3.4. Calculating patch variables and landscape structure

To evaluate the possible differential effects of habitat loss in the core and periphery, we applied a patch-landscape approach and analyzed the influence of variables representative of landscape structure and patch characteristics on patch occupancy. We differentiated between four types of variables: landscape configuration, landscape composition, patch geometry and patch habitat quality. Variables defining the landscape configuration around each patch included distance to river (dist_river), distance to urban areas (dist_urban) and distance to crops and pastures (dist_crop), and two measures of isolation, the edge-to-edge Euclidean distance to the nearest patch (np_dist) and proximity index (prox).The proximity index (Gustafson and Parker 1994) is a scale dependent measure of isolation and is calculated as the sum of the ratios patch area / distance to the focal patch for all patches that fall, at least partially, into the buffer of a given distance around the focal patch.

Variables related to landscape composition were calculated at different buffer-distances (hereafter, “scales”) around each patch in each region. The different scales were selected based on reported dispersal distances for *L. viridis* (Elbing 2001; Grimm et al. 2014; Mangiacotti et al. 2013). Scales selected were: 50m, 150m, 250m, 500m, 750m, 1km, 1.5km, 2km, 2.5km and 3km. At each scale, we calculated the proportion of urban, crop_pas and habitat (the sum of all habitat types).

Patch geometry variables included area, perimeter, perimeter to area ratio (Per_area) and shape index (Shape_index). Patch habitat quality was defined based on the most important parameters found for this species (Moser 1998; Prieto-Ramírez et al. 2018; Waitzmann and Sandmaier 1990): vegetation structure, radiation and slope. Vegetation structure was calculated based on available information at the microhabitat scale. At each single transect in each patch, percentage of vegetation coverage was taken in at least one plot of 25 m^2. Vegetation coverage classes included herbs < 30 cm, herbs between 40 and 80 cm, herbs > 90 cm, woody plants < 2 m, woody plants > 2 m, dry leaves, rocks and fallen trunks, bare soil, and branches coverage. Plots correspond either to the area around the specific point where a lizard was detected or to the area around random points blindly selected in the GPS along each transect. For each plot we calculated the foliage height diversity’ index (FHD; MacArthur and MacArthur 1961), which is a modification of the Shannon index applied to vegetation structure. Because most of the patches had a heterogeneous habitat composition, the plots of a single patch might belong to different habitat types. Therefore, we averaged the FHD values of the plots belonging to the same habitat type across patches to obtain the averaged FHD of each habitat type. Vegetation structure (Veg_str) of each patch was then calculated as the sum of the FDH of each habitat type weighted by the area that each specific habitat type occupied within the patch. To calculate the topographic slope we used software SAGA (Conrad et al. 2015) to derive slope maps from digital elevation models (DEMs) with 30 m resolution available from the U.S Geological Survey. We averaged pixel values corresponding to each patch. We calculated radiation from the DEMs with the 'Potential incoming solar radiation' module of SAGA (Conrad et al. 2015). Radiation value of each patch hence corresponded to the average annual radiation during the 5 years preceding the field work in each region, calculated from April to September, from 8am to 6pm and with a temporal resolution of 10 days and two hours. All other calculation procedures were carried out with ArcMap version 10.3.1 (ESRI 2015), except for shape_index and prox which were calculated with FRAGSTATS version 4 (McGarigal et al. 2012.

4.3.5. Statistical analysis

To evaluate the occupancy patterns of populations of *L. viridis*, we applied the occupancy model proposed by MacKenzie et al. (2002) as implemented in the package 'Unmarked' (Fiske and Chandler 2011) in the software R (R Core Team 2018). This model calculates the probability of occupancy (p) by correcting for the probability that an individual will actually be detected (psi). The first step was to fit a detection probability model to be used in all subsequent steps. For this, we tested the effect of vegetation structure, day of survey and patch area on detection probability. As previously shown, vegetation structure can affect the detectability by reducing the visibility for the observer. Day influences lizards' activity, given it is determined by annual seasonality, increasing with the advance of the spring and starting to decrease at the beginning of the summer in the core, and at mid-summer in the periphery. Higher activity can increase the encounter rate and, therefore, the probability of detection. Finally, big patches can be expected to hold larger populations, which might increase the probability of detecting a lizard. Thus, to find out the model that better explained detection probability, we built models with constant p and with all possible variable combinations among vegetation structure, day of survey and patch area as predictors of detection . Then, we compared models based on AIC and selected those with ΔAICc < 2 (Burnham and Anderson 2002). The model including the three variables was the best in the core, and the second best model in the periphery (ΔAIC=0.38) (Appendix S4). Consequently, all three variables were used as predictors of detection probability in all subsequent analysis in both regions.

In order to find out which were the relevant scales at which occupancy is explained in each region we tested whether occupancy patterns are explained at single scale(s) or simultaneously at multiple scales. Single-scale models included all composition variables measured at the same scale, plus configuration and patch variables, and multi-scale models included each composition variable at its scale of effect, together with configuration and patch variables. Therefore, before building multi-scale models we needed to find out which was the scale of effect of each composition variable -percentage of habitat, crops_pastures and urban- in each region. For this purpose, we fitted univariate models with each of these variables at each scale as predictor of occupancy (p) and selected the scale with the highest Nagelkerke R^2 (RN^2) as the scale of effect. In cases when the highest RN^2 value was present in several scales, the smallest scale was selected. For proximity index (prox), which is a scale-dependent configuration variable, the same procedure was applied to find its scale of effect in each region.

Then, to avoid collinearity among variables included in the same model, we applied a Spearman rank correlation test (Appendix S5) to each single-scale and multi-scale dataset. Among correlated variables ($rs > 0.60$) we selected the one with the strongest effect on occupancy probability. Additionally, we calculated the variance inflation factor (vif) of selected covariates, and retained those with $vif < 10$ (Martin and Fahrig 2012). In both regions we found strong collinearity among some variables that might have an important ecological role on occupancy. Therefore, in order to avoid skipping relevant variables from the analysis due to collinearity, we run several sets of single-scale and multi-scale models in each region (Appendix S6). Each set included all non-correlated variables, and only one from the pair of correlated variables. In the core, Np_dist was correlated with prox at all scales, as well as crop_pas with urban. Both, Crop_pas and urban, might exert strong pressure on the occupancy, and proxy is a scale dependent measure of isolation that might have different explanatory power compared to Np_dist. Therefore, we run four sets of single-scale models for this region: Np_dist and crop_pas, Np_dist and urban, prox and crop_pas, or prox and urban. For the multi-scale model in the core, crop_pas was not correlated with urban; thus, both variables could be simultaneously included and only two multi-scale models were fitted, one with np_dist and one with prox. In the periphery, habitat was negatively correlated with urban at all scales, as well as in the multi-scale dataset. Therefore, for this region we fitted two single-scale models at each scale and two multi-scale models, one with habitat and the other with urban.

After having found the best model for detection probability, the scale of effect of composition based variables and prox to be used in multi-scale models, and having tested for collinearity among variables, we could then proceed with building single-scale and multi-scale global models. All global models were tested for Spatial Autocorrelation of Residuals (SAC) to avoid underlying spatial processes to affect our results. For this, we calculated Global Moran's I and when significant SAC was found, an autocovariate parameter was calculated by means of principal components of neighbor matrices (PCNM) and added to the global model (Augustin et al. 1996). Goodness-of-fit test and overdispersion parameter (c-hat) were estimated by applying the parametric bootstrap procedure proposed by MacKenzie and Bailey (2004) and implemented in the 'AICcModavg' package of R (Mazerolle 2019).

Finally, to find out the best model(s) explaining occupancy patterns in each region, we generated all possible models starting from each single-scale and multi-scale global model, with the function dredge of MuMiN package in R (Bartón 2015). Then, we selected the models with $\Delta AIC < 2$ (Burnham and Anderson 2002). Selected models were evaluated based on indicators that can be derived from a confusion matrix, which contains observed and predicted presence/absence (1/0) values of a given model (Fielding and Bell 1997). We calculated the percent correctly classified (PCC), the area under the receiver operator characteristic curve (AUC) and Kappa statistics. All indicators have values ranging from 0 to 1. Kappa measures the agreement between the observed presence/absence values and those expected by chance, and can be calculated at different thresholds used to translate predicted probabilities into 0/1 values. We calculated two Kappa measures, one at threshold of 0.5 ($Kappa_{0.5}$) and another one at the optimized threshold ($Kappa_{opt}$), where the optimized threshold was determined by calculating Kappa at each threshold from 0 to 1 at intervals of 0.01. All indicators were calculated with the 'PresenceAbsence' package of R (Freeman and Moisen 2008). Additionally, we also calculated the RN^2 of each selected model. We then selected the models with the highest value for most of the model indicators, and compared among all the single-scale models, and with the multi-scale models. Lastly, we determined which variables influenced the most occupancy patterns in each region, and whether the multi-scale models outperformed the single-scale models.

4.4. Results

A total of 172 lizards were detected in both regions, 135 in the core and 37 in the Periphery. From 42 patches visited in the core, lizards were detected in 17 patches in both surveys and in 7 patches in one survey, for a total of 24 patches occupied. In the periphery, 7 out of 33 patches were occupied, and lizards were detected in 5 patches in both surveys and in 2 patches in one survey.

4.4.1. Scales at which occupancy is explained in each region

The effect of composition-based variables (urban, crop_pas, habitat) and the proximity index (prox) on occupancy probability as single variables is shown in Figure 4.2. At all scales, the effect of urban, crop_pas and prox was higher in the periphery (Figure 4.2a) compared to the core (Figure 4.2b). At the core, crop_pas and prox showed a low, almost constant effect across scales, and the effect of urban at its scale of effect (50m) was just slightly higher compared to the other scales. By contrast, in the periphery the difference among scales was much more marked for these variables. Here, the scale of effect of urban was found at 500m, and the effects of crop_pas and prox at 1000m and 2000m, respectively, but their effects did not change considerably across scales. The effect of habitat at small scales (<500m) was similar between regions, but increased with scale in the periphery, reaching its maximum at 2000m, and decreased with scale in the core. The effect of natural covers that do not represent habitat in the periphery was strongest at large scales (Figure 4.2c). The effect of densewood showed a tendency to increase with scale up to 2000m, after which a slight decrease in the effect is found. A tendency to increase with scale was observed for humid_grass after 250m, reaching its peak at the scale of 3000m.

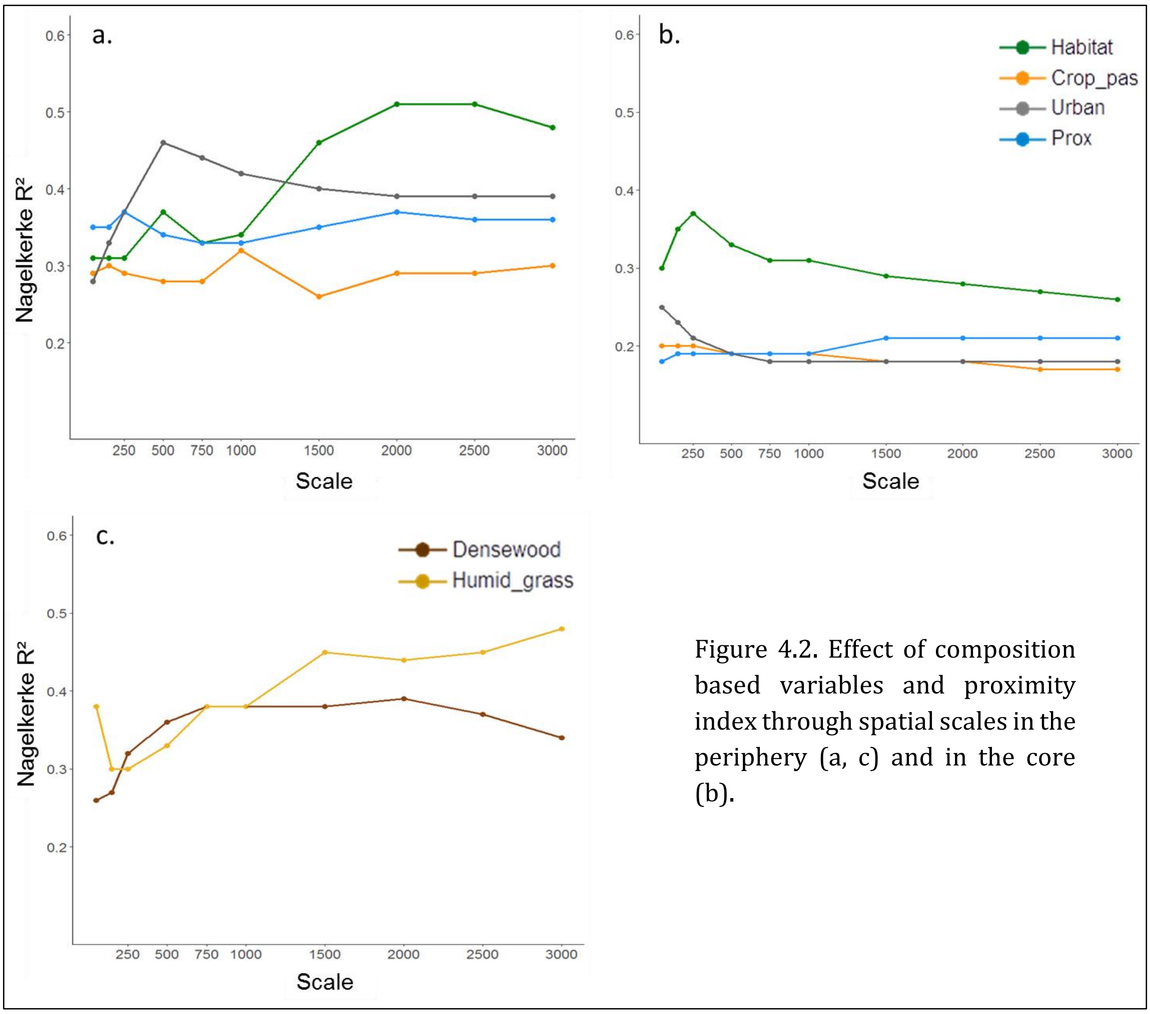

Figure 4.2. Effect of composition based variables and proximity index through spatial scales in the periphery (a, c) and in the core (b).

4.4.2. Most important variables at single scales

We found differences between regions regarding the variables that consistently had an effect on the occupancy probability across scales in SS models. In the core, most important variables were those defining landscape configuration and patch geometric characteristics (Table 4.2). Dist_river appeared consistently in all SS models, as well as a measure of isolation, either np_dist or prox. Perimeter and shape_index were also included in most models across scales. Area was not as commonly included as the variables mentioned above but was present in half of the SS models (15 out of 31), principally in models from 500m to 2000m. In the core, occupancy probability across single scales increased with isolation and perimeter and decreased with distance to the river, patch area and shape index. Although all indices across single scales had very close values, the best model was found at 750 m, which additionally included habitat, a variable that appeared only in few SS models. Prediction curves of the best model in the core showed that occupancy probability starts to decrease with a distance of 150m from the river, and reaches a value of 1 already with 10m distance from nearest patch and 20% of habitat coverage (Figure 4. 3).

Comparably, in the periphery, a combination of variables related to landscape composition, patch geometry and habitat quality defined the occupancy probability across single scales (Table 4.3). Densewood and crop_pas had a positive effect on occupancy and were present in the majority of SS models, as well as perimeter and slope. As in the core, area appeared in half of the SS models (13 out of 25), and was concentrated in scales above 500m, having a negative effect on occupancy probability. In the periphery, almost all indices had the same value across SS models. Based on the prediction curves, occupancy was above 0.5 when the proportion of densewood was between 0.4 and 0.6 and the proportion of crop_pas between 0.3 and 0.7 (Figure 4.4).

Other variables had a lower representativeness across single scales in each region. In the core, the effects of composition-focused variables were mostly concentrated at larger scales. Urban was present in most of the models at 1000m and 3000m and crop_pas appeared in very few models, from which the majority belonged to the 2500m scale. Habitat also had a low representativeness in SS models in the core with most of them being at the 2000m and 2500m scales. Thus, habitat was not very consistent in explaining occupancy probability across scales in this region, despite being present in the best model at 750m. In the periphery, variables that appeared in much fewer models were np_dist, prox and veg_str. Isolation effects, either as np_dist or prox, were concentrated at large scales and appeared in all models above >1000m having a positive effect on occupancy. Veg_str was common in models at small scales (50-250m) and its effect on occupancy was negative.

Table 4.2. Multiscale (ms) and single scale selected models at the core region. Only variables explaining occupancy probability are presented, and the direction of their effects is shown as positive (+) or negative (-). In bold is signalized the model with the highest values for most of the model performance indicators.

Scale	RN^2	PCC	AUC	Kappa$_{0,5}$	Kappa$_{opt}$	Dist_river	Np_dist	Prox	Habitat	Crop_pas	Urban	Area	Perimeter	Shape_index	Veg_str	Radiation
ms	0.4	0.761	0.824	0.513	0.559				+							
	0.43	0.761	0.821	0.513	0.559				+							
	0.33	0.761	0.821	0.513	0.513				+							
	0.37	0.761	0.824	0.513	0.513				+							
500	0.7	0.928	0.902	0.851	0.851	-		-			-		+	-	+	-
	0.7	0.928	0.902	0.851	0.851	-		-		+		-	+	-	+	
750	0.68	**0.952**	**0.918**	**0.901**	**0.901**	**-**	**+**		**+**				**+**			
	0.62	0.928	0.878	0.851	0.851	-	+		+			+	+			
1000	0.69	0.928	0.871	0.851	0.851	-	+				-	-	+	-		
	0.69	0.928	0.8855	0.851	0.851	-	+				-	-	+	-		
	0.7	0.928	0.902	0.851		-	+					-	+	-		-
1500	0.69	0.92	0.895	0.851	0.851	-	+					+	+	-		
	0.68	0.928	0.868	0.851	0.851	-	+				-	-	+	-		
	0.7	0.928	0.902	0.851	0.851	-	+					-	+	-		-
	0.66	0.928	0.895	0.851	0.851	-	+		+				+	-		
2000	0.69	0.92	0.895	0.851	0.851	-	+					-	+	-		
	0.67	0.928	0.895	0.851	0.851	-	+				-	-	+	-		
	0.7	0.928	0.902	0.851		-	+					-	+	-		-
	0.7	0.928	0.902	0.851	0.851	-	+		+				+	-		-
	0.67	0.928	0.895	0.851	0.851	-	+		+				+	-		
	0.67	0.928	0.902	0.851	0.851	-		-	+				+		+	-
2500	0.69	0.928	0.891	0.851	0.851	-	+		+							
	0.69	0.928	0.898	0.851	0.851	-			+							-
	0.67	0.928	0.895	0.851	0.851	-		-			-		+	-		
	0.7	0.928	0.895	0.851	0.851	-		-			-	-	+	-	+	
	0.69	0.928	0.895	0.851	0.851	-		-		+			+	-		
	0.64	0.928	0.895	0.851	0.851	-		-		+			+	-		

	0.63	0.928	0.895	0.851	0.851	-		-		+			+	-		
	0.66	0.928	0.855	0.851	0.851	-			-	+		-	+	-		
3000	0.7	0.92	0.899	0.851	0.851	-	+				-	-	+	-		
	0.69	0.928	0.902	0.851	0.851	-	+				-		+	-		
	0.69	0.928	0.895	0.851	0.851	-	+					-	+	-		
	0.69	0.928	0.895	0.851	0.851	-		-			-		+	-		
	0.68	0.928	0.895	0.851	0.851	-		-			-		+	-		
	0.68	0.928	0.895	0.851	0.851	-		-	+	+			+	-		

Note: Models with the same set of variables represent models with different combinations of the three variables explaining detection probability.

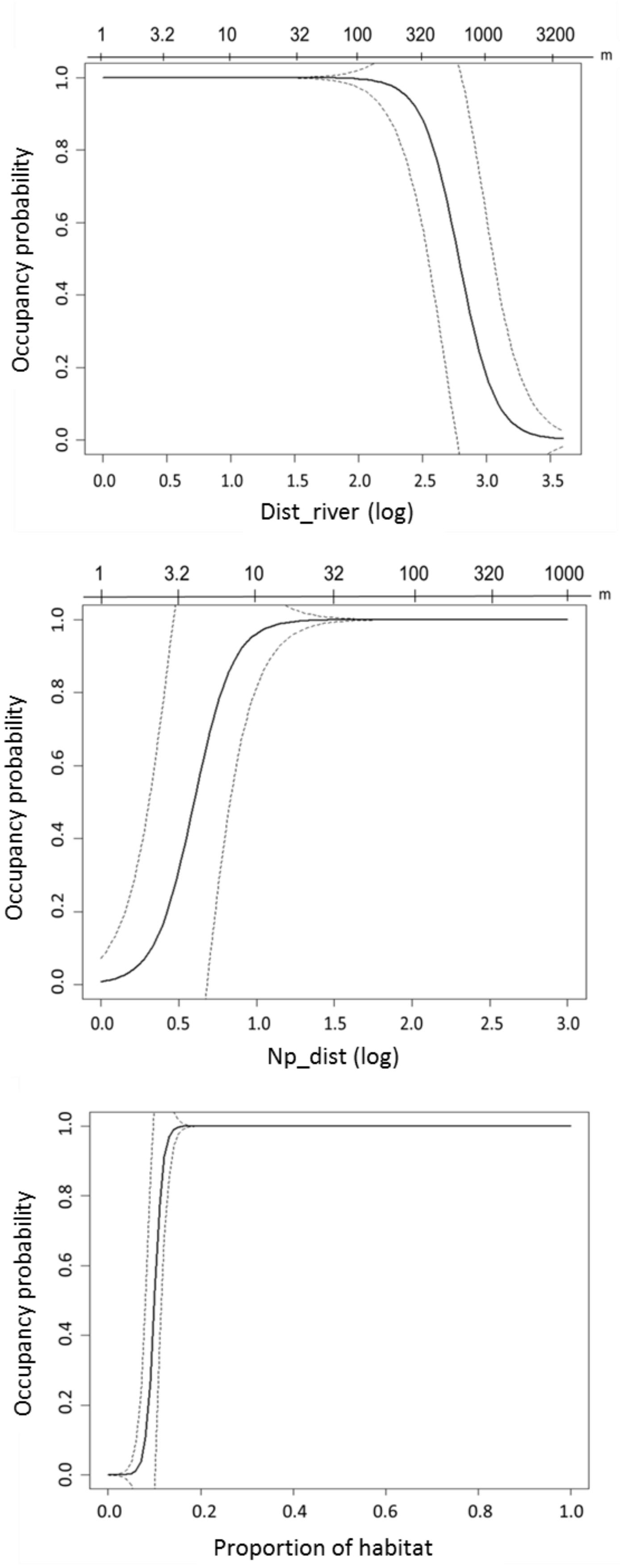

Figure 4.3. Predicted occupancy probability as function of distance to river (Dist_river), distance to nearest patch (Np_dist), and proportion of habitat in the best model at scale 750m. For Dist_river and Np_dist the x axis at the top represents distance values in meters.

Table 4.3. Multiscale (ms) and single scale selected models in the periphery region. Only variables explaining occupancy probability are shown and the direction of variables' effect is marked as positive (+) or negative (-).

Scale	R_N^2	PCC	AUC	Kappa$_{0,5}$	Kappa$_{opt}$	Dist_river	Np_dist	Prox	Habitat	Densewood	Humid_grass	Crop_pas	Urban	Area	Perimeter	Shape_index	Veg_str	Slope
ms	0.86	1	1	1	1		+	-		+				-	+			+
	0.83	1	1	1	1	+				+	-		-		+		-	
	0.79	1	1	1	1		+			+	-				+		-	
50	0.83	0.939	0.928	0.835	0.835				+		-	+			+		-	
150	0.85	1	1	1	1					+		+			+		-	+
	0.88	1	1	1						+		+			+		-	+
	0.82	1	1	1					-	+		+				-		+
250	0.86	1	1	1		-				+		+		-	+			+
	0.85	1	1	1	1		+			+		+			+		-	+
	0.85	1	1	1	1				-	+		+			+		-	+
	0.84	1	1	1	1					+	-	+			+		-	+
	0.84	1	1	1	1				-	+		+			+	-		+
	0.83	1	1	1	1				-	+		+		-	+			+
	0.85	1	1	1	1					+		+	+		+		-	+
	0.84	1	1	1	1					+		+	+		+	-		+
	0.83	1	1	1	1					+		+	+	-	+			+
500	0.85	1	1	1		-				+		+		-	+			+
750	0.86	1	1	1	1	-				+		+		-	+			+
	0.79	1	1	1	1						-	+		-	+			+
	0.83	1	1	1	1						-	+		-	+		-	+
1000	0.83	1	1	1	1		+	-		+				-	+			+
	0.8	1	1	1	1		+	-		+					+		-	+
1500	0.85	1	1	1	1		+	-		+				-	+			+
2000	0.86	1	1	1	1		+	-		+				-	+			+
2500	0.86	1	1	1	1		+	-		+				-	+			+
3000	0.86	1	1	1	1		+	-		+				-	+			+
	0.83	1	1	1	1		+			+				-	+		-	+
	0.84	1	1	1	1	+		-			-		-		+		-	

Note: Models with the same set of variables represent models with different combinations of the three variables explaining detection probability.

4.4.3. Multi-scale versus single-scale models

In the core region, when including composition-focused variables at its individual scale of effect in MS models, those with only habitat as predictor of occupancy probability performed better than models with any other combination of variables. However, in this region the best MS models did not outperform the best SS models at all scales for any of the model indicators (Table 4.2).

At the periphery, the performance of the MS models was equal to that of all SS models (Table 4.3). MS models in the periphery were partially similar to those in SS models, with dense-wood and perimeter still being very important and present in all MS models. Additionally, veg_str , np_dist and humid_grass were found to gain importance and were present in most of the MS models in the periphery. Humid_grass had a strong effect on occupancy probability, which dropped to zero at a very low coverage of this land cover class (Figure 4.4).

4.5. Discussion

This study supports the hypothesis that the landscape structure and patch characteristics resulting from habitat loss affect differently the occupancy probability of *Lacerta viridis* in core versus peripheral populations. When comparing study areas with nearly similar landscape structure, we found that landscape composition had an overall stronger effect in the periphery compared to the core when land-cover classes were analyzed individually. In spite of the fact that the scale of effect of urban areas and crops and pastures was smaller in the core compared to the periphery, the effect of these variables was higher in the periphery at all scales (Figure 4.2). Similarly, the amount of habitat around patches had a stronger individual effect across all scales above 500m in the periphery compared to the core, while at smaller scales the strength of the effect was similar between regions. Therefore, our evaluation of the individual effects of landscape composition variables confirms the hypothesis of peripheral populations being more sensitive to habitat loss, not due to stronger effects appearing at smaller scales compared to the core, but because effects are stronger across all single scales.

Lower effects of individual landscape composition variables in the core compared to the periphery reflect what we found later in multivariate models: occupancy probability in the core was influenced by landscape configuration across single scales, whereas in the periphery occupancy was much more determined by landscape composition (Tables 4.2 and 4.3). The characteristics of the landscape surrounding a patch (patch context) affect occupancy probabilities mainly through their influence on the dispersal of individuals among patches (Fahrig 2001; Cushman et al. 2013), an essential component for population persistence in structured landscapes (Brachet et al. 1999). Therefore, based on our study, it can be inferred that the most relevant parameter that might affect

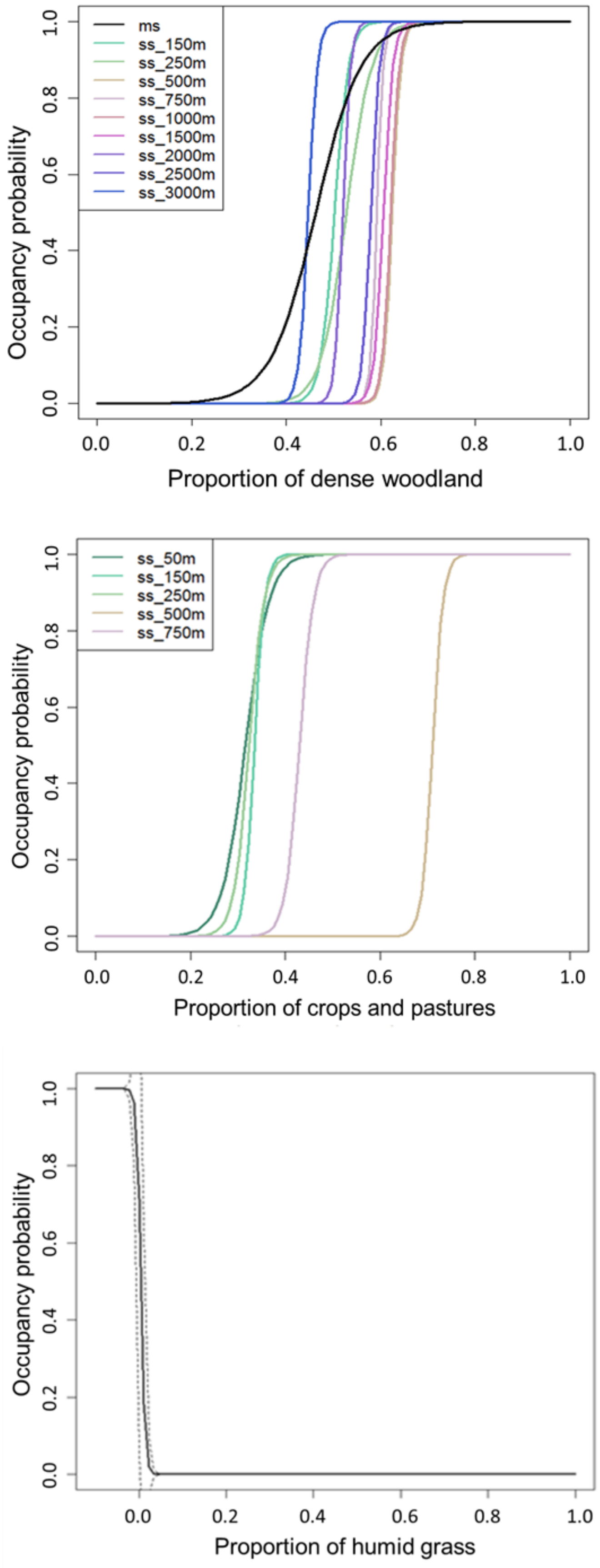

Figure 4.4. Predicted occupancy probabilities in the periphery as function of the proportion of dense woodland and crops and pastures across single scales. Probability curves plotted for each single scale (ss) correspond to the best model among the models in which the variable appears. Humid_grass curve correspond to the best MS model in which this variable was present.

dispersal in the core is the spatial relation between patches and the river, while in the periphery our findings indicate a key parameter to be the proportion of different land covers in the matrix across scales. Thus, in the core, dispersal would be facilitated through connectivity defined by spatial configuration, while in the periphery it is overall landscape permeability that affects occupancy.

This sensitivity to matrix permeability in the periphery might be principally associated to the positive effect of crops and pastures on occupancy probability up to the 750 m scale (Table 4.3, Figure 4.4), suggesting that up to medium dispersal distances lizards in the periphery can cope with these land covers. Interestingly, although the variable crops and pastures was not ranked as important parameter in the core, when present in any model, its effect was positive as well (Table 4.2). The positive effect of crops and pastures on occupancy might be related with their effect on ecological processes that can occur during dispersal, like feeding, thermoregulation and predators' avoidance (Baguette et al. 2014; Vasudev et al. 2015). Despite higher exposure to predators, crops and pastures might offer food resources, as well as thermoregulation possibilities in the peripheral region, given a need for microhabitats with lower vegetation structure in this region. Open land covers might also be suitable for juvenile dispersal, as they are less conspicuous for predators than adults; and seasonal changes of crops might allow lizards to use different vegetation structures throughout the year. Moreover, age of individuals and vegetation structure of crops can have a positive interactive effect on the movement of some species. For example, in the case of the Franklin's ground squirrel (*Poliocitellus franklinii*), crops have been shown to have low resistance to movement, especially for juveniles in late summer and autumn, when vegetation is higher and can hide them from predators (Martin and Heske 2005; Duggan et al. 2011). This might be especially important for the persistence of populations of Lacertid species, in which juvenile dispersal is one of the most important dispersal events in life (Ronce et al 1998; Cote and Clobert 2007), occurring precisely in late summer and autumn.

Tolerance to agricultural land cover might also be related with the maintenance of specific structures in the landscape that can increase the connectivity among populations, like vegetation in riparian zones, which are often inhabited by Lacertid species. For instance, the distribution of *Lacerta schreiberi* in Portugal was found not to be negatively affected by agriculture as long as vegetation along watercourses is maintained (Brito et al. 1998). Our results suggest a similar finding in the core, with crops and pastures not having a negative effect and distance to river being one of the most important factors explaining population persistence (Table 4.2, Figure 4.3). Indeed, the vegetation at the banks of the Maritsa River, as well as those of tributary rivers like the Tshaja River, is continuous along most of the river, thus potentially serving as an important corridor among patches. Hedges between fields are another landscape feature that might reduce the resistance of crops and pastures to the movement of lizards. Hedges were already found to play an important role for lizards at the community level, with cultivation patterns that include hedgerows sustaining higher species richness in a natural reserve in Cyprus (Michaelides and Kati 2009). Hence, in this region, the restoration of hedges around fields may improve connectivity and, with it, potentially occupancy probabilities. Regarding dense woodland in the periphery, which was present in all models in the periphery, its consistent positive effect (Table 4.3, Fig 4) might be due to the high correlation with prevalence of open woodland at all scales, which is one of the habitat types that *L. viridis* occupies in the periphery, rather than with permeability to dispersal.

In both regions, isolation had a positive effect on occupancy probability of habitat patches when combined with other variables. It was present across most single scales in the core but only above 1000 m in the periphery (Tables 4.2 and 4.3). Although the Island Biogeography Theory (IBT; MacArthur and Wilson 1967) and the meta-populations dynamics model (Hanski 1998) predict a negative effect of isolation, other conceptual models propose that the sensitivity to habitat configuration -isolation and patch area- vary depending on the overall amount of habitat in the landscape. The 'fragmentation threshold' hypothesis (Andrén 1994), for instance, states that habitat configuration is important when habitat amount is below ~30%; and the habitat amount hypothesis (HAH; Fahrig 2013) postulates that due to a sample area effect, habitat configuration can perfectly be replaced by habitat amount surrounding the sampled site, with isolation having either any or positive effect (eg. Melo et al. 2017). However, in our study, habitat amount did not have a paramount effect on occupancy probability across single scales in any region, and therefore, the HAH does not apply to our case.

A conceptual model that could explain our results, is the one proposed by Villard and Metzger (2014). They propose that habitat configuration is important for the persistence of populations at intermediate levels of habitat amount. At low levels of habitat destruction the species' density is high irrespective of isolation; as habitat reduction proceeds, populations become dependent on configuration and dispersal among patches; finally at high levels of habitat loss -and subsequent increase in isolation- the species pool in the landscape has considerably decreased and populations' rescue is not possible anymore, even if connectivity is improved. The breadth and position of the range of intermediate values of habitat amount at which habitat configuration is important depends on the species sensitivity to both, habitat loss and habitat configuration. In our study, habitat amount was not important across models and isolation did not have a negative effect. Hence, following the model of Villard and Metzger (2014; see Appendix S8), populations of *L. viridis* in the core and the periphery seem to have low sensitivity to both, habitat reduction and isolation, which predicts a broad intermediate level that starts after considerable habitat loss. In other words, lizards' populations seem to be able to cope with habitat loss independently of habitat configuration up to high levels of habitat reduction. With further habitat loss populations depend on configuration, but due to low sensitivity to it, they persist until considerable levels of isolation resulting from further reduction of habitat amount.

In terms of patch characteristics, the most important variable was perimeter, which was present in all models in both regions and had a positive effect on occupancy probability (Tables 4.2 and 4.3). Also, patch area was found in half of the models in each region, having in all but two cases a negative effect on occupancy probability. Positive perimeter effects coupled with negative effects of area are closely related to positive edge effects, (Fletcher et al 2007), due to perimeter-to-area ratio increasing with decreasing area. In the core, additionally, shape index, which in our study increases with patch irregularity, had a negative effect on occupancy probability. Negative effects of shape index are related to decreasing core patch area (Helzer and Jelinski 1999; Ries et al. 2004). Thus, our results suggest that in the core occupancy probability might be influenced by positive edge effects together with sensitivity to core area, a pattern that has been found in species that use both, interior and patch edges (Bender et al. 1998). Comparably, in the periphery, where shape index did not affected occupancy across scales, lizards might have preference for edges.

Differential preference in the use of patch edges between peripheral and core populations of *L. viridis* might result from differences in microhabitat selection between regions (Prieto-Ramírez et al. 2018). In the periphery, overall radiation is lower compared to the core, and lizards compensate by selecting open microhabitats with low vegetation structure in order to maximize the exposure to radiation. In the core, where radiation and temperatures are higher, lizards use microhabitats with higher vegetation structure that provide shadow and allow lizards to cool after basking hours. Thus, lizards in the periphery might use edge more often along the day and throughout the year, while in the core the preference of lizards for edges may correspond to basking hours in the early morning and late afternoon, and more often in early spring compared to late spring and summer. The relation between the effect of patch characteristics on occupancy probability and microhabitat selection and thermoregulatory behavior of lizards was also indicated by vegetation structure, which had a positive effect on occupancy probability in the core but a negative effect in the periphery. These results suggest that ecological processes at the individual level, like microhabitat selection and thermoregulation, might affect population persistence in the patch and generate occupancy patterns at the landscape scale.

Although vegetation structure was important for the occupancy probability in both regions in models at small scales (<500 m; Tables 4.2 and 4.3), it was only in the periphery where another variable defining habitat quality, which is slope, was important across all single scales and retained in multi-scale models, suggesting a stronger dependency of peripheral populations of *L. viridis* on habitat quality when interacting with other parameters at multiple scales. Northern peripheral populations of *L. viridis* have a smaller niche size compared to core ones, which makes them more stenoecious or habitat specialist than core populations (Prieto-Ramirez et al. 2018), a pattern also found in insects (Svensson 1992; Thomas et al. 1999), fishes (Lappalainen and Soininen 2006) and other lizards (Thomas et al. 1999). Furthermore, habitat specialization is closely related with higher dependency on habitat quality (Ye et al. 2013), and occupancy probabilities have been found to be strongly influenced by habitat quality in specialist species of insects (Biedermann 2004; Münsch et al. 2019, small mammals (Gardiner et al. 2018; Gomez et al. 2018) and lizards (Thompson et al. 2018) inhabiting modified landscapes, in comparison with generalist species. In this regard, our study supports the existence of this pattern, but this time at the intraspecific level, with populations differing in their degree of habitat specialization depending on their geographic position in the distribution range of the species.

Several studies have linked the position in the distribution range with vulnerability to extinction, and pointed out, that peripheral populations might be at higher risk of local extinction (Donald and Greenwood 2001; Yackulic et al. 2011). Moreover, specific traits of peripheral populations, like lower abundance (Brown 1984), lower genetic variability (Hampe and Petit 2005; Peterman et al. 2013) and smaller niche (Lappalainen and Soininen 2006; Yurkowski et al. 2016), have been proposed to explain its higher vulnerability. Position in the range and vulnerability of extinction have also been linked with sensitivity to human modified landscapes (e.g. Lucas et al. 2016), and extensive multispecies approaches have demonstrated higher sensitivity to habitat loss of peripheral populations in the Palearctic region (Boakes et al. 2018). However, only very few studies have made the complete link between position in the range, species traits and vulnerability of extinction in modified landscapes. For instance, (Henle et al. 2016) found that peripheral populations of the lizard *Lacerta agilis* had a lower genetic variability and also a higher sensitivity to patch size, compared to core populations. In this context, our work also throws some light upon the possible ecological mechanisms behind the relationship between position in the range, sensitivity to habitat loss and populations' traits, by identifying the parameters of landscape structure and patch characteristics to which northern peripheral and more specialized populations of a broad ranging species are more sensitive compared to core populations.

With respect to the analysis performed and the model selection procedures, it is important to note that the high values obtained for model evaluation indices in all of our models, can be strongly related to the fact that we tried as much as possible to cover the range and type of variables that might influence occupancy. Also, it might be strongly related to the model selection procedure that we applied, in which models were first selected based on $\Delta AIC < 2$ and then, from this group of best models, we selected those with the highest values for the indices evaluated. High indices values indicate that the models can discriminate very well between patches where the lizard is present and those where it isn't, which in a binary classification scheme can be expected for models that explain also high levels of variance (> 63% in the single scale models in the core, and >79% in all models in the periphery), and thus, our results highlight even more the fact that the inclusion of specific variables (the most common ones found in the models) might be important for model accuracy. In the periphery very high indices values of selected models (=1) might also be due to the fact that the majority of the patches in the sample were not occupied, and then, the classification ability is higher. However, given models presented in the results represent an extremely reduced group among all the models initially run, we still consider that the predictive and classification abilities of selected models, by themselves and not due to sample distribution, is very high.

An additional important remark regarding models' output, is that in multivariate models the direction of the effect of each variable can change depending on other variables present in the model (Banner and Higgs 2017). For some of the variables that we considered, like isolation in the core and crops and pasture in both regions, the individual effect was negative (Appendix S9), but in combination with other variables the effect was positive. Positive effects of these variables were systematic in all multivariate selected models where these variables were present, and therefore, we rely on our results, and highlight the importance of testing coefficients direction when variables are alone or in combination with other variables.

Regarding the land cover classification approach that we apply, it is important to consider that although the ideal methodological approach to compare among landscapes is to produce classified maps with data obtained from the same source, our approach was perfectly sufficient to perform the ecological analysis that we carried out. As stated by Fynn and Campbell (2019), possible shortcomings of landscape ecology studies using imagery from different sources might come out in cases when images with coarse resolution are compared with finer resolution imagery. However, in our study the resolution of both, the IPR map used for the periphery and the rapid eye satellite imagery used for the core, was the same (5m), and additional information used for the classification in both regions had the same source (Urban atlas, TCD and imperviousness layers of CORINE) and resolution; orthophotos used for some parts of the map in the periphery were rectified by IPR and had also a very high accuracy. Dissimilar sources of information might as well represent a disadvantage due to the different methods used for the classification process in the IPR map of the periphery compared to those we applied to the Rapid Eye satellite imagery in the core region. However, given the high specificity of the original classification of the IPR map (> 60 classes), which we afterwards reclassified in broader classes, we consider that the output of both maps had similar accuracy (>90%), and therefore, perfectly allowed to compare between landscapes and precisely calculate percentages of land cover classes. Comparability was also achieved through careful examination of maps by the first coauthor who knows both study sites extremely well after having spent several months in both regions, and therefore had trustable on-the-ground information, and by means of thorough and systematic application of specific criteria to classify each land cover in both regions (Table 4.1).

4.5.1. Implications for conservation measures

In the periphery, the most important was the landscape composition and the permeability represented mostly by the presence of crops and pastures. Our results show that these effects are present already at very low scales, and that in scales between 50 to 500m occupancy probability increases already over 0.8 with percentages of crops and pastures between 30 to 40%. On the other side this permeability decreases very fast with already a low percentage of humid grasses. Therefore, we strongly recommend increasing matrix permeability by applying a more heterogeneous cultivation pattern that includes hedges and line structures with vegetation corresponding to the habitat of the species, as well as the inclusion of such structures through areas with humid grassland.

With respect to patch characteristics, it is very important to increase the availability of edge in the patches. This can be achieved by increasing patch size with linear structures to maintain a high perimeter to area ratio. In parallel, these linear structures can also serve to connect through the agricultural landscape. Finally, maintaining high levels of habitat quality is also very important in this region, and can be achieved by keeping low levels of vegetation structure, and specially by protecting valley's slopes from overgrown vegetation. Similarly, overgrown vegetation should be avoided in open woodlands, which are usually located in slopes and at the borders of dense woodland areas.

In the core, regarding configuration of the landscape, the most important management measures are, first to protect the patches that are close to the river, or at the riverside, and second to structurally connect with the river those patches that are further. Based on our analysis, patches with a distance to the river lower than 320m have an occupancy probabilities over 0.8, and patches with distances longer than ~650 m have probabilities lower than 0.5. Then, we recommend to protect -and restore where necessary- the river bank vegetation along the Maritsa River and its tributary rivers, as this areas might act as important corridors for the species, and to connect further habitat remnants with this large riverside corridor, through additional structures with habitat vegetation. As in the periphery, hedges and habitat lines surrounding crops could improve connectivity through the landscape.

Regarding composition, it is very important to protect the habitat surrounding patches, principally at a scale of 250m, which is the scale of effect of this land cover and at which the variable was included in multi-scale models, being the only variable present in these models. Habitat was also present in the best model at the scale of 750m, and our results show that with only a small increment in the percentage of habitat at this scale (~ 10%) the probability of occupancy substantially increases (Figure 4.3).

With respect to patch characteristics, we found that the shape of the patches is very important for both, maintaining a large perimeter and also sufficient core area. Therefore, we strongly recommend to not alter the shape of remnant patches that already have a regular shape, and to restore habitat at the direct borders of patches with irregular shapes, in order to increase perimeter and core area by 'softing' angular and irregular shapes. Regarding habitat quality, we suggest to protect the vegetation structure in remnant patches, avoiding practices that can diminish it. This means, maintaining different vegetation levels that include grasses, shrubs, rocks, fallen trunks, trees, etc. Grazing, for instance, can have a very rapid negative effect in the quality of the patches by substantially reducing vegetation structure (pers. observation), given cows and goats feed on the low and medium strata, and goats also on lower branches of woody plants. As a consequence lizards lose refuge and structures to bask. Also, as vegetation structure decreases radiation incidence increases, consequently augmenting temperatures and diminishing humidity, with the habitat becoming drier and less suitable for the species.

In both regions we recommend to monitor the populations. Further insights in the abundance and condition status of individuals would be very useful to more deeply asses the status of populations.

4.6. Conclusions

Our study shows that northern peripheral, more specialized populations of *L. viridis* are also more sensible to the effects that habitat loss has on the landscape structure and on the characteristics of remnant habitat patches. In comparison with populations in the core, the occupancy probability of populations in the periphery was found to be more affected by landscape composition, which suggests substantial dependency on matrix permeability; also, habitat quality had a stronger influence on populations in the periphery and our results regarding patch geometric characteristics in this region suggest a preference of the species for patches with more edge in relation to patch core area. Comparably, in the core, we found that persistence of populations is mainly affected by the possible connectivity that the river bank vegetation offers through the landscape. Also, the species in this region seems to be an omnipresent species regarding its use of the patch, requiring both long edges and also enough core area in the interior of the patch. Finally, in both regions the species had low sensitivity to habitat amount and to habitat configuration, an outcome that strongly differs from the expectations of the IBT, the meta-populations dynamic models and also from the HAH, but one that fits conceptual – and empirically tested – models that describe a more gradual relationship between habitat amount and isolation.

4.7. Acknowledgments

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4.8. Supporting Information

Appendix S1. Distribution of variables representative of habitat configuration in each region.
Appendix S2. Location of habitat patches surveyed in each region
Appendix S3. Maps of classified land cover classes in each region.
Appendix S4. Models for detection probability in each region.
Appendix S5. Spearman rank correlations of no scale dependent variables in each region.
Appendix S6. Different sets of models ran in each single scale and multiscale models in each region.
Appendix S7. Best selected models at small scales from 50m to 250m in the core region.
Appendix S8. Conceptual model of habitat configuration and habitat amount effects proposed by Villard and Metzger (2014).
Appendix S9. Individual effects of non-scale and scale dependent variables.

5. Possible early warning indicators of negative effects of habitat loss on core populations of *Lacerta viridis*

Subadult eastern green lizard *Lacerta viridis* in Plovdiv, Bulgaria. Photo credits: AMPR

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5.1. Abstract

Habitat loss increases the stress that individuals of species inhabiting fragmented landscapes experience. Morphological and physiological parameters can serve as early warning indicators of stress before persistence of populations be threaten. In this study we tested effects of patch characteristics, isolation and landscape composition resulting from habitat loss on body condition (BC), fluctuating asymmetry (FA) of metric and meristic traits, and tick load of individuals from central populations of the eastern green lizard *L. viridis*. We evaluated the effects of each landscape composition parameter at its scale of effect for each indicator. BC was negatively affected by habitat loss and conversion into cropland. FA of different traits was affected by interactions among patch and landscape parameters and increased with loss and conversion of habitat, reduction of patch size and isolation, with responses being highly sex and age dependent. Tick load increased with habitat availability and decreased with habitat conversion and isolation. No correlations were found among evaluated indicators. BC and FA can be used as suitable early indicators of stress for populations of *L. viridis* and tick load may be a suitable indicator for the isolation of host populations in fragmented landscapes. At the landscape scale, conservation measures should focus on the protection of habitat at broader scales to compensate negative effects of cropland and urban areas occurring at small scales.

5.2. Introduction

Habitat loss imperils species' persistence due to reduction of area providing suitable habitat, isolation of remnant habitat patches and changes in landscape structure, including habitat configuration (Fahrig 2003). These effects are accompanied by changes in environmental conditions, through the modification of fluxes of wind, water and solar radiation (Saunders et al. 1991), which therefore affect vegetation structure (Laurance et al. 1998), microclimate (Kapos et al. 1997) and ground cover (Didham et al. 1998). As a result, populations embedded in patchy fragmented landscapes are expected to suffer from enhanced environmental stress, facing the transformation of parts of their habitat into a hostile environment where their ecological requirements are not met anymore (Hanski and Ovaskainen 2000). Also, populations exposed to reduced patch area and increased isolation decline in size and gene flow among them is reduced, leading to a loss of genetic variability (Frankham 2009; Hitchings and Beebee 1998; Tallmon et al. 2002). Additionally, these conditions can promote mating among close relatives (Charlesworth and Willis 2009), increasing the risk of inbreeding depression (Saccheri et al. 1998) and extinctions (Henle et al. 2004a).

Both, environmental and genetic stress resulting from habitat loss can affect morphology and physiology of individuals before populations irreversibly decline (Ellis et al. 2012), and therefore, parameters related to these characteristics can be used as early warning indicators of population status (Leary and Allendorf 1989; Seebacher and Franklin 2012). For instance, environmental stress due to changes in microclimatic conditions in fragmented landscapes can affect developmental stability of individuals (Beasley et al. 2013; Braña and Ji 2000; Lazić et al. 2013). In bilateral symmetrical traits, small random deviations from perfect symmetry called fluctuating asymmetry (FA) are used as a measure of developmental instability (Beasley et al. 2013; Van Dongen 2006). Increase FA has been found to be related to environmental stress resulting from habitat loss and fragmentation, and therefore, is extensively applied as an early indicator of stress in fragmented populations (Crnobrnja-Isailovic et al. 2005; Helle et al. 2011; Lens and Eggermont 2008). In the long term, loss of genetic variability and inbreeding resulting from small population size can also generate developmental instability, and then FA is also used as warning signal about long term effects of habitat loss related to genetic stress (Leary and Allendorf 1989; Pertoldi et al. 2006).

Body condition is a physiological parameter also frequently used as indicator of the status of populations in fragmented landscapes (Delciellos et al. 2018; Janin et al. 2011). Body condition can decrease short after fragmentation, due to increased competition resulting from a transient initial increase in population density (Krasnov et al. 2007), known as crowding effect (Debinski and Holt 2000; Tischendorf et al. 2005). This phenomenon has been observed in several taxa, including snakes and lizards (Mitrovich et al. 2009; Stow et al. 2001), and is known to last up to two years in birds and seven years in invertebrate species (Debinski and Holt 2000). On the other hand, independent of crowding effects, shortage of resources due to loss of area with available food, refuge and space can also generate reduction in body condition (Battles et al. 2013; Bucher and Entling 2011; Zanette et al. 2000). Lower body condition, in turn, makes individuals more susceptible to parasitic infections due to immunosuppression (Sánchez et al. 2018). This leads to a higher investment of energy in immune defense, which consequently reduces mass or fat depositions, reducing body condition even more, and increasing susceptibility to parasitic infections (Bower et al. 2019). Therefore, additional to FA and body condition, parasite load and/or prevalence are also used as an early indicator of population stress in fragmented landscapes (Gillespie et al. 2005; Santos et al. 2018). In the long term, low physiological status related to limited resources can have negative effects on the survival of individuals and, consequently, on the persistence of the populations, increasing the risk of extinction (Collinge and Forman 1998, Henle et al. 2004b).

These possible indicators of population status have been shown to be sensitive to different parameters that characterize habitat patches. In lizard populations, FA has been found to be negatively affected by habitat quality (Lazić et al. 2013), and to increase with fragmentation and, specifically, with isolation (Ljubisavljević et al. 2005; Sarre 1996). By its side, body condition of lizards has been reported to increase with habitat quality (Amo et al 2007a,b; Gallego-Carmona and Bernal 2016; Stellatelli et al. 2015). On this parameter effects of patch area or isolation have not been tested on lizards, but in spiders Bucher and Entling (2011) found body condition to decrease with increased isolation. Finally, parasite load in lizards has been shown to increase with decreasing habitat quality (Amo et al. 2007a; Gwiazdowicz et al. 2020), and in small and mid-size mammals parasite prevalence and intensity was found to increase with fragmentation (Raharivololona and Ganzhorn 2009; van der Mescht 2011).

Furthermore, although rarely tested, the impact of landscape composition, in terms of the amount of different land cover types (habitat, urban and cropland) in the landscape, has also been linked to these indicators. Reduced habitat amount in the landscape has been found to have negative impacts on body condition of toads and small mammals (Janin et al. 2011; Püttker et al. 2008), positive effects on fluctuating asymmetry of birds and marsupials (Helle et al. 2011; Teixeira et al. 2006) and on parasite load and prevalence in small mammals (Püttker et al. 2008; Santos et al. 2018; Thamm et al. 2009). However, the effects of landscape composition have never been tested on lizards. Moreover, with very few exceptions (Janin et al. 2011; Kusack et al. 2020; Thamm et al. 2009), most studies evaluating effects of landscape composition on these parameters set a specific buffer zone surrounding the area of interest (e.g. patch) in which the percentages of the cover types of interest are calculated. However, not all land cover types have the strongest ecological effect at the same spatial scale. The scale of effect is the extent of area at which the strongest effect of a variable is found (Jackson and Fahrig 2012). This is a concept developed in the arena of landscape ecology and is extensively used in studies evaluating the effect of landscape composition on other ecological parameters like occupancy and abundance (Garmendia et al. 2013; Prieto-Ramirez et al. 2020; Remm et al. 2017). The application of this approach to evaluate effects of modified landscape composition, resulting from habitat loss, on morphological and parasite-related parameters could increase the precision of the analysis and give more insights into the relation between processes occurring at the landscape scale and at the individual level of biological organization (Ellis et al. 2012)

Lacerta viridis is a generalist species with a distribution range extending from northern Turkey to central Czech Republic, with the historical core of its distribution range being located in Bulgaria (Marzahn et al. 2016). *L. viridis* is listed in the European Habitats Directive (2007) under Annex IV, which requires strict protection of the species. Although at the national level it is the most abundant lizard species in Bulgaria (Popgeorgiev and Mollov 2005), it does face reduction of habitat due to agriculture and urban expansion in the central part of the country – the Thracian plateau (Mollov and Georgiev 2015).

In this study we evaluated the effects of patch characteristic variables, isolation, and landscape composition on the body condition, FA of metric and meristic traits, and tick load (*Ixodes ricinus*) of individuals of *L. viridis* inhabiting a fragmented landscape in central Bulgaria. The present study was carried out in the context of a broader investigation regarding microhabitat selection and effects of habitat loss. So far, findings have shown that the studied populations are not genetically differentiated and have high genetic variability (Nemitz- Kliemhen et al. 2020). However, the occupancy patterns of populations in the area has already been affected by habitat loss, and extant populations depend on specific landscape structures and patch parameters to persist (Prieto-Ramírez et al. 2018; Prieto-Ramírez et al. 2020), and this implies that populations are already being subject to environmental stress. Thus, this system offers an excellent opportunity for understanding early effects of habitat loss on persisting populations and to investigate the suitability of morphological and physiological parameters as early warning indicators of effects of habitat loss.

We predict parameters that increase resources at patch and landscape levels, regulate environmental conditions into the patch and ensure connectivity (patch area, habitat quality and habitat amount in the landscape) to have positive effects on body condition and negative effects on tick load and fluctuating asymmetry on individuals of *L. viridis.* On the contrary parameters that can negatively affect environmental conditions into the patch, reduce resources availability and connectivity (isolation, patch edge, and cropland and urban areas in the landscape) are expected to have the opposite effects Fisher and Lindenmayer 2007; Hatfield et al. 2020; Pardini et al. 2017). Additionally, we expect habitat amount in the landscape, patch area and habitat quality to reduce effects of isolation and cropland and urban areas in the landscape, and edge effects to be intensified by non-habitat land covers surrounding patches (Hatfield et al. 2020). The results of this study will contribute relevant information about the ecology of the species, and allow to recommend conservation measures for the species in this region, especially regarding monitoring programs, and to make inferences about possible early warning indicators that could be used in other regions where the species is more vulnerable to habitat loss, like northern peripheral regions (Prieto-Ramirez et al. 2020).

5. 3 Materials and methods

5.3.1. Study area

The study was conducted in the surrounding of Plovdiv, Bulgaria, in the Thracian plateau. It is an alluvial plain dominated by the banks of the Maritza River and of tributary rivers. In this region, which corresponds to part of the current and historical core of the distribution range of the species (Marzahn et al. 2016), *L. viridis* inhabits a broad range of natural and semi-natural habitat types with high vegetation structure, including river banks, shrublands and mesophilic mixed forest (Mollov 2011). Due to urban and agricultural expansion the species faces severe habitat loss in this region (Kambourova-Ivanova et al. 2012; Mollov and Georgiev 2015). Most of the habitat is configurated in fragments of variable size separated one from another by a matrix of unsuitable land covers. Based on other studies in the same area, the process of conversion and fragmentation of habitat started early in the 30's, intensifying during the 90's (Mollov and Georgiev 2015), and current landscape structure might have change very little, if at all, during the last decade (Mollov 2011; Mollov and Velcheva 2010).

5.3.2. Study design and data collection

In the context of a broader study we visited 42 habitat patches (Prieto-Ramirez et al. 2018) and based on observations in these patches, six patches were selected to develop the present study; an additional patch was selected in a later visit (Figure 5.1; see Appendix S1 for patches' coordinates). The main criteria for this selection were: 1. patches with an encounter rate during the occupancy survey ≥ 2 individuals per hour to ensure catching individuals for the present study in a reasonable period of time; 2. selected patches should cover the ranges of patch area and isolation in the study region; and 3. selected patches should be broadly distributed throughout the landscape such that they are surrounded by different land cover types. All selected patches are separated from each other by agricultural landscape, urban areas and/or highways.

Field work was performed from beginning of April to mid-May in 2015 and from mid-June to beginning of July in 2017. In this region males become active after the winter pause in mid-March and females start to become active at the beginning of April. The reproduction season lasts until mid or late May, and during this time both sexes are active and have a unimodal activity pattern (Grimm et al. 2014). As temperature increases with the advance of spring and the beginning of summer, both sexes stay active but the daily activity pattern shifts to bimodal with a pause during midday. Thus, survey was adjusted depending on the season in which the region was visited: in the spring of 2015 surveys were performed from 9:00 until 19:00, and in the summer of 2017 surveys started very early in the morning at 7 a.m., when temperatures were already suitable for activity (~27°C) and extended until 8 p.m. with a pause of two or three hours during midday depending on temperature.

Figure 5.1. Patches where surveys were carried out in the surroundings of Plovdiv, Bulgaria. Map source: Base map ArcGIS desktop (ESRI 2015).

Each population was visited multiple days until 20 individuals were caught. Populations 1, 2, 3, and 4 were sampled only in 2015, populations 5 and 6 in both years and population 7 was only visited in 2017. For each captured individual sex, age (adult or subadult) and number of ticks (*Ixodes ricinus*) were recorded. Individuals were weighted with a digital balance to the nearest 0.01 g and snout-vent length (SVL) measured to the nearest 1 mm. Individuals were classified by sex and age based on visual inspection of size, color pattern and reproductive organs in the field. Then, we checked for SVL distribution and our classification in the field matched the information provided by Sagonas et al. (2018) for Greek populations of *L. viridis* about minimum size of sexually mature individuals (adult males >80 mm; adult females> 76 mm). For analysis of fluctuating asymmetry data on two metric characters –length of front and hind legs– and five meristic traits –femoral pores and infralabial, supralabial, supraciliary and supraocular scales– was gathered. Length of front and hind legs was measured with a caliper to the nearest 0.02 mm.

5.3.3. Calculating Body Condition and Fluctuating Asymmetry

Body Condition Index (BCI) and Scaled Mass Index (SMI) calculations

As body condition index (BCI) we calculated the scaled mass index proposed by Peig and Green (2009). The main advantage is that it takes into account the scaling relationship between mass and a selected measure of linear size. This is achieved by calculating the scale parameter via standardized major axis regression (SMA), which afterwards can be implemented to calculate the BCI of any individual. The scaled mass index is calculated as follows:

$$\hat{M}_i = M_i \left[\frac{L_0}{L_i}\right]^{b_{SMA}}$$

where M_i and L_i are the body mass and linear measurement of size of individual *i*; L_0 is any value of L in the range of values measured, and is suggested to be the mean or median; and b_{SMA} is the scaling exponent. The question that is answered by calculating the SMI is which would be the BCI of any given individual if it had a certain linear size (L_0) by applying the scaling exponent. For our calculation of BCI we selected SVL as linear measure of size. Following Peig and Green (2009), we performed a first SMA to check for outliers and remove them with the purpose of getting the best possible fit of the line in the definitive SMA regression and calculate the scale parameter. Based on Cook's distances we removed five individuals (Appendix S2, Figure S2.1) and refitted the SMA (Appendix S2, Figure S2.2) obtaining a scale parameter of 3.285. Then, we calculated the SMI for all individuals using the mean of SVL (87 mm) as L0. Finally, BCI was log transformed for further analysis.

Test of fluctuating asymmetry

Two out of five recorded meristic symmetrical traits had enough individuals with asymmetric counts to perform the analysis – femoral pores and supraciliary scales. For infralabial and supralabial scales only 23 and 24 individuals out of 166 from the total sample including all populations presented asymmetry and the number of individuals with asymmetry in supraocular scales was only ten. Such low proportion of individuals with FA of these traits led to very low sample heterogeneity, which is indispensable to test population level FA against anti-symmetry (Van Dongen 2000), and hence, these three meristic traits were omitted from the analysis of fluctuating asymmetry. The correlation between FA of front and hind leg length was low (ρ=0.116), and therefore, both traits were analyzed separately.

Deviation from symmetry does not necessarily correspond to fluctuating asymmetry, and can also be present in the population due to directional asymmetry or antisymmetry

(Palmer and Strobeck 1986; Tomkins and Kotiaho 2001). Directional asymmetry is the case when the average tendency of the asymmetry in the population is to the same direction and has a frequency distribution of the signed right-left (R-L) values skewed towards one direction (Palmer and Strobeck 1986). Antisymmetry is present when about half of the population has asymmetry in one direction and the other half in the other direction, and is seen as a platikurtic frequency distribution of the signed R-L difference (Palmer and Strobeck 1986). We applied the D'Agostino skewness test to test for directional asymmetry and the Anscombe-Glynn kurtosis test to test for antisymmetry in front and hind leg length (Komsta and Novomestky 2015). For count data, like in the case of femoral pores and supraciliary scales, we visually inspected the frequency distribution of the data (Palmer and Strobeck 1986). As shown by the tests and by the frequency plots (Appendix S3 - S5) the deviations from asymmetry that we found in our data correspond to fluctuation asymmetry. We tested for body size (SVL) dependency of FA for all traits. For FA in front legs, hind legs and femoral pores we additionally tested for trait size dependency, calculated as the average of leg length. No body size or trait size dependency was found for any trait.

5.3.4. Environmental Variables

To assess the impact of habitat loss on developmental stability, body condition and parasite load we evaluated the effect of variables characterizing patches, habitat configuration and landscape composition. For populations 1-6, values of all variables included in the present study were extracted from a previous study (Prieto-Ramirez et al. 2020) for which patch digitalization was done with ArcMap version 10.3.1 (ESRI 2015) to calculate patch characteristics and habitat configuration variables, and land cover classification was performed in order to calculate landscape composition variables. For population seven digitalization of the patch was done in this study in the same way in order to calculate patch characteristics and habitat configuration, but neither habitat quality nor landscape composition variables were available for this patch. Geometric characteristics of each patch include area, perimeter and perimeter/area ratio. Perimeter/area ratio is one of the most common metric to study edge effects in habitat loss and fragmentation (Fletcher et al. 2007), and therefore hypothesis regarding edge effects were tested by evaluating effects of this variable. To evaluate the influence of habitat quality, we tested the effects of vegetation structure. *L. viridis* is a mesothermophile and mesophile species, and in the study region is highly dependent on enough vegetation cover that offers shadow and humidity, as well as refuge and open spots to bask (Mollov and Velcheva 2015; Vacheva et al. 2020). Thus, it uses habitats with comparatively higher vegetation structure than those used by other lizard species in the region (Petrov 2007; Vacheva et al. 2020). Vegetation structure was calculated as a foliage height diversity' index (MacArthur and MacArthur 1961) based on information gathered at the microhabitat scale in several plots in each patch (Prieto-Ramírez et al. 2018). Habitat configuration was characterized by patch isolation, calculated as the edge-to-edge Euclidean distance to the nearest patch (isolation). For each patch, the isolation values were calculated with respect to the real nearest neighboring patch. Neighboring patches are not necessarily included in the present study, but were part of an occupancy study performed earlier in the same region (Prieto-Ramirez et al. 2020). Landscape composition variables included proportion of crops and pastures (cropland), proportion of urban areas and proportion of habitat surrounding patches. These predictors were calculated at different buffer distances around patches (scales) selected based on dispersal distances reported for *L. viridis* (Grimm et al. 2014; Mangiacotti et al. 2013; Elbing 2001). Selected scales were: 50 m, 150 m, 250 m, 500 m, 750 m, 1 km, 1.5 km, 2 km, 2.5 km and 3 km (Prieto-Ramírez et al. 2020). The values of variables corresponding to each patch are summarized in Appendix S6.

5.3.5. Statistical analyses

All statistical analyses were performed with R (R Core Team 2018) using the relevant functions (see below). In the second year, only very few juveniles that were born in that year were caught, and therefore, for all subsequent analyses, we classified individuals into two age classes: adults and subadults (including juveniles).

Mixed models with patch identity as random effect were applied to analyze the data of all traits. Data of BCI was normally distributed (Shapiro – Wilkonson normality test: W=0.985, p-value=0.103) and was analyzed with linear mixed models (LMM). Data of FA of front and hind legs was not transformed (Palmer and Strobeck 1986) and was analyzed with generalized linear mixed models (GLMM) with gamma distribution. For the two meristic traits – femoral pores and supraciliary scales – we tested for differences between Poisson and negative binomial distribution of the count data, and found no differences (femoral pores: $\chi^2=0$, p-value=1; supraciliary: $\chi^2=0$, p-value=1). Additionally, we tested for zero inflation in supraciliary data, given we had only 45 individuals with FA; no zero inflation was found (ratio observed to simulated: 0.988, p=0.878). Thus, the data of femoral pores and supraciliary scales were analyzed with GLMM with Poisson distribution. Finally, count data of tick load was also analyzed with GLMM with Poisson distribution.

For each trait we tested the effect of sex and age applying mixed models. Then, the scale of effect of each landscape composition variable – cropland, urban and habitat – on each trait was assessed by fitting univariate mixed models with each of these variables at each scale. The scale with the highest Nagelkerke R^2 (RN^2) value was selected as scale of effect (Martin and Fahrig 2012) and used in subsequent analysis.

We evaluated the individual effects of each patch and landscape parameter on BC, tick load and FA. Also, the effects of the interaction between each parameter and sex and age, separately, were evaluated. To test hypothesis regarding effects of interactions among parameters, we constructed models with first order interactions among patch area, perimeter/area, vegetation structure, isolation, proportion of habitat, proportion of cropland and proportion of urban areas. Additionally, the effects of interaction terms were evaluated in combination with sex or age (second order interaction terms). To avoid collinearity, we tested correlations among variables using a Spearman rank test. Only models including non-correlated variables ($r<0.60$) were tested.

As we performed a large number of multiple comparisons, our analysis had a risk of error Type I, and therefore, a family-wise error rate (FWER) correction, like the Bonferroni alpha adjustment, has to be done (Pedhazur and Schmelkin 1991). However, the application of Bonferroni corrections has two main shortcomings: first, it increases Type II error rate, and second, the significance of a single test depends not solely on the strength of the effect itself, but on the number of subsequent tests (Perneger 1998; White et al. 2019). Therefore, in order to reduce these risks while avoiding also high type I error rates, we followed the common null hypothesis principle (Miller 1981; Rice 1989), and defined 'family' as the subgroup of models corresponding to a single prediction (Bender and Lange 2001). Hence, a family of models includes the model testing the effect of a single patch or landscape parameter or of an interaction among parameters, and two models testing the difference of that effect among sex or age classes. Thus, we applied an alpha threshold of 0.016 to all models tested. Additionally, to identify the stronger effects, we applied a Cohen's f^2 test to evaluate effect sizes of significant variables or interaction terms (Selya et al. 2012). Results are focused on those variables (or interaction terms) that had mid to high effect sizes (>0.1) (Cohen 1988).

5.4. Results

A total of 166 lizards were caught in all populations, 119 adults and 47 subadults. Sex identification was possible in 151 lizards, of which 71 were females and 80 were males. No significant differences were found among years for any response variable analyzed (Appendix S7) except for FA of supraciliary scales. Hence data was combined for all subsequent analyses.

The scales of effect of the three land cover types evaluated – habitat, cropland and urban– were in most cases below 500 m (Figure 5.2). The exceptions were habitat, with a scale of effect of 3000 m on BCI, hind legs and supracialiary scales, and cropland with a scale of effect of 3000 m on tick load. Urban presented scales of effect below 250 m for all response variables.

5.4.1. Body condition

Males had significantly higher body condition than females ($t=1.979$, $p=0.049$). Body condition increased with proportion of habitat ($t=2.428$, $p=0.016$) and decreased with proportion of cropland ($t=-2.554$, $p=0.011$) (Figure 5.3). Both variables had medium-high effect size (habitat: Cohen's $f^2=0.204$; cropland: Cohen's $f^2=0.214$) and did not show significant differences among sexes or age classes (habitat*sex: $t=-1.307$, $p=0.193$;

habitat*age: t=1.041; p=0.300; cropland*sex: t=0.071, p=0.943; cropland*age: t=-0.155, p=0.876).

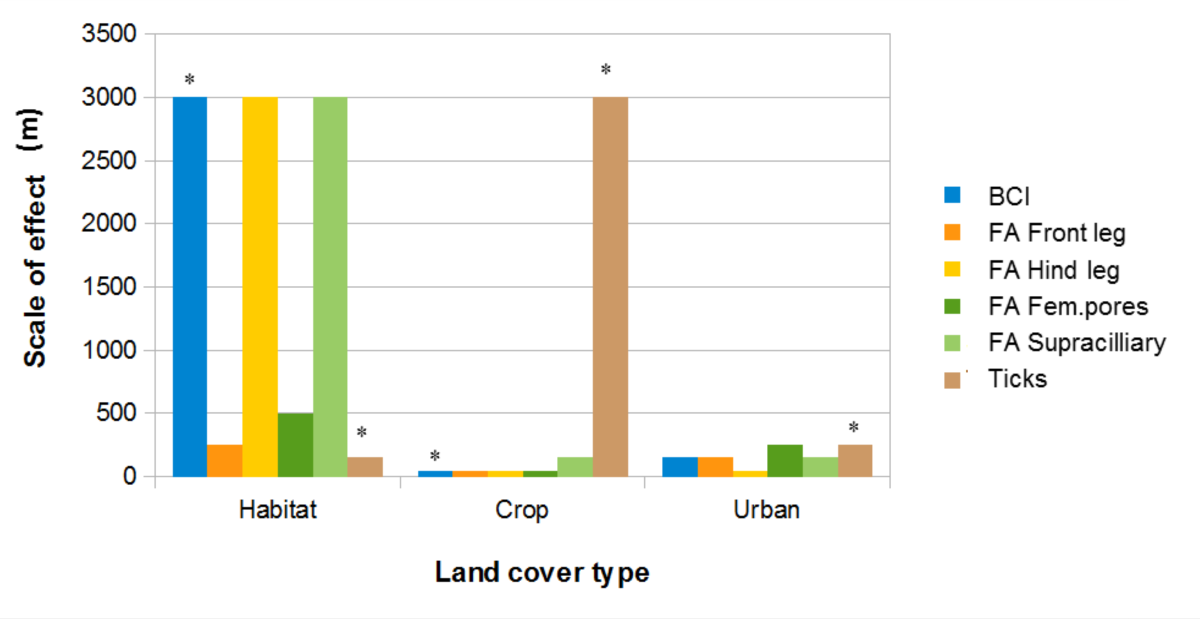

Figure 5.2. Scale of effect of each land cover type on body condition (BCI), fluctuating asymmetry (FA) and ticks load (Ticks). Selected scales of effect correspond to the distance in meters (m) from the border of patches, at which a given land cover type (Habitat, Cropland, Urban) had the strongest effect on an indicator. Significant effects are marked (*). Fem. pores: Femoral pores.

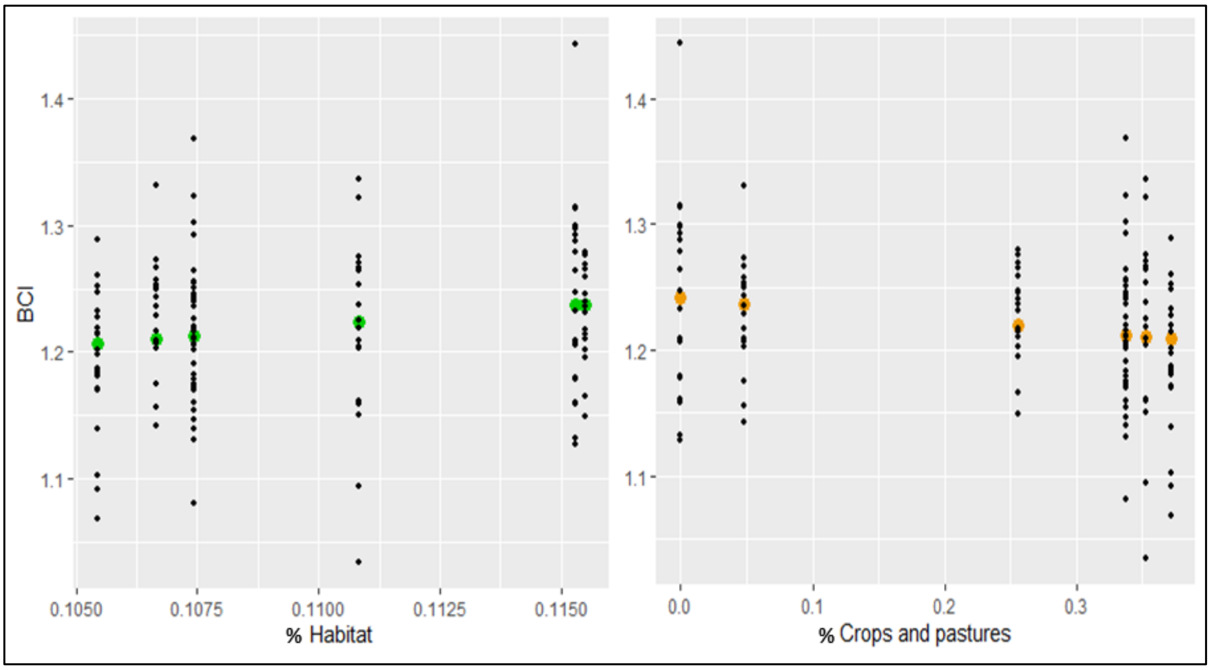

Figure 5.3. Effect of percentage of habitat and percentage of crops and pastures surrounding patches on the body condition index (BCI). Percentages of both land cover types correspond to values calculated at their scales of effect. Green and yellow dots represent mean values. For BCI, the scale of effect of the percentage of habitat is 3 km and the scale of effect of crops and pastures is 50 m.

5.4.2. Tick load

Tick load were higher in males compared to females ($t=6.178$, $p= 6.5e^{-10}$) and in adults compared to subadults ($t=-13.784$, $p<2e^{-16}$). Tick load increased with proportion of habitat, proportion of cropland and patch area (Figure 5.4a-c; % of habitat: $t=4.891$, $p=1e^{-06}$, Cohen's $f^2=0.208$; % of cropland: $t=3.692$, $p=0.0002$, Cohen's $f^2=0.138$; patch area: $t=3.328$, $p=0.0008$, Cohen's $f^2=0.104$).

In contrast, tick load decreased with proportion of urban areas ($t=4.275$, $p=1.91e^{-05}$, Cohen's $f^2=0.154$), isolation and the perimeter/area ratio (Figure 5.4d-f). In the case of isolation, tick load decreased at different rates for each sex ($t=-5.681$, $p=1.34e^{-08}$, Cohen's $f^2=0.191$) and age class ($t=5.313$, $p=1.08e^{-07}$, Cohen's $f^2=0.194$). The decreasing rate of tick load in response to the perimeter/area ratio was significantly different between adults and subadults ($t=4.553$, $p=5.29e^{-06}$, Cohen's $f^2=0.164$). Both, the effects of isolation and the perimeter/area ratio, were found to be much stronger in adults compared to subadults.

Tick load also increased with vegetation structure at low levels of isolation, but its effect decreased with increasing isolation (Figure 5.5a; $t=-3.674$, $p=0.0002$, Cohen's $f^2=0.159$). Similarly, the effect of vegetation structure decreased with increasing perimeter/area ratio (Figure 5.5b; $t=-2.944$, $p=0.003$, Cohen's $f^2=0.117$). The effect of urban areas was influenced by patch area ($t=3.238$, $p=0.001$, Cohen's $f^2=0.143$), with tick load increasing with patch area at any proportion of urban areas, but at a lower rate at high proportion of this land cover for both sex, with this difference being more marked for males (Figure 5.5c). The effect of perimeter/area ratio was influenced by proportion of urban areas (Figure 5.5c), with the interaction having a negative effect on tick load of both, males and females, with tick load being much higher for males at low but not at high levels of proportion of urban areas ($t=-3.613$, $p=0.0003$, Cohen's $f^2=0.143$).

5.4.3. Fluctuating asymmetry

No significant differences in FA were found between males and females for any of the evaluated traits. Subadults were found to have significantly higher FA compared to adults in the two linear traits, front and hind legs ($t=2.009$, $p=0.044$; $t=2.824$, $p=0.004$, respectively). Regarding effects of patch and landscape variables, no single predictor had alone a significant effect on the FA of any trait, but interactions among variables did. Most interaction effects had significantly different effects between sex or age classes.

An interaction between proportion of habitat and vegetation structure was present in several traits evaluated for FA (Figure 5.6a, b). In the case of front legs ($t=3.025$, $p=0.002$, Cohen's $f^2=0.119$) FA decreased with increasing proportion of habitat independent of vegetation structure for adults (Figure. 6a) and in subadults this was

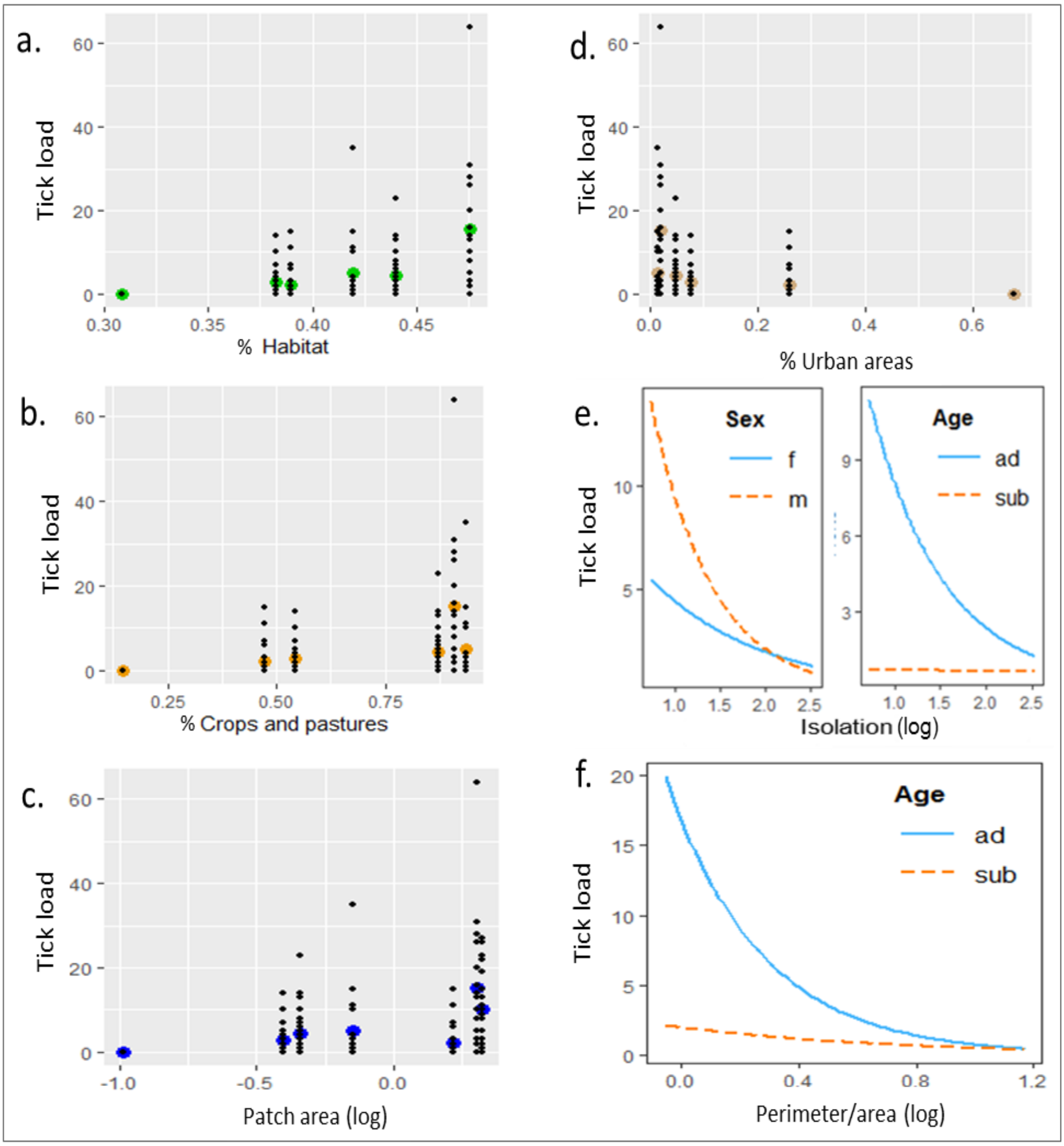

Figure 5.4. Effects of patch characteristics, isolation and landscape composition variables on tick load of individuals of *Lacerta viridis*. Colored dots in a, b and c represent mean values. Units of untransformed values: patch area in Km^2 and isolation in m.

the case only at the highest level of vegetation structure; for lower levels of vegetation structure the reverse was true. Similar results was found for hind legs, with FA decreasing with increasing vegetation structure and proportion of habitat for both age classes, but this interaction had a smaller effect size (Cohen's f^2= 0.097; see Appendix S8 for graphic). For femoral pores, FA decreased with increasing proportion of habitat at median and high levels of vegetation structure for females and at low and median levels of vegetation structure for males (Figure 5.6b; t=4.209, p=2.5e^{-05}, Cohen's f^2=0.192). The effect of isolation was affected by proportion of habitat and patch area in some traits (Figure 5.6c, d). FA in front legs increased with isolation in adults at low proportion of habitat (t=2.444, p=0.014, Cohen's f^2= 0.195), and decreased with isolation at medium and high proportion of habitat; in the case of subadults the response to the interaction was the opposite (Figure 5.6c). For supraciliary scales the effect of isolation on FA was influenced by patch area (t=-3.636, p=0.0002, Cohen's f^2=0.337). In this trait, isolation had a positive effect on FA but only when patch area was small; when patch area was large FA decreased strongly with isolation (Figure 5.6d).

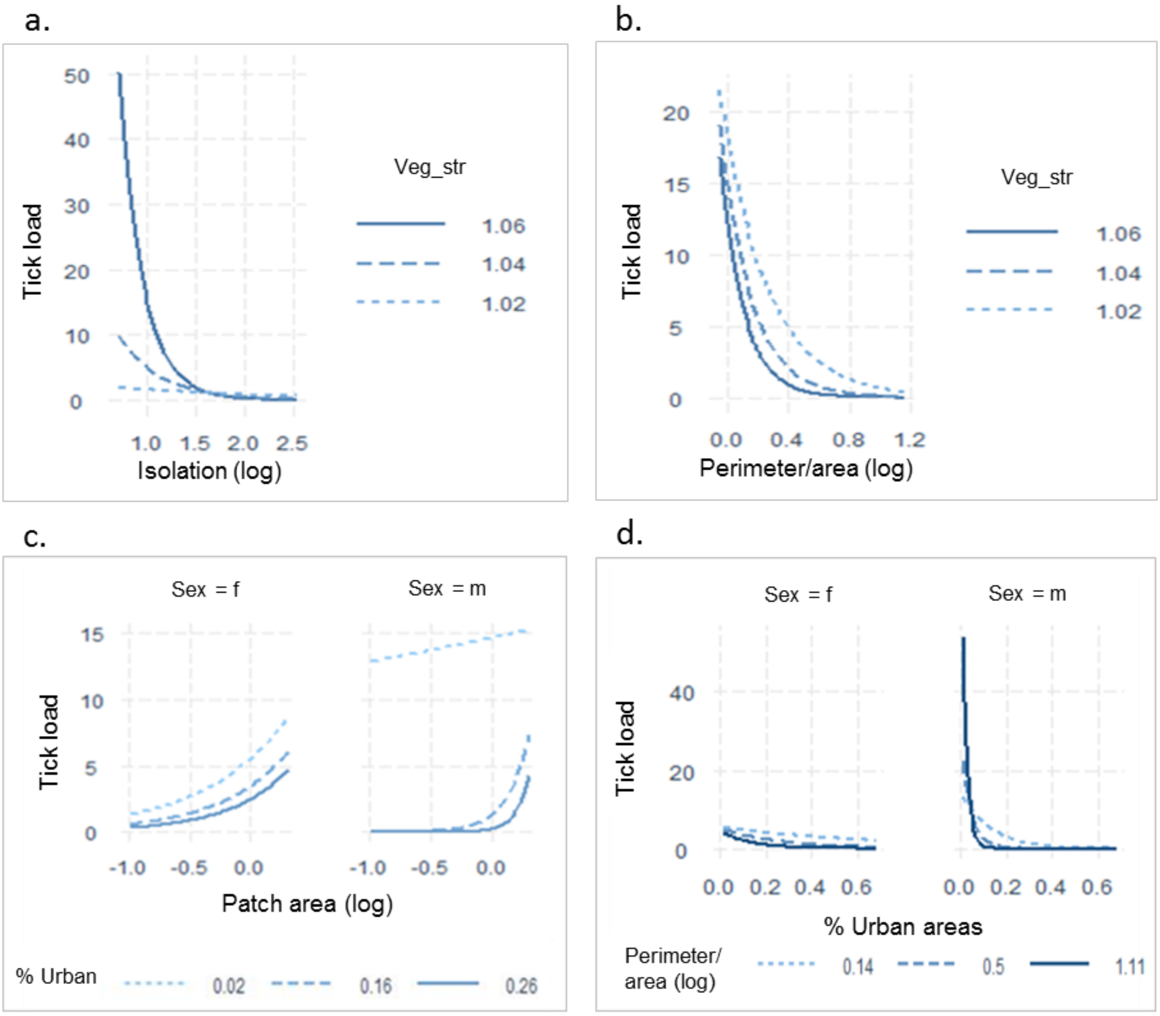

Figure 5.5. Effect of interaction terms on tick loads in individuals of *Lacerta viridis*. The values of vegetation structure (veg_str), % urban areas in c and perimeter/area ratio in d and are the first quantile, mean and third quantile of the data. Units of untransformed values: patch area in Km^2 and isolation in m.

The effects of proportion of urban areas and proportion of cropland on FA were influenced by patch area, vegetation structure and proportion of habitat (Figures 5.7 and 5.8). FA of front legs of adults increased with urban only in small or medium values of patches area, but decreased with increasing patch area (t=-2.646, p=0.008, Cohen's f^2=0.211), with no clear pattern being found for subadults (Figure 5.7a). Similarly, FA of front legs increased with cropland in subadults only when patch was small or mid-size, and decreased at large patch area (t=2.711, p=0.006, Cohen's f^2=0.216) in comparison to adults were the pattern was the opposite (Figure 5.7b). The effect of urban on FA of supraciliary scales was influenced by vegetation structure (t=-2.779, p=0.005, Cohen's f^2=0.114). In males, compared to females, proportion of urban areas had a positive effect on FA at low and medium levels of vegetation structure and the effect was reversed at high levels of vegetation structure (Figure 5.7c).

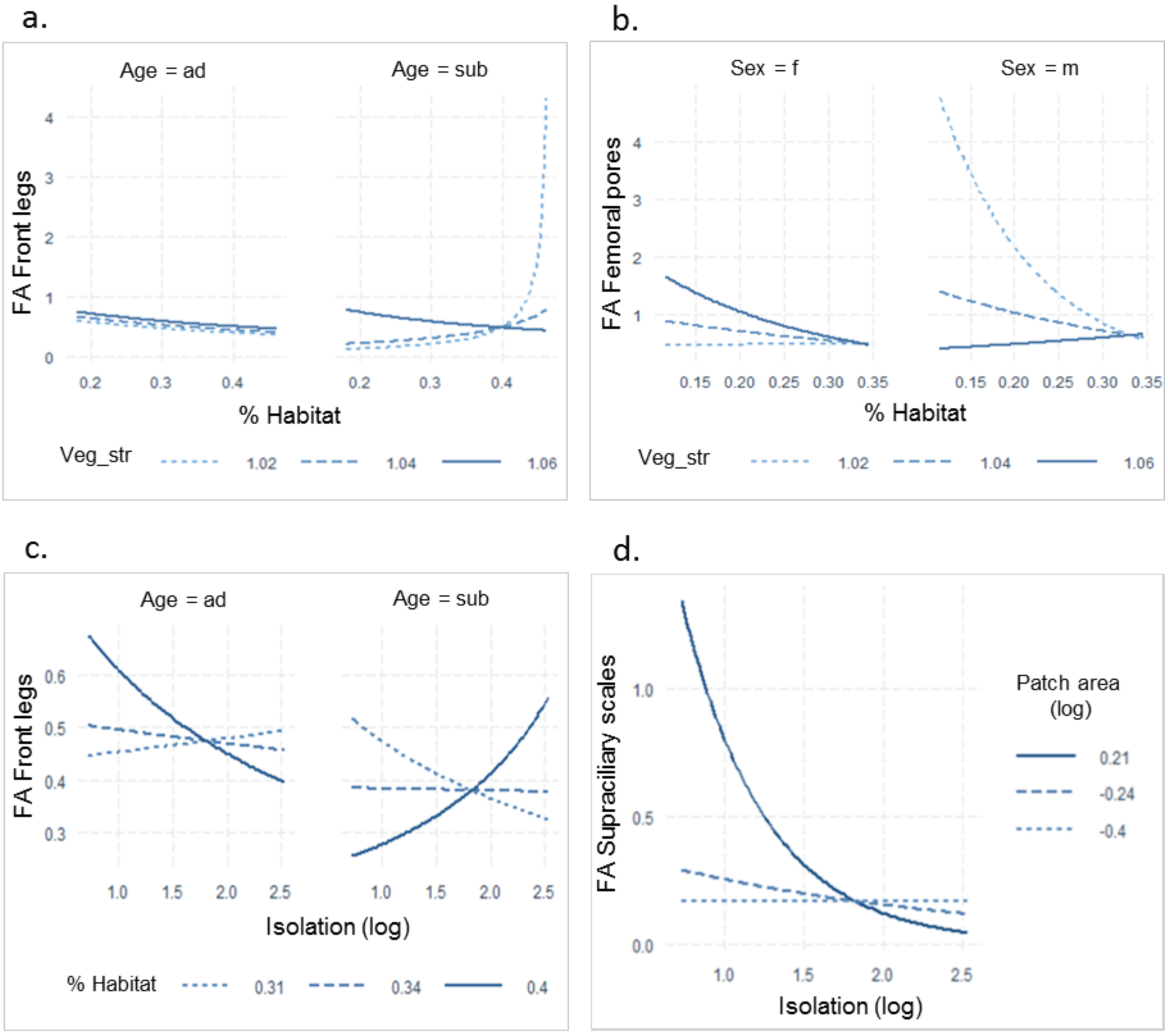

Figure 5.6. Effects of interactions among proportion of habitat, patch characteristic variables and isolation on fluctuating asymmetry (FA) of *L. viridis.* Values of vegetation structure (veg_str) in a and b, and of proportion of habitat in **c**, correspond to first quantile, mean and third quantile of the data. Units of untransformed values: isolation in m and patch area in Km^2.

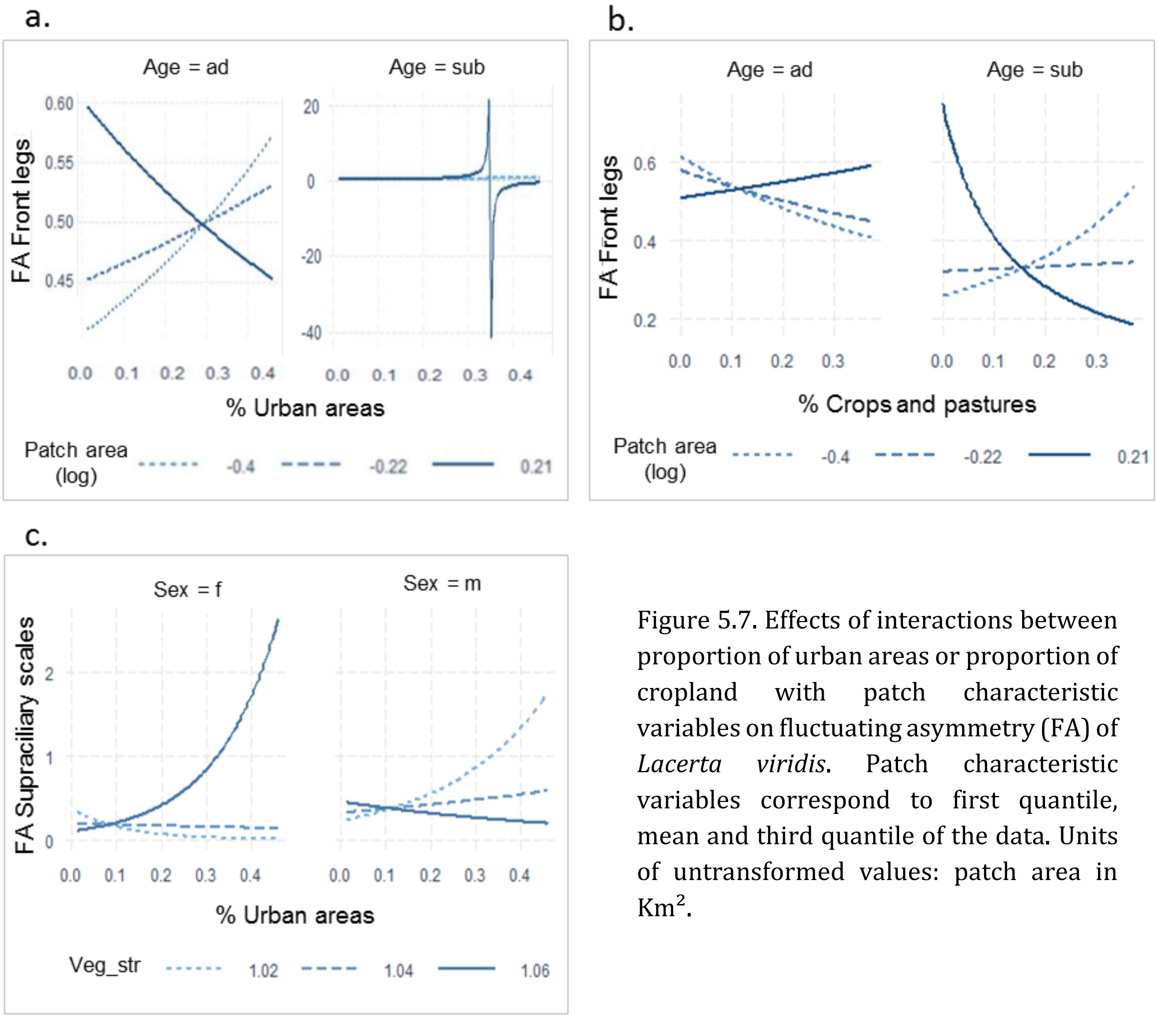

Figure 5.7. Effects of interactions between proportion of urban areas or proportion of cropland with patch characteristic variables on fluctuating asymmetry (FA) of *Lacerta viridis*. Patch characteristic variables correspond to first quantile, mean and third quantile of the data. Units of untransformed values: patch area in Km^2.

The effect of proportion of urban areas on FA of supraciliary scales was affected by proportion of habitat ($t=12.779$, $p<2e^{-16}$, Cohen's $f^2=0.176$), with an strong influence of sex class, with FA decreasing with proportion of urban areas at any proportion of habitat in males whereas it increased in females especially at low proportion of habitat (Figure 5.8a). FA of hind legs increased with proportion of urban areas at any proportion of habitat for females, but at high proportion of habitat the rate of increment was smaller ($t=-9.647$, $p=2e^{-16}$, Cohen's $f^2=0.142$); for males no clear pattern was found (Figure 5.8b). The effect of proportion of cropland on FA of hind legs (Figure 5.8c) was negative at any proportion of habitat for females, and only when proportion of habitat was medium or high in the case of males, with the effect also being smaller than for females ($t=2.591$, $p=0.009$, Cohen's $f^2=0.16$).

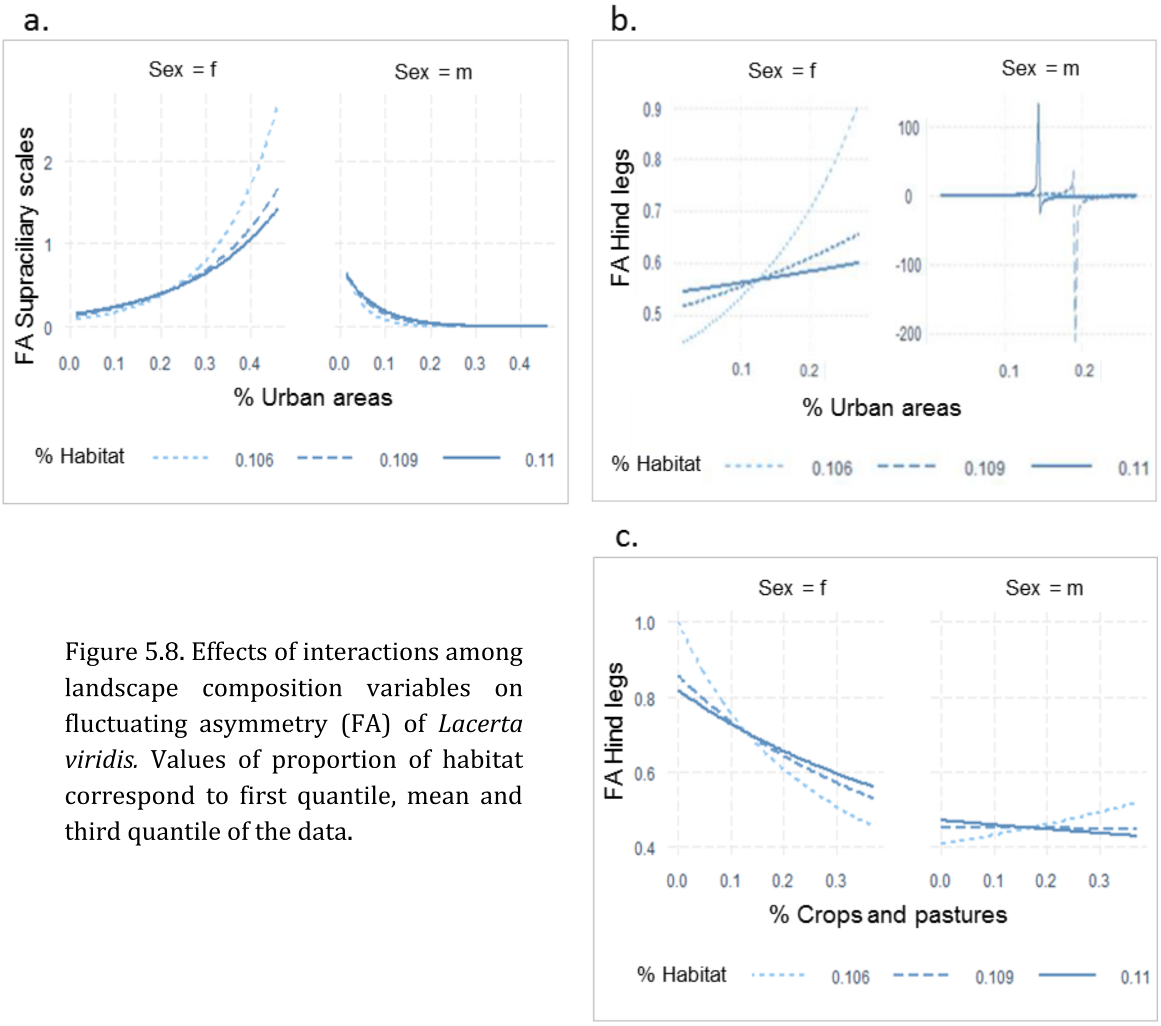

Figure 5.8. Effects of interactions among landscape composition variables on fluctuating asymmetry (FA) of *Lacerta viridis.* Values of proportion of habitat correspond to first quantile, mean and third quantile of the data.

5.5. Discussion

The effects of patch characteristics, isolation and landscape composition resulting from habitat loss on three morphological and physiological parameters – body condition, tick load and fluctuating asymmetry of metric and meristic traits – were evaluated, in order to assess the possible suitability of these parameters as early warning indicators of negative effects of habitat loss on central populations of *Lacerta viridis.* Our main results showed that BC and tick load have a direct link with some of the predictor variables analyzed. In contrast, FA of all traits was either sex or age dependent and was affected by interactions of predictor variables rather than by single variables alone, making it challenging to use FA as indicator of the effects of a particular predictor variable.

5.5.1. Body condition

In agreement with our predictions regarding landscape composition parameters, body condition (BC) increased with the proportion of habitat in the landscape and decreased with the proportion of cropland. Effects of landscape composition on morphology or physiological state of individuals are rarely found in the literature (Ellis et al. 2012) and no studies have analyzed before these effects on lizards.

Shortage of resources has been directly linked with reduced BC in *Lacerta viridis* (Bajer et al. 2012). In several lizard species, intraspecific competition is positively correlated with density (Donihue et al. 2016; Pafilis et al. 2009; Savvides et al. 2019) and higher competition leads to lower BC (Mugabo et al. 2011). Shortage of resources can also result from direct detrimental effects of habitat loss on food availability for lizards (Battles et al. 2013). Arthropods are the main source of food for lacertid lizards (Arnold 1987), and habitat loss can have negative impacts on their community structure and density (Bucher and Entling 2011; Dormann et al. 2007), thus reducing prey availability for lizards.

Besides the effects of the conversion of habitat into cropland, a possible cause for the negative effect of cropland on BC might be the exposure to pesticides. Studies with other two lacertid lizards, *Podarcis bocagei* (Amaral et al. 2012) and *Podarcis muralis* (Mingo et al. 2017) demonstrated that dermal and/or oral contact of lizards with pesticides have direct negative effects on their physiological performance and BC. A higher proportion of cropland can also increase the exposure to predators, and this might elevate the risk perception of lizards, forcing them to change their movement patterns and reducing their BC, as found in *Iberolacerta cyreni* (Amo et al. 2007b).

The scale of effect of cropland on BC was much smaller (50 m) than that of habitat (3000 m), which would suggest, that the presence of enough habitat at a much broader scale, is necessary to counteract the negative effects of cropland on BC, occurring at a much smaller scale. Furthermore, the lack of significant effects of local patch predictors indicates that body condition in the study system is affected by processes occurring at the landscape scale rather than at the local scale. This highlights the importance of assessing the impact of landscape predictors when studying effects of habitat loss on physiological parameters (Janin et al. 2011; Ellis et al, 2012). Also, although we did not find a negative effect of isolation, measured as Euclidean distance, proportion of cropland is a composition-based measure of isolation (Fahrig 2013; Martin and Fahrig 2012), which could better reflect impacts of shortage of resources at the landscape scale than distance-based measures.

Finally, females had lower BC than males, a pattern also found in other lizard populations living in modified landscapes (Lazić et al. 2013; Stellatelli et al. 2015). Males are bigger and their dominance over females is found in many lizard species (Alberts 1994; Mugabo et al. 2011), which increases the competitive pressure for limited resources on females (Lecomte et al. 1994).

5.5.2. Tick load

Parasite load on a given host mostly depends on the abundances of parasites in the landscape, which in turn depends on hosts' diversity and abundance (Krasnov et al. 2007; Fenner and Bull 2008). Contrary to our predictions, tick load on *L. viridis* was positively affected by proportion of habitat and patch area, but in agreement to our expectation, also by proportion of cropland. Thus, tick load was positively affected by predictors that can increase the burden of ticks in the landscape, either directly affecting ticks' populations or through effects on its host species.

Proportion of habitat in the landscape and the size of patches can positively affect the occupancy and abundance of both, ticks (Allan et al. 2003; Lawrence et al. 2018; Ledger et al. 2019; Simpson et al. 2019) and lizards (Díaz et al. 2000; Hokit and Branch 2003; Sumner et al. 1999). Additionally, these predictors can also increase immigration and emigration rates in lizards' populations (Doherty et al. 2019; Stow et al. 2001), resulting in spreading of ticks through the landscape (Taggart et al. 2018). Similar results were found by Carbayo et al. (2019), who reported a higher prevalence and intensity of tick (*Ixodes* sp) infection in *Psammodromus algirus* lizards in areas with better habitat conditions for the lizards, compared to highly disturbed areas, explaining that possible better microhabitats for ticks in better conserved areas would be the most plausible factor influencing their results.

Effects on other hosts species like rodents can also influence the burden of ticks in the landscape. Cropland is known to enhance presence and abundance of rodents (Benedek and Sîrbu 2018; Fras et al. 2014; Mendoza et al. 2019), thus could increase density of ticks in the landscape. Moreover, rodents are known to be 'bridge hosts' – host species that cross ecosystem boundaries (Borremans et al. 2019; Renwick and Lambin 2013) and are among the most possible reservoirs transferring *Ixodes ricinus* ticks from ecosystems like pastures and hedgerows around crops into woodlands (Boyard et al. 2008), hence influencing parasite load in other species (Bolaños-García et al. 2018). Additionally, some of the forested patches visited in this study hold populations of deer, a tick host whose presence is a key determinant of ticks' burden in the habitat (Gilbert et al. 2012; Hofmeester et al. 2017).

Predictors negatively affecting tick load in lizards are also related to negative effects on tick abundance and lizard population density. Opposite to our predictions, tick load was reduced by proportion of urban areas, isolation and perimeter/area ratio. Ticks may be less prevalent among urban wildlife due to lack of habitat for them (Murray et al. 2019) even if host abundances are high (DeVore et al. 2020), and might be affected by the lack of habitat connectivity that reduces hosts' movement in the landscape (Püttker et al.

2008). Moreover, in the long term, small patches with a high perimeter/area ratio could hold smaller lizard populations and cause negative edge effects on ticks' populations related with higher turnover and extinction events (Simpson et al. 2019)

The scale of effect of proportion of urban areas and proportion of habitat on tick load was smaller (150 m and 250 m, respectively) than that of proportion of cropland (3000 m). This might reflect differences on how direct are the effects of these land covers on tick abundance, and in turn, on lizards' tick load. While habitat and urban areas can directly affect ticks' distribution in the landscape, cropland effects would be mediated by its influence on other host species. Landscape predictors reflecting complex species interactions have scales of effect that reflect the mobility of all the species involved, which is expected to be detected at large rather than localized scales (Martin and Fahrig 2012). In this case, the high mobility of other hosts like small mammals through cropland areas might be possible to be captured only at broader scales.

5.5.3. Fluctuating asymmetry (FA)

FA was affected only by interactions among predictors and in several cases effects were sex or age dependent. As expected, proportion of habitat and vegetation structure reduced FA in some traits, but only when interacting with each other. This was the case for FA of front legs and femoral pores (Figure 5.6a,b). Vegetation structure is among the most important local factors regulating temperature and humidity and buffering the influence of the surrounding landscape (Suggitt et al. 2011). Furthermore, the comparably higher vegetation structure of habitats of *L. viridis* in the Thracian plains in relation to the habitats used in the northern periphery (Prieto-Ramirez et al. 2018), and to habitats occupied by *L. trilineata* in the same area, which are drier and opener (Strijbosch 2001), indicate that it might be an important regulator of environmental conditions necessary for the species in the region, thus reducing the environmental stress that could cause developmental instability. By its side, habitat amount is related to the regulation of environmental conditions at the landscape scale, avoiding increases in the temperature and reduction of humidity levels (Arroyo-Rodríguez et al. 2017). Moreover, both of these parameters are related with availability of food resources for lizards (Amo et al. 2007a,b; Bucher and Entling 2011; Dormann et al. 2007), which could be an important ecological parameter influencing physiological mechanisms that reduce FA. For instance, there is evidence that developmental stability in early life stages can be compensated in subsequent development (Möller and Thornhill 1998) through compensatory growth by allocating energy in the development of symmetrical parts of the body allowing for a controlled homeostatic development (Boersma and Wit 1997; Eyck et al. 2019). Then, enough availability of resources would improve the chances of a successful reduction of FA through compensatory growth.

In agreement with our prediction, effects of isolation were reduced by proportion of habitat and patch size, but only in some traits. In front legs the effect of isolation on FA of adults was positive only at low proportion of habitat, while at high proportion the effect was reversed (Figure 5.6c). Also, isolation had a positive effect on FA of supraciliary scales in small patches (Figure 5.6d), and this effect was reversed with increasing patch size. In lizards, positive relationship between isolation and FA has only been reported in studies comparing populations in islands with those in the mainland (Crnobrnja-Isailovic et al. 2005; Băncilă et al. 2010), but not in fragmented landscapes. Genetic stress in isolated populations resulting from loss of genetic variability and inbreeding depression due to reduced population size can lead to developmental instability and increased FA (Leary and Allendorf 1989; Pertoldi et al. 2006). However, Nemitz-Kliemchen et al. (2020) found high genetic variability and low genetic differentiation among populations for all population surveyed in the present study. Thus, environmental stress might be a more plausible explanation for the FA that we found. Isolated patches are expected to be surrounded by a higher proportion of non-habitat land covers (Fahrig 2003) that can affect abiotic environmental conditions within patches and availability of resources (Fischer and Lindenmayer 2007; Hatfield et al. 2020), which could be compensated in large patches by a higher availability of resources and a lower edge effect, and therefore lower exposure to external non-suitable environmental conditions (Ewers and Banks-Leite 2013; Fletcher et al. 2007).

In our results we found that the effects of proportion of urban areas and proportion of cropland were influenced by patch size, vegetation structure and proportion of habitat. This was the case for FA of front legs (Figure 5.7a,b), supraciliary scales (Figure 5.7c, Figure 5.8a) and hind legs (Figure 5.8b,c). Our results show negative effects of proportion of urban areas and cropland on FA occurring already at a small scale (<250m), which can be compensated by proportion of habitat in the landscape, patch area or vegetation structure. Depending on the trait, a specific age or sex class is more strongly affected by cropland or urban areas, and benefited by a reduction of their negative effects due to an increase in the percentage of habitat, patch area or vegetation structure. However, although highly trait- and sex or age class-dependent, negative effects of proportion of cropland and/or urban areas were reduced for every single class in at least one trait.

Urban areas have higher temperatures in comparison with natural or semi-natural areas (Arnfield 2003), and agricultural landscape might increase the exposure of patches to wind and water fluxes, causing strong daily temperature shifts. In *Podarcis muralis*, for instance, urban populations have higher FA of metric and meristic traits compared to rural ones (Lazic et al. 2013; 2015; Mirc et al. 2019), and for *Podarcis muralis* (Braña and Ji 2000) and *Lacerta agilis* (Zhdanova and Zakharov 2006) high temperatures have been correlated with higher FA in several traits. Moreover, very low or high incubation temperatures are known to negatively affect developmental stability during lizards' embryogenesis (Hare et al. 2002; Shine and Harlow 1996). Compensatory mechanisms of increased habitat amount, patch area and vegetation structure might act through the effects on population size (larger patches, enhanced dispersal through the landscape and increased availability of resources) and regulation of abiotic conditions discussed above.

Moreover, the scale at which proportion of habitat in the landscape would compensate for these effects could differ among traits. Differences in the scale of effect of proportion of habitat among traits (Front legs and femoral pores ≤500 m; hind legs and supraciliary scales = 3000 m) would reflect the variable sensitivity of traits to possible environmental stress, and therefore, its responsiveness to positive effects of habitat.

Finally, our results reflect strong differences in sensitivity to possible environmental stress among sex and age classes. In most models with differences among sex or age classes, females are more sensitive to stress compared to males, and subadults compared to adults. For instance, in FA of supraciliary scales the effect of proportion of urban areas seems to be stronger for females than for males (Figure 5.7c, Figure 5.8a) and in FA of front legs the effect of isolation appears to affect more subadults than adults (Figure 5.6c). If developmental stability in early life stages is reduced through compensatory growth, then adults would have a lower FA as response to environmental stressors compared to juveniles, a pattern also found in other species (Eyck et al. 2019). Furthermore, the negative correlation between fluctuating asymmetry and sexual selection has been found to be weaker in females compared to males for traits not involved in mobility in various species (Möller and Thornhill 1998), and investment of energy in development can be an energetic trade-off with important life-history traits (López and Martín 2002). Thus, males might have a higher pressure for investing energy on stable development, while females not having this pressure would trade-off stable development for energy available for reproduction.

5.5.4. Correlations between BC, FA and tick load

We did not find correlations among the studied traits, FA, BC and parasite load. In the case parasite load, other studies in lizards testing its correlation with FA did not find any (Garrido and Pérez-Mellado 2013). Regarding the correlation between parasitism and BC, evidence available is disparate. For *Lacerta agilis* a correlation between resistance to parasitism and body condition was found (Olsson et al. 2005); for *Lacerta monticola* the correlation between parasites prevalence and intensity and body condition was negative only during the reproductive season, and for *Lacerta lepida* no correlation was found (Amo et al. 2005; Amo et al. 2004); finally, for *Podarcis melisellensis* immune response to parasites was not correlated to body condition (Huyghe et al. 2010). Possible reasons for the lack of correlation between BC and FA with tick load are hosts' compensation of infection with more food intake (Tripet and Richner 1997), preference of ticks for individuals in better shape to increase their own fitness (Chapman et al. 2005; Dudek et al. 2016), and positive effects of the vegetation at local and landscape scale on both, lizards and ticks (Amo et al. 2007a; Ledger et al. 2019).

The relationship between FA and BC also varies among studies (Shamiminoori and Bull 2016; Winchell et al. 2019), probably because under limited levels of stress, the relationship between developmental stability and fitness can be more difficult to detect

(Van Dongen and Lens 2000). Given no single local or landscape predictor was stressful enough to alone affect FA, the level of stress the populations are experiencing might not be sufficient to find correlations between BC and FA, although it is so, to find single or interactive effects on each of these traits separately.

5.6. Conclusions

We found evidence of patch and landscape parameters affecting morphological and physiological parameters in *L. viridis* populations. Body condition was directly affected by reduction of habitat amount in the landscape and conversion into cropland. FA of different traits was found to be especially affected by synergies among patch and landscape parameters representative of habitat amount at local and landscape scale; in general FA increased with loss and conversion of habitat, reduction of patch size and increased isolation, and responses were sex and age dependent for some traits. Finally, mechanisms behind the effect of habitat loss on tick load seem to be related with how ticks experience the landscape, and how they are affected by the density of both, lizards and other hosts, with predictors that are expected to positively influence lizards' populations also having a positive effect on tick load and vice versa.

Body condition and tick load were directly affected by single parameters of habitat loss whereas FA was impacted only when interactions among parameters were accounted for. These might reflect differences in sensitivity to habitat loss, but also differences in the time lag at which each trait is affected. In the case of FA, possible genetic stress generated by habitat loss might take longer time, probably corresponding to several generations, until a single predictor has a direct effect (Holzhauer et al. 2006; Spear and Storfer 2008).

We strongly suggest the analysis of patch and landscape parameters when evaluating effects of habitat loss on possible individual-based indicators of stress. We conclude that BC and FA are suitable early indicators of stress for populations of *L. viridis* facing habitat loss. For rapid assessment studies, the suitability of tick load would depend on its correlation with physiological parameters which can go beyond BC, and in the long term, this trait would be definitely necessary for the monitoring and unraveling of complex ecological interactions among ticks and hosts populations in fragmented landscapes affecting the tick load of lizards. Finally, based on the scales of effect obtained for each landscape composition parameter, we suggest conservation measures to focus on the compensation of negative effects of habitat loss and conversion occurring already at a small scale by protecting and increasing habitat at a much broader scale.

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5.8. Supporting information

Appendix S1. Location of patches where surveys were carried out in the surroundings of Plovdiv, Bulgaria.
Appendix S2. Calculation of scale parameter through standardize major axis regression (SMA).
Appendix S3. Antisymmetry and directional asymmetry tests for the two metric traits.
Appendix S4. Frequency distribution of signed differences in the number of femoral pores in each population and in all populations.
Appendix S5. Frequency distribution of signed differences in number of supracialliary scales in each population and in all populations.
Appendix S6. Predictor variables for each patch
Appendix S7. Levene's Test for homogeneity of variance applied to test differences among years.
Appendix 8. Effect of interaction between proportion of habitat, vegetation structure and age on fluctuating asymmetry of hind legs.

6. Synthesis

6.1. From the niche to the impact of habitat loss

The theoretical context of many ecological studies is markedly divided between two different approaches: neutral and deterministic models. Studies about effects of habitat loss, land use change and landscape modification are no exception.

Neutral theoretical models are based on the ecological equivalence of species and predict species distribution and abundance based on spatial characteristics of the landscape and stochastic processes like ecological drift and genetic and demographic stochasticity (Bell 2000; Hubbell 2001). On the contrary, deterministic approaches account for the uniqueness of species, their relations with the environment and the interactions with other species to predict distribution and abundance of species. One of the most important and influential deterministic ecological theories is the Niche theory, which states that distribution and abundance of a species are determined by the set of biotic and abiotic conditions that allow populations to grow or persist, having birth rates equal or greater than death rates. Thus, the N-dimensional hypervolume of species' requirements, known as the niche, will define all factors (e.g. competition, enemy avoidance, resource gathering) that have an influence on species' birth and death rates (Hutchinson 1957).

Habitat loss has been mainly studied in the context of neutral theoretical approaches (Püttker et al. 2015). The two main theories influencing studies of habitat loss and fragmentation, Island Biogeography Theory (IBT, MacArthur, 1965) and Metapopulation Dynamics Models (MDM, Hanski, 1998; Hanski and Ovaskainen, 2000), are neutral theories. IBT assumes ecological equivalence among species and predicts species abundance and persistence based solely on patch size and patch isolation, without any regards for species specific requirements or dispersal abilities. In the dynamics of local extinctions and recolonizations of MDMs, extinction rate is a function of patch size and colonization rate depends on patch isolation and size of occupied patches. With increased isolation and reduced patch size local populations become small and eventually extinct due to demographic and genetic stochasticity and/or ecological drift. Although some studies applying principles of IBT or MDM include parameters that account to some extent for the ecological and environmental requirements of species, like habitat quality (Baguette et al. 2011; Moilanen and Hanski 1998) or presence of competitors (Lobelle et al. 2013), or isolation measures that account for the dispersal ability of the species and its relation with the land covers of the modified landscape, like least-cost path distance (Creech et al. 2014), the principles of these two theoretical approaches, on which most frameworks to study habitat loss and fragmentation are based, is neutral. However, habitat loss is a species specific process, in which most factors affecting species sensitivity, like ecological, life history and biological traits, are species specific (Fischer and Lindenmayer 2007). As such, habitat loss generates both, spatial and environmental effects, whose impact will depend on species-specific environmental requirements and dispersal capacity (Betts et al. 2014).

Thus, apart from species distribution models (SDM), whose theoretical basis is the Niche theory, and which have been widely applied to predict species distributions in fragmented landscapes, the application of Niche theory to study effects of habitat loss has been very limited and mostly limited to the use of binary specialization traits for the identification of most vulnerable species. However, in spite of the key contributions of the specialist/generalist classification to the understanding of effects of habitat loss and the vast evidence supporting higher sensitivity of specialist species(Henle et al. 2004b), it is now increasingly acknowledged that the study of habitat loss would better benefit from mechanistic niche-based approaches that, in comparison with specialization-trait based approaches, not only describe a static characteristic of a species, but the range of environmental conditions necessary for an organism to have a positive population growth (Frishkoff et al. 2015). This is especially important in the face of landscape modification, because the response of species to habitat loss is landscape dependent, and the range of possible responses will be then better captured by a species characterization that is not simply a binary trait but an ecological continuum representing the degree of specialization. Furthermore, this approach allows for the inclusion of differential sensitivity among populations of the same species related to their location in the distribution range of the species (Prieto-Ramirez et al. 2020) and to the portion of the environmental gradient that occurs in each location (Prieto-Ramírez *et al.* 2018)

The works of Swihart *et al.* (2003, 2006) and of Kellner *et al.* (2019) conducted in the fragmented landscape of the Middle Wabash–Little Vermillion watershed of Indiana, USA, are among the few approximations to the link between niche breadth, position in the distribution range and species sensitivity to habitat loss and fragmentation. For a broad range of taxa, including mammalian predators, rodents, bats, amphibians and aquatic turtles, they found that occupancy rates were lower for species with comparably narrower niche breadths and for which the study region represented the edge of the distribution range compared to those that were at their distribution centers. In all these studies the estimation of habitat niche was based on the range of habitat types used at the species level reported in the literature, thus disregarding intraspecific differences in niche breadth in their hypothesis and in the interpretation of results. For instance, Swihart *et al.* (2003) hypothesized that the role niche breadth plays in the effect of position of populations within their range on occupancy probability will be stronger when range is formed by biotic factors (southern border) rather than by abiotic (northern border), because in a range boundary formed by intraspecific interaction the specialist species would be left with less habitat to maintain its competitive superiority; while, in a boundary formed by abiotic factors it would be physiological tolerance to abiotic conditions that would be more important than niche breadth. However, in their hypothesis they did not only fail to explain the scenario in which a specialist species is present near a border formed by abiotic stressors, but also to directly link niche breadth with position in the range. Therefore, they explain their finding of a stronger decline in occupancy due to proximity to a range boundary formed by abiotic stressor compared to biotic ones, based on physiological tolerance. However, this result can also be due to a narrower niche breadth of populations located in the northern border of the distribution range (Lappalainen and Soininen 2006; Prieto-Ramirez et al. 2018; Yurkowski et al. 2016), with more specialized peripheral populations being more vulnerable because the alteration of preferred habitat would leave them comparably less area to inhabit (Henle et al. 2004b; Keinath et al. 2017). Later, Swihart *et al*. (2006) found that none of the mean occupancy rates of species located near their range boundary was predicted by niche breadth, supporting again the hypothesis that niche breadth has no important role in the link between position in the range and sensitivity to habitat loss and fragmentation. I argue below that this statement cannot be supported without a measurement of niche breadth that accounts for intraspecific differences precisely related to position in the range (Prieto-Ramirez *et al.* 2018). Thus, the approach would not be to test for the influence of niche breadth in the effect of position in the range on occupancy rates, but, on the contrary, for the effect of niche breadth as a trait that depends on the position in the range on occupancy rates.

In the specific case of ectotherms some progress has also been done to link niche breadth with sensitivity to habitat destruction, with a focus on thermal biology. Frishkoff *et al.* (2015) studied the effects of forest clearing on community composition of herpetofauna in tropical forests in Costa Rica, by linking increased local temperature after forest clearing with thermal niche centers of species and testing response differences along altitudinal thermal gradients. They found that species track their thermal niche along the altitudinal gradient by shifting habitat use from forested areas at low elevations to deforested warmer pastures at high elevations, and that in general species with warmer thermal niche centers had higher tolerance to deforestation. Although in agreement with my findings they conclude that tolerance to deforestation is not a species-level trait and is dependent on the geographical position of species, Frishkoff *et al.* (2015) interpret changes in species' tolerance to habitat loss as a response to an extrinsic factor, the elevation-dependent shift in the temperature after deforestation, assuming niche centers as a static characteristic of species along the altitudinal distribution range. However, the generalization they made might not apply, because as I showed (Prieto-Ramirez et al. 2018), in the border of the environmental gradient, niche might not only be smaller but also shifted, meaning that the niche centers in different locations of the distribution range of species might not overlap each other.

Then, as explained above, the inclusion of intraspecific niche differences improves the possibilities of the application of a mechanistic niche approach for the study of effects of habitat loss, and has the capacity to increase our understanding of the ecological processes taking place at the borders of species' distribution ranges. Furthermore, the advantages of this niche-based, intraspecific-centered approach can be extended to the effects of habitat loss at higher levels of biological organization. For instance, our understanding of biotic homogenization - the replacement of more vulnerable specialized species by more tolerant ones after habitat loss occurs, that leads to changes in community composition and reduces ß-diversity (Devictor et al. 2008) – could also greatly benefit from accounting for intraspecific differences in specialization degree. It has been argued that common measures of species richness could mask biotic homogenization by overlooking effects of habitat loss on community composition, which are based on effects on single species (Filippi-Codaccioni et al. 2010). Thus, if intraspecific differences in specialization degree are ignored, processes occurring in regions corresponding to the periphery of the distribution range of species might be identified solely as species richness loss, and not as both species richness loss and biotic homogenization due to the loss of species that are specialist only in the periphery.

6.2. Linking microhabitat selection to occupancy patterns

I showed that specialization degree in peripheral populations can differ from that in the core, and that this difference can lead to variable sensitivity to habitat loss among regions. Realized habitat and abiotic factors niches of northern peripheral populations of *L. viridis* located in Germany and Czech Republic were smaller than and shifted from those of core populations in Bulgaria (Prieto-Ramirez et al. 2018). I also found that microhabitat selection in peripheral populations of *L. viridis* reflects a compensation for suboptimal biophysical conditions and a narrower range of available habitats with respect to the core (Prieto-Ramírez et al. 2018). Then, in Prieto-Ramírez *et al*. (2020), I linked these differences in specialization degree and microhabitat selection with occupancy patterns resulting from habitat loss in each region. By applying a patch-landscape approach I found differences in the characteristics of habitat remnant patches and of the landscape structure surrounding patches that affected patch occupancy probability the most in the periphery compared to the core. Moreover, I also found that the spatial scale from which those effects are stronger was smaller in the periphery compared to the core (Prieto-Ramirez et al. 2020).

In the following paragraphs I discuss my results of niche size and microhabitat selection in the context of thermal ecology in reptiles, the interlinked relation between the parameters governing processes occurring at the microhabitat scale and those affecting patch occupancy patterns in the landscape, and the connection between intraspecific differences in specialization degree and persistence of populations in modified landscapes.

The fact that the realized niche in the northern periphery was shifted from the niche in the core suggests that there might be some degree of physiological phenotypical adaptation in peripheral populations (Castilla et al. 1999; Chevin and Lande 2011; Van Damme et al. 1986), which follows the pattern of a higher, latitudinal-related, intraspecific variability in low thermal limits compared to upper thermal limits found in several ectotherm species including lizards (Addo-Bediako et al. 2000; Araújo et al. 2013; Sunday et al. 2010). Moreover, in the case of relict peripheral populations located in Prague, which are genetically differentiated from other peripheral populations connected to the continuous range of the species (Böhme and Moravec 2011), local genetic adaptation might also explain the shifted realized niche in this region relative to the core (Kawecki 2008). However, realized niche shifts can also be the result of differences in the environmental space that the species experience in different regions (Soberón and Peterson 2011). My results regarding strong differences in microhabitat use and factors affecting microhabitat selection in each region indicate that a great part of the differential response of the species to different climatic and habitat constrains in each region corresponds to behavioral thermoregulatory mechanisms. This was most clearly showed by the relation between radiation and vegetation structure in each region. Radiation was consistently lower in both peripheral regions compared to the core, and thus microclimatic conditions in comparable habitat types regarding vegetation structure, like mixed forest, were suitable in the core but not in the periphery (Prieto-Ramírez et al. 2018). Therefore, microhabitats used in the core had higher vegetation structure than those in the periphery. On the contrary, in the periphery where radiation was lower, lizards seemed to maximize thermoregulatory opportunities by selecting places with lower vegetation structure, less shadow and more exposed to sunlit. This pattern is also known in other lacertid lizards, like *L. agilis*, who inhabits heathlands with a high proportion of bare ground available near the northern margin of its range, while in the core, where there is a broader range of habitats available, it inhabits heathlands at any seral stage and with comparably more vegetation structure (House and Spellerberg 1983; Thomas et al. 1999).

Microhabitat selection is a niche-based process that responds to species requirements, habitat and resources distributions, and biotic ecological constrains like presence of competitors and/or predators (Angert et al. 2002; Turlure et al. 2009; Michael et al. 2015). However, in reptiles as in other ectotherm taxa, microhabitat selection has additionally a strong direct link to species' thermal biology and represents a major strategy of behavioral thermoregulation (Castilla et al. 1999; Huey et al. 2003). Behavioral thermoregulation is the main mechanism through which reptiles balance heat exchange with their biophysical environment in order to achieve body temperatures that allow them to be active (Huey, 1982). Hence, the process of selecting microhabitats in reptiles involves not only actively tracking for habitat with enough resources and refuges against predators, but also for habitat that offers suitable microclimatic conditions in order to fulfill their thermal physiological requirements (Brusch et al. 2015; Grimm-Seyfarth et al. 2017). The range of available habitats that the species can use in order to meet its ecological and microclimatic requirements is determined by broad climatic conditions, and defines species' degree of habitat specialization. Then, as climatic conditions change along the distribution range of species, it should also be expected that the range of habitats the species can use and select to fulfill their requirements also change geographically (Böhme and Rödder 2014; Thomas et al. 1999). Moreover, thermoregulatory priorities can change between regions, with 'cooling down' being more important in subtropical and tropical regions, while ‘warming up’ being the priority in high latitudinal temperate regions (Kearney et al. 2009; Muñoz et al. 2016). This is especially important for species with broad distribution ranges, because different priorities at high latitudinal versus low latitudinal regions might exist, as well as different patterns of (micro) habitat selection. Patterns of variable habitat selection and narrower niche breadth towards the northern periphery had earlier been found in several ectotherm taxa, like insects (Oliver et al. 2009; Svensson 1992; Thomas et al. 1999; Thomas et al. 1998), lizards (Thomas et al. 1999), fishes (Lappalainen and Soininen 2006), seals and whales (Yurkowski et al. 2016).

The availability of suitable ecological and thermal conditions at fine spatial scales also determines activity patterns of reptile species, thus influencing vital processes like food intake and reproduction, and therefore, birth and death rates in the population, and consequently, its persistence (Huey 1982; Meek 1995). Hence, in the face of habitat loss, the availability of suitable microsites and microhabitat selection can have impacts in the response and sensitivity of species to habitat reduction (Huang et al. 2014; Nowakowski et al. 2018). The importance of microhabitat for the resilience of reptiles to disturbance has mostly been studied in climate change research, with several studies demonstrating that fine scale microclimatic conditions can greatly differ from conditions at wider scales in habitats and ecosystem, and have an enormous impact in the tolerance or vulnerability of species to extreme climatic events (Kearney et al. 2009; Scheffers et al. 2014). Moreover, some studies have integrated not only microclimatic data but also microhabitat information, and have demonstrated that the conservation of vegetation types, whose structure offers microsites with sunlit and shaded spots, is of enormous importance to increase tolerance of reptile species to climate change (Grimm-Seyfarth et al. 2017; Kearney 2013; Suggitt et al. 2011). Habitat loss is known to often have a related increase in temperature as vegetation cover is modified (Arroyo-Rodríguez et al. 2017; Laurance 2004), and the destruction of habitat directly implies the loss of available microhabitats (Saunders et al. 1991). However, in spite of the consensus about the direct links between thermal biology and microhabitat selection (Brusch et al. 2015), and about the importance of ecological processes at fine scales for the response of species to broader scale disturbances (Chiacchio et al. 2020), a full link between effects of habitat loss and species microhabitat selection as a mechanistic response related to thermal biology, is still missing in reptile species literature.

I used microhabitat information to define local patch habitat quality by upscaling values of vegetation structure, slope and radiation. Then, I tested the effects of these parameters at the patch level on occupancy (Prieto-Ramírez et al. 2020). I found that in each region some factors had consistent effects for both individuals’ microhabitat selection and population persistence, while others differed in their importance among processes, thus reflecting different challenges at different spatial scales and levels of biological organization. Vegetation structure, which was higher in microhabitats at the core compared to the periphery, had a positive effect on occupancy in the core. On the contrary, vegetation structure had a negative effect on occupancy in the periphery, where microhabitats have opener vegetation. By its side, radiation and slope, which were important for microhabitat selection in the core, were not important for occupancy in this region. And in the periphery in Prague, slope had a moderate effect for microhabitat selection but a higher one for occupancy probability.

Regarding vegetation structure, I found a pattern in which into each separate region, this parameter had the same effect for both microhabitat selection and population persistence into patches. Similar results were obtained by Santos *et al.* (2008), who studied the microhabitat selection of the lacertid lizard *Psammodromus algirus* in a fragmented landscape and upscaled microhabitat features to calculate patch habitat quality and to test the effect of different habitat types with different vegetation structures on occupancy at the landscape level. They found that effects of the vegetation structure of different forest type fragments (deciduous vs. evergreen) on occupancy probabilities of *Psammodromus algirus* were consistent between microhabitat and patch levels, with lizards preferring deciduous over evergreen forest. In an analogous study, Fisher et al. (2004) tested the multi-level response of several lizard species in a fragmented landscape in Australia to effects at different spatial levels, with variables collected at the microhabitat level, including vegetation structure, being up-scaled to define site characteristics. Contrary to my results and those obtained by Santos *et al*. (2008), they found that plot (microhabitat) and site occupancy were affected by different parameters for all species, which they explained based on the possible differences in habitat perception and response to disturbance that species might have at different spatial scales. Thus, in the case of *L. viridis*, specifically regarding vegetation structure, this implies that its perception of habitat is consistent across levels and ecological processes.

By its side, the loss of importance of radiation and increased importance of vegetation structure for occupancy in the core suggests that the vulnerability of *L. viridis* to habitat loss in that region follows the same pattern found in other reptile species, in which sensitivity is related to the local increase in temperature due to loss of vegetation cover and shaded areas (Kearney, 2013). However, this vulnerability in the core might be buffered by the broad range of habitats available for the species that provide microclimatic conditions necessary for thermoregulation. On the contrary, based on my results, the vulnerability of *L. viridis* to habitat loss in the periphery might not be related with negative effects of increased temperature due to loss of vegetation cover. In fact, my results show that in the periphery suitable microclimatic conditions are provided by few habitat types with open vegetation (Prieto-Ramirez et al. 2018). Therefore, although of course some thermoregulatory needs imply that lizards in the northern periphery use at the hottest time of the day, especially during summer, shaded spots (Strödicke 1995), the priority is most likely to be 'warming up' (Kearney et al. 2009) as found in northern peripheral populations in other reptile species (Dubois et al. 2009). Then, the sensitivity of *L. viridis* to habitat loss in this region is related to the specialization degree of the species caused by the availability of few vegetation cover types providing essential thermoregulatory conditions for the species.

The increased importance of slope in the periphery for occupancy probability in comparison with microhabitat selection might reflect changes in ecological processes when populations are at risk. Decline in population density can lead to reduced encounter rates among individuals and to an increase in the time lizards need to invest seeking for mates (Wosniack et al. 2014). This implies a necessary change in activity budgets, which might be energetically achievable only in habitats in which the heat balance is most efficiently reached (Díaz et al. 1996). Hills' slopes in Prague corresponding to the Vltava river valley are mostly conformed by litho-resources -rocky grounds and outcrops. Slope is one of the most important factors influencing microclimatic conditions (Suggitt et al. 2011) that result thermally beneficial for ectotherms at high latitudes (Lawson et al. 2014), and has an strong influence on habitat quality of northern lizards' populations, including *L. viridis* (Fischer and Rehak 2010; Frör 1986; Märtens et al. 1996; Waitzmann and Sandmaier 1990). By its side, litho-resources are especially important for temperate species (Michael et al. 2015), and are related with high rates of temperature increment and high lizards' heating rates through thygmothermy (Belliure and Carrascal 2002). Thus, it is probably in the rocky slopes where individuals of *L. viridis* inhabiting the rocky slopes along the Vltava River could achieve activity body temperatures faster and maintain them for longer time, allowing them to invest enough time looking for mates. This would then have impacts on reproduction, birth rates, and persistence of the population.

Among the few studies that directly link environmental information at a fine scale with effects of habitat loss and/or fragmentation in reptiles are those of Santos et al. (2008) and (Fischer et al. 2004) mentioned above. Additionally, other approaches (Frishkoff et al. 2015; Nowakowski et al. 2018) have linked fine scale climatic information with thermal traits of species like critical thermal limits to predict species sensitivity to habitat loss and the probability of using the matrix. However, although microclimatic data can be used to characterize habitat suitability for reptile species, these studies lack the mechanistic link between the ecological process of microhabitat selection and effects of habitat loss. Moreover in most studies the connection between microhabitat selection, effects of habitat loss and regional differences is missing. For instance, although Frishkoff *et al.* (2015) included climatic variability to test intraspecific differences in species' occurrence probability in modified habitat (from tropical forest to pastures) along an altitudinal range, they based their analysis solely on species thermal tolerances and microclimatic data, without considerations of differences in microhabitat selection in different parts of the range.

Differences in niche size among regions derived from information at the microhabitat scale were also linked with the effects of landscape structure on occupancy patterns in each region. In the periphery, individual land cover classes had a stronger effect on occupancy across scales compared to the core, and in the models combining landscape structure and local patch factors the scale from which habitat loss had the strongest effect was much smaller in the periphery (50 m) than in the core (500 m). This means that a smaller amount of area surrounding patches being subject to anthropogenic modification will have an impact on the persistence of populations in the periphery compared to the core. I also found differences in the parameters of the landscape to which the species responded in each region, and that could eventually influence dispersal. In the core, landscape configuration was more important for occupancy probability than landscape composition, whereas it was the opposite in the periphery.

The link between specialization and effects of landscape composition has earlier been done at the species level. For instance, the amount of habitat in the landscape surrounding patches has been found to have a stronger positive effect on dispersal and abundance of specialist small mammal species (Püttker et al. 2013) and on persistence of specialist bird species (Carrara et al. 2015) compared to generalist species. Additionally, scale of effect of landscape composition parameters has been found to be smaller in some invertebrate specialist species compared to generalist (Chaplin-Kramer et al. 2013), and is expected to be smaller for other specialist species due to a comparably lower dispersal ability (Miguet et al. 2016). Environmental constrains can influence and modify movement behavior, consequently affecting dispersal process (Vasudev et al. 2015). Moreover, the interaction between species traits, like specialization, and the characteristics of the landscape define species' sensitivity to habitat loss (Fahrig 2007; Püttker et al. 2013; Swift and Hannon 2010). Thus, in populations of *L. viridis* in the periphery, which have a comparably higher specialization degree, a lower dispersal capacity compared to core might be environmentally-induced, with a narrower spectrum of habitats available to disperse through the landscape resulting in a higher vulnerability to habitat loss.

Furthermore, the attributes of the landscape that possibly govern dispersal differ among regions. In both regions may exist a meta-population structure, but it is influenced by landscape configuration in the core and by landscape composition in the periphery. I found that distance to the river was one of the most important factors influencing occupancy probability in the core, suggesting that riparian vegetation is a corridor maintaining the connectivity of populations through the landscape, as found in other European lizards (Brito et al. 1998; Sahlean et al. 2020). Additionally, in the core, Nemitz-Kliemchen et al. (2020) evaluated the genetic structure of populations in this region, including samples of all the populations studied in Prieto-Ramírez *et al.* (in Review), which were also part of the sample in Prieto-Ramírez *et al.* (2018, 2020), and found low genetic differentiation among populations, indicating that there is gene flow among populations. On the other hand, in the periphery, the consistent positive effects of cropland on occupancy probability across small and medium scales (50 - 750 m) suggest also that up to medium dispersal distances populations might be connected due to some degree of permeability of cropland to lizards' movement, probably related to thermal and nutritional benefits (Baguette et al. 2014; Vasudev et al. 2015). Thus, although connectivity among populations might be present in both regions, the fact that configuration and composition have dissimilar importance in each region reflects differences in the possible mechanisms governing dispersal and the possible maintenance of connectivity in each region.

Despite the fact that niche breadth has been found to decrease toward the northern periphery in other taxa (Lappalainen and Soininen 2006; Svensson 1992; Thomas et al. 1998; Yurkowski et al. 2016), specialization in relation to vulnerability to habitat loss has always been investigated as a species level trait. Recognizing intraspecific differences in specialization degree break some 'dogmatic' beliefs regarding species traits, or the use of certain traits as proxy for other. For instance, in a recent work including a large number of reptile species Doherty et al. (2020) tested which species traits predict sensitivity to habitat loss. Among the traits included are species specialization and the size of the distribution range of species, a trait that is usually predicted to have an inverse correlation with specialization and sensitivity to habitat loss because species with broader ranges are assumed to have higher dispersal capabilities and higher tolerance to ecological and environmental disturbance (Slatyer et al. 2013). My research challenges these common beliefs by showing that the negative correlation between distribution range and specialization and sensitivity to habitat loss does not necessarily meet. In species with broad distribution ranges the differences between peripheral and core populations can be larger due to a greater difference in climatic conditions and in the range of available habitats among regions, and thus, specialization in the periphery can be masked in broad scale analysis that do not include the location of a study in the distribution range of species, hence leading to wrong traits' predictions of sensitivity to habitat loss. In their (Kellner et al. 2019) global analysis Doherty *et al.* (2020) did not find any correlation between specialization and sensitivity to habitat loss. Similarly, Kellner et al. (2019) did not find consistent evidence of negative correlation between specialization degree of birds, small mammals, bats and turtles and response to habitat conversion. Both studies concluded that specialization is a poor predictor of species response to habitat loss, precisely because the response might differ along the distribution range of the species. Other studies on birds (Hatfield et al. 2018) and mid and large-sized (Thornton et al. 2010) have also failed on finding a consistent relation between species level specialization trait and sensitivity to habitat loss when evaluating several locations across distribution range of species. These studies argued that the predictability of specialization is highly location-specific probably due to the specific landscape structure of the study site. However, any of these studies discussed the possibility that geographic specificity be due to intraspecific differences in specialization degree related to the position in the distribution range. Rather than leading to the abandonment of specialization degree as a useful ecological tool to predict species response to habitat loss, the recognition of regional differences should lead to acknowledge that the problem might not be the trait but the level (species) and the scale (complete range) at which it is measured, and that accounting for the intraspecific variability of the trait along the distribution range of species can improve its predictive power.

6.3. Links between effects of habitat loss on different ecological processes

Population decline due to habitat loss and fragmentation is a process that starts with effects at the individual level, through endogenous threatening processes that lead to the disruption of the morphology and biology of individuals, and ends with the extinction or increased vulnerability to extinction of local populations (Ellis et al. 2012; Fischer and Lindenmayer 2007). Occupancy patterns reflect the spatial patterns of local populations' persistence or extinction resulting from habitat loss in modified landscapes, and it is a key link between disturbance and population-level response. However, the usefulness of occupancy is only apparent once (some) populations have gone extinct, thus not throwing information about the processes occurring at earlier stages of population affectation (Ellis et al. 2012).

At an early stage of the population decline process, less habitat available and reduced habitat quality, together with other impaired environmental conditions, can lead to increased competition among individuals and/or shortage of resources, which causes diminished physiological and nutritional status, and hence lower body condition (Battles et al. 2013; Mugabo et al. 2011; Smyth et al. 2014). Also, as a result of impaired environmental conditions, levels of developmental instability can increase leading to higher levels of fluctuating asymmetry (FA; Lens et al. 1999; Lazic et al. 2013; Mirc et al. 2019). Subsequently, modified morphological characteristics can lead to changes in life-history traits, like clutch size and clutch frequency (Brewster et al. 2018), and in individuals' survival probabilities, which can be sex- and/or age-dependent, thus causing changes in the populations' demographic structure, reproduction and survival rates (Díaz et al. 2005; Keehn et al. 2019; Walkup et al. 2017). Eventually, these processes can cause a reduction in population size, thus increasing the risk to inbreeding depression or genetic drift. Finally, small population size and loss of genetic variability increase the vulnerability to demographic and environmental stochasticity, and the extinction risk (Benson et al. 2016; Soulé 1987)

Coupling effects of habitat loss on early stages, such as those on individual morphological parameters, with later stage effects on population persistence may provide insights into processes occurring at different times and spatial scales and their importance for the survival of species.

In my study I found that the role of some landscape and local patch predictors was equally important at different stages, while for others its effect in the response was stage-dependent (Prieto-Ramirez et al. 2020; Prieto-Ramirez et al. in review). In the following paragraphs I discuss the most important emergent patterns found.

Occupancy vs. body condition: configuration vs composition

My results showed that persistence of populations of *L. viridis* in the Thracian plains depends mostly on landscape configuration and connectivity, but also that the start of the declining process might be triggered by landscape composition. Thus, for instance, cropland was not determinant of occupancy, and in the few models in which it was present its effect was positive (Prieto-Ramírez et al. 2020). In contrast, it had a negative effect on body condition (Prieto-Ramírez et al. in review). Similarly, the importance of habitat amount differed between occupancy and body condition, although contrary to cropland, the direction of its effect was consistent, being positive for both responses. Amount of habitat was not determinant for occupancy across scales, but it had a significant positive effect on body condition (Prieto-Ramirez et al. 2020; Prieto-Ramírez et al. in review).

These results suggest that the importance of habitat amount in the landscape decreases towards the end of the population decline process, at which population extinction risk is higher, but is high when population starts declining. Low sensitivity of occupancy to reduction in habitat amount is supported by some hypothesis and models. On the basis of empirical support with birds and mammals the random-sample hypothesis (Andrén, 1994), the regime-shift model (Pardini et al. 2010) and the conceptual model of Villard and Metzger (2014) state that at under certain threshold of total habitat amount in the landscape (~ 30%), the amount of habitat surrounding patches losses importance for species persistence in the patch, because immigration rates become solely dependent on habitat and/or landscape configuration. Betts et *al*. (2006, 2007) and Martensen et al. (2012) have provided additional empirical support for this pattern studying the distribution of forest bird populations in Canada and Brazil, respectively.

However, although habitat amount is less important for occupancy than for body condition, its effect on occupancy might be more direct than that on body condition. This was indicated by the small scale of effect (SoE) of habitat amount on occupancy (Prieto-Ramírez et al. 2020), in contrast with the large SoE it had on body condition (Prieto-Ramírez et al. in review). Large SoE of habitat amount on body condition may reflect its influence on ecological processes determining prey abundance and availability (Bucher and Entling 2011; Dormann et al. 2007), or on the exposure of lizards to euryoecous predators, which, in case of being increased, reduces the time they can invest for feeding activities, and therefore their body condition (Amo et al. 2007b). These processes may occur at a large spatial scale and would indirectly affect the response of body condition to habitat amount in a long time lapse (Manzer and Hannon 2005; Miguet et al. 2016). On the contrary, the small SoE of habitat on occupancy (250 m) might reflect the necessity of populations at the limit of persistence of having increased habitat amount in the vicinity of the patch to support processes like foraging, which usually occur a small scales of effect (Miguet et al. 2016; Suorsa et al. 2005). Additionally, as habitat amount is correlated with attributes of landscape configuration like connectivity (Fahrig 2003), and habitat configuration exerted an strong influence in occupancy of *L. viridis* in the core (Prieto-

Ramírez *et al.* 2020), the small SoE of habitat amount of occupancy can also reflect the importance of increasing habitat in the direct surrounding of patches to improve connectivity.

In spite of the acknowledged importance of the relatively new research area of Conservation Physiology (Cooke et al. 2013; Seebacher and Franklin 2012; Wikelski and Cooke 2006) and its efforts to make spatially explicit links between anthropogenic disturbances and physiological responses (Ellis et al. 2012), very few studies have related aspects of species distribution (occupancy or abundance) with parameters of individuals' physiological state (Maron et al. 2012; Navarro-Castilla et al. 2014). Moreover, this link has never been reported for reptiles (Bergman *et al.* 2019) and only one study has tested effects of habitat amount on both types of responses, distribution and physiological state, across scales (Janin *et al.* 2011).

From the few available studies, the findings of Maron et al. (2012) are similar to the results I obtained (Prieto-Ramírez *et al.* 2020; Prieto-Ramírez et al. in review). They tested effects of local and landscape parameters on the occupancy and physiological state of the eastern yellow robin (*Eopsaltria australis*) in Australia, and found that occupancy was not influenced by habitat amount, while physiological state was determined by the amount of habitat surrounding each patch. On the contrary, results obtained by Janin et al. (2001), who also tested effects of habitat amount across scales, are opposite to mine. In a fragmented landscape in France, they found that the occurrence of the common toad (*Bufo bufo*) in ponds was affected by the surrounding habitat amount (forest) at a large scale, but not by habitat configuration, while its body condition was affected by habitat amount at a small scale. Occupancy is highly dependent on inter-population processes, and therefore, in the case of being more dependent on habitat amount than on configuration, it is expected that the SoE of habitat amount capturing these processes be large. Additionally, in the case of the common toad the response of pond occupancy to loss of forest can be delayed by the fact that the pond to which adults come back to reproduce is still available; this delayed response would then most probably be captured at a large spatial scale (Janin et al. 2011). On the other hand, physiological state of amphibians is highly dependent on pond conditions and within population processes, which are more influenced by the directly adjacent habitat, resulting in a small SoE of habitat amount on body condition (Janin *et al.* 2011; Unglaub *et al.* 2018). Effects of habitat amount on different responses are highly species- and landscape-specific (Fischer and Lindenmayer 2007; Miguet et al. 2016), which makes it difficult to find trends through taxa, regions and levels of habitat loss. However, the lack of studies linking information about individuals' physiological state and populations' distribution is the main impediment to progress on the understanding of proximal mechanisms related to the population decline process in modified landscapes (Bergman 2019; Ellis et al. 2012)

Lastly, the populations I surveyed for morphological analysis (Prieto-Ramírez *et al.* in review) were not genetically differentiated, which suggests some degree of connectivity (Nemitz-Kliemchen et al. 2020), and they were among the largest ones (high encounter rates and density, unpublished data). Despite this, my results can be extrapolated to the other populations studied for occupancy (Prieto-Ramírez *et al.* 2020), because in more isolated populations the amount of cropland surrounding patches would be much higher and their effects on body condition likely would have the same direction and probably would be stronger. The decline of these populations would then be exacerbated by even lower connectivity and exchange of individuals, generating then an stronger effect on body condition.

Occupancy vs FA: Edge effect, isolation, habitat quality and habitat amount

My results from occupancy analysis (Prieto-Ramírez *et al.* 2020) and FA (Prieto-Ramírez et al. in review) show differences in the effects of isolation, edge, habitat quality and habitat amount. I found that occupancy in the core was positively influenced by edge (positive perimeter effect and negative patch area effect), while its effect on developmental stability was negative (positive effects of perimeter/area ratio and negative effects of patch area on FA). Also, my results show a positive effect of isolation on occupancy but negative effect on developmental stability (positive on FA). Furthermore, habitat amount and vegetation structure (characteristic of habitat quality) were not of paramount importance for occupancy, but their interaction had significant positive effects on developmental stability (negative effect on FA), and were important factors reducing, and in some cases even reversing, the negative effects of isolation, cropland and urban areas on developmental stability.

Positive edge effects on the persistence of lizards' populations are often found to be related to thermoregulatory benefits (Delgado García et al. 2007; Sato et al. 2014, Vignoli et al. 2009). However, small patches with a greater portion of edge have a higher exposure to the abiotic conditions in the matrix, and thus, are more susceptible to changes in microclimatic conditions (Hatfield et al. 2020; Murcia 1995; Ries et al. 2004) that can eventually affect the development of individuals, as demonstrated in experimental studies in lizards (Braña and Ji 2000; Ji et al. 2002; Zhdanova and Zakharov 2006). In other species, geometric characteristics defining edge have also been found to increase levels of FA. Pilia (2011) found that FA of carabid beetles increased with the proximity to patch edge, and in the fence lizard (*Sceloporus occidentalis*) Tull and Brussard (2007) found a negative effect of edge on FA of bilateral head-scale patterns due to environmental stress related to proximity to roads. Also, Møller (1995) and Helle et al. (2011) found increased FA of feather length with reduced patch size on blackbirds (*Turdus merula*) and treecreepers (*Certhia familiaris*), respectively.

Regarding isolation, for several species, including lizards, it has also been reported not to have a negative effect on occupancy (Bell and Donnelly 2007; Krauss et al. 2004; Moore and Swihart 2005; Santos et al. 2008; Urban and Swihart 2009), an outcome that is highly landscape-dependent, because effects of isolation are moderated by the landscape structure (eg. habitat amount) resulting from habitat loss (Fahrig, 2003; Andrén, 1994; Pardini et al. 2010; Villard and Metzger, 2014). On the contrary, in the case of FA, most studies testing effects of isolation have found negative impact (Băncilă et al. 2010; Helle et al. 2011; Ljubisavljević et al. 2005; Sarre 1996). Moreover, the few available information about the effects of isolation on both occupancy and FA in other species is in agreement with my results. Patch occupancy of the Eurasian treecreeper (*Certhia familiaris*) in central Finland was found not to be affected by an index of habitat fragmentation which included isolation (Suorsa et al. 2005), but in the same study area FA of primary wing feathers was affected by isolation (Helle et al. 2011). Similarly, the occupancy of habitat remnants by the gecko *Oedura reticulate* in the Western Australian wheatbelt was found to be unaffected by isolation (Sarre et al. 1995), while, in the same study area, the levels of FA of supra and infra labial scales in isolated populations were higher compared to those of populations in inhabiting continuous habitat (Sarre 1996).

The lack of importance of habitat amount and vegetation structure for occupancy is most probably related to the fact that *Lacerta viridis* in this region is a generalist species and can use a broad variety of habitats with different vegetation structures (Vacheva et al. 2020), and therefore these parameters are not limiting factors for the persistence of populations in this region (Prieto-Ramírez et al. 2020), a pattern also found in other species (Devictor et al. 2008; Püttker et al. 2013; Carrara et al. 2015). However, habitat amount and vegetation structure were found to be important for the developmental stability of individuals. The habitat surrounding patches and the vegetation structure into patches are important factors regulating temperature and humidity within patches and buffering the influence of external conditions (Arroyo-Rodríguez et al. 2017; Suggitt et al. 2011), thus reducing environmental stress affecting developmental stability. In the treecreeper populations (*Certhia familiaris*) in Finland habitat amount surrounding patches was also reported to reduce levels of FA (Helle et al. 2011), and Lens et al. (1999) found that reduced vegetation structure increased levels of FA in afro-tropical bird species in Kenya.

Some of the symmetric traits that I studied have direct links with fitness parameters in lacertid lizards, and have the potential to trigger effects on population status. FA in front and hind legs is associated to reduced locomotor performance (Braña and Ji 2000) and escape behavior (Martin and Lopez 2001), and in *Podarcis siculus* Vervust et al. (2009) reported a negative relation between FA in several meristic and metric traits in the head and exertion capacity -the time before exhaustion when being chased. Reduced escape capacity can affect survival probability, especially if lizards are exposed to increased predation risk. By its side, femoral pores have an important role in mate choice in lizards due to the secretion of pheromones, which serve as chemical cues informing females about males' quality and age (Martín and López 2006; Nisa-Ramiro et al. 2019), hence FA in this trait can significantly reduce the chances of males of being selected by females (Martin and Lopez 2000), and thus could affect males' reproductive output. For some symmetric traits, like supracilliary scales, the link with fitness parameters might be more indirect (Leung and Forbes 1996) through linkage to organism-wide processes (Gangestad and Thornhill 1999) that coordinate developmental stability and homeostasis of characters that directly affect fitness traits (Zakharov et al. 2001), like growth rate and patterns of oxygen consumption and energy expenditure for development (Braña and Ji 2000; Ji et al. 2002).

Thus, I found that isolation and edge effects, although not having negative effects on the distribution of populations of *L. viridis*, do have the potential of negatively affect populations through their effects on individuals' developmental stability at an early stage of the population decline process. Moreover, those effects might be principally modulated by the environmental conditions in the landscape surrounding the patch (determined by the amount of habitat around the patch), by the exposure of the patch to those conditions (defined by patch geometric characteristics) and by the quality of the patch, which increases with increasing diversity of vegetation layers. Information about effects of landscape structure and configuration on both, occupancy and FA, is only available for very few species. Therefore, the discussion regarding the possible trade-offs to be met in landscape management plans when contrasting effects of a given landscape parameter on occupancy and FA exist, is still missing. In the specific case of *L. viridis* (but also applicable to other reptile species), a middle way between the environmental demands for stable development, thermoregulation and availability of resource demands and population persistence necessities can be met by increasing habitat in the surrounding landscape and increasing patch size and reducing edge, while maintaining levels of vegetation structure that offer sufficient open spots, but also refuge and shaded places, to fulfill thermoregulatory demands of lizards.

Finally, although a common link between population decline and FA reported in the literature is through reduced developmental stability due to genetic stress caused by small population size (e.g. Berggren, 2005), it is important to consider that the opposite direction in the cause – effect relation can also be possible, especially in populations that still have relatively high levels of genetic variability but that are exposed to impaired environmental conditions.

6.4. Perspectives for species distribution models

Habitat loss in the periphery and species' response to climate change

Theory predicts that stable range limits are formed when populations in the periphery lack adaptive potential to further expand. Spatial range expansion models suggest this is due to a decreasing abundance gradient from the core to the periphery that results in peripheral populations being smaller, having lower genetic variability, being more isolated, and therefore, having higher vulnerability to genetic drift and demographic stochasticity, which hamper adaptation and expansion, thus creating a range limit (Bahn et al. 2006; Guo et al. 2005; Vucetich and Waite 2003). Additionally, models based on environmental heterogeneity suggest that environmental suitability decreases from the core to the periphery and that range limits are at the edge of the fundamental niche of species, what is called range limits at equilibrium (Pulliam 2000). The lower environmental suitability, together with lower population size and genetic variability, will reduce even more the adaptive capacity of these populations (Sexton et al. 2009).

Non-locally adapted reptile populations in temperate regions usually experience maximum temperatures that are further from their physiological upper thermal limits, compared to low latitudinal and core populations (Araújo et al. 2013; Sunday et al. 2010). Therefore, under climate change northern peripheral populations are predicted to profit from novel, more climatically suitable environments that would be similar to conditions closer or at the core (Deutsch et al. 2008; Le Galliard et al. 2012), thus expanding or shifting the species' range. In order to track climatic conditions individuals must be able to move through the landscape, and therefore habitat availability and landscape structure in peripheral regions is enormously important for species' ability to cope with climate change by range shifts (Hof et al. 2011; Opdam and Wascher 2004). Hence, several studies predicting range shift under scenarios of climate change have included measures of habitat availability as predictor factors for future species distribution (e.g. Ballesteros-Barrera *et al.* 2007; Melles *et al.* 2011). However, such measures are usually calculated at large scales and lack of the landscape perspective necessary to understand the effect of landscape structure on dispersal, demographic parameters and (meta)population dynamics at the scales at which these processeses occur (Sexton *et al.* 2009). Hence, the inclusion of landscape structure parameters in peripheral regions (e.g. Naujokaitis-Lewis *et al*., 2013, Fourcade *et al.* 2017) where the species might be more vulnerable to habitat loss due to a higher specialization degree, can potentially change predictions of future range shifts under climate change.

Inclusion of intraspecific differences to model regional species distribution

Another potential for the improvement of predictive power of species distribution models (SDM) is the inclusion of the difference in the realized niche and (micro)habitat selection in the periphery compared to the core. The vast majority of SDM infer niche from correlation between presence data and environmental conditions (usually climatic and/or habitat), and assume a homogeneous sensitivity and response of species across the distribution range, thus failing to capture intraspecific differences that can highly influence model output. Recently, some studies have proposed the inclusion of intraspecific differences by constructing separate models for different lineages, habitats or climatic zones (Chardon et al. 2019; Lecocq et al. 2019; Martin et al. 2020; Peñalver-Alcázar et al. 2021), using these parameters as proxy for intraspecific niche differences. All of these approaches report important improvement of intraspecific-based SDMs in contrast to species-based SDMs. However, first, the ecological and spatial grain of those studies is still very coarse, and therefore proxy measures like habitat and climatic zones might lack ecological specificity, and second, these approaches apply the same basic parameters to separate among groups without accounting for differences in the relative importance of different environmental parameters in each region.

I propose that further improvements could be achieved through either increasing the spatial resolution of proxy parameters like habitat or climatic zones, or by directly including specific realized niche factors that are of higher relative importance in different regions. The inclusion of high-resolution environmental data for SDMs has not only proven to improve model's accuracy, but also to increase ecological relevance by directly relating to species microhabitat (Nezer et al. 2017). These could then more efficiently capture differences among regions in a high spatial resolution approach. On the other hand, generating information about realized niche differences between core and peripheral regions allows knowing in advance, which are the most important factors to be included in the SDMs in each region (e.g. radiation, vegetation type, slope, temperature), thus solving spatial transferability problems of classical SDMs, which usually do not incorporate differences in local habitat availability and local preferences (Torres et al. 2015; Yates et al. 2018), and therefore do not reflect possible higher specialization degree in peripheral regions.

Implication for predictions of Lacerta viridis' range

Lacerta viridis experienced a rapid range expansion during the Holocene from several Pleistocene refugia in the Balkans (Böhme et al 2007b; Marzahn et al. 2016). Approximately 5000 years ago, populations are thought to have experienced a range contraction during postglacial climatic oscillations and vegetation succession, giving origin to the relict populations known today in Brandenburg and Bohemia (Böhme et al. 2006; Joger et al. 2010). Although local adaptation in both peripheral regions, Prague and Passau, cannot be ruled out without experimental studies, my results on differential microhabitat selection in each region (Prieto-Ramírez et al. 2018) together with the known differences in seasonal activity patterns (Fischer and Rehak 2010; Grimm et al. 2014; Sagonas et al. 2018; Václav et al. 2007), suggest that plastic thermoregulatory behavior might be an important mechanism responsible for the persistence of these populations and the maintenance of possible stable range limits in the northern edge. This means that in the periphery *L. viridis* might follow the pattern of reptile species at higher latitudes tracking novel suitable environments during climate change (Joger et al. 2010; Massot et al. 2012), and then the higher sensitivity of the species to habitat loss in this region will play a very important role in the range shift response of the species.

6.5. Conservation measures for *Lacerta viridis* in each region

In both peripheral regions (Passau and Prague) are being implemented protection measures for some populations of *L. viridis*. In Passau the main applied measures are related to the maintenance of open vegetation in Passau (Assmann 2002), and in Prague most populations are located in nature conservation reserves where their habitat is protected (Miroslav et al. 2008) and a monitoring and management program is being applied for a single *L. viridis* population that inhabits the area where the Zoo of Prague is located (Rehák 2015). Additional conservation measures to be implemented at broader spatial scales, like the creation of corridors, have been suggested by other authors (Böhme and Moravec 2011; Elbing et al. 1997; Nettmann and Rykena 1984), but until now no conservation programs have been design with the purpose of protecting *L. viridis* across the landscape. My research supports the importance of the currently applied measures and suggests additional ones, which include the landscape and monitoring perspectives.

In all regions it is important to protect the remnant habitat for the species to prevent further local extinctions. Additionally, I suggest to implement a monitoring program in each region that evaluates the response of possible early warning indicators of negative effects of habitat loss, especially of body condition and fluctuating asymmetry. Specific conservation and management measures for each region are listed below.

Peripheral populations in Passau

- Maintain low vegetation in sites where the species already occurs in the valley below cliffs, and also in the upper border of the cliff to increase the potentially suitable area for the species.
- Create corridors along forest tracks or powerlines that facilitate connections between suitable habitats below and above the cliffs, as well as with the habitat along the riverbed of the Danube River.

Peripheral populations in Prague

- Increase matrix permeability by including hedges and line structures with vegetation corresponding to the habitat at the borders of croplands, as well as the inclusion of such structures through areas with humid grassland and dense woodland, especially at small scales (<500 m).
- Increase the availability of edge in the patches by increasing patch size with linear structures to maintain a high perimeter to area ratio.
- Keep low levels of vegetation structure especially in valley slopes, and prevent overgrown vegetation in open woodlands and at the borders of dense woodland areas to avoid losing habitat.

- Evaluate the possibility of connecting populations in the valley slopes with river bank vegetation of the Vltava River, currently separated by streets, as it might be an important corridor augmenting connectivity.

Core Populations in Plovdiv and surroundings

- Protect the patches that are close to rivers and structurally connect with the river bank those patches that are more distant to rivers, as well as protect and restore river bank vegetation along the Maritza River and its tributary rivers.
- As in the periphery, hedges and habitat lines surrounding crops could improve permeability of the landscape.
- Protect the habitat surrounding patches, principally at a scale of 250 m, and increase at least 10% of habitat at 750 m scales, as derived from predicted occupancy probabilities at this scale.
- Maintain patches with large perimeter and also sufficient core area.
- Protect the vegetation structure in remnant patches, avoiding practices, like grazing, that can diminish it.

7. Summary

Habitat destruction due to land cover and land use changes is currently the most intense pressure threatening global biodiversity, (Maxwell, 2016). As ectotherms, reptiles are especially vulnerable to it due to its dependency on environmental conditions, which can be affected by landscape modification (Meek, 1995; Larson, 2014; Keinath et al. 2017; Saunders et al. 2017;), and to their lower dispersal abilities and smaller home ranges compared to other vertebrate taxa (Kearney et al. 2009). Species' traits like specialization have extensively been applied to identify species that might be more vulnerable to habitat loss. However, traits cannot always be extrapolated across the distribution range of species and failing to account intraspecific differences (eg. Brown, 1996) can lead to erroneous predictions of species sensitivity. The Kühnelt principle of regional stenoecy (Kühnelt, 1965) states that due to a narrower range of available suitable habitats and conditions in the periphery compared to the core, populations living at the periphery are comparably more stenoecious or specialized than populations at the core. This geographical-dependent intraspecific difference in specialization degree implies that there are also differences in the sensitivity to habitat loss among peripheral and core populations of the same species and that different conservation measures should be applied in each region.

In my project I quantified niche size, microhabitat selection and vulnerability to habitat loss of populations of the eastern green lizard *Lacerta viridis* living at the core and at the northern periphery of its distribution range. I also identified individual's morphological and physiological parameters that are suitable as early warning indicators of negative effects of habitat loss before populations dramatically decrease in size and eventually go extinct. To do this, I combined extensive field data gathering in different regions of the distribution range of *L. viridis* with advance statistical and spatial analysis approaches. This allowed me to link processes occurring at different spatial levels (micro, remnant habitat patch, landscape, region), different levels of biological organization (individuals and populations) and different times (initial vs late stages of population decline), and to identify the most important conservation measures to be applied for the protection of *L. viridis* in each region.

I found that northern peripheral populations have a higher specialization degree than core populations, resulting not only from known climatic constraints, but also from habitat restrictions, with a narrower range of habitats available to fulfill ecological and thermal requirements. Thus, in the periphery, populations of *L. viridis* have a smaller and differentiated niche compared to the core, and microhabitat used and parameters that define microhabitat selection also differ among regions. *L. viridis* in the core used microhabitats with a higher vegetation structure and microhabitat selection was defined solely by abiotic parameters, while in the periphery, where radiation is lower, the species responds to this pressure by selecting microhabitats with lower vegetation structure, and

microhabitat selection is defined by vegetation structure parameters alone or in combination with abiotic parameters.

Furthermore, I found that differences in specialization degree among regions have direct links with differences in vulnerability to habitat loss. First of all, persistence of peripheral populations (occupancy probability) was more influenced by parameters of habitat quality compared to the core. Second, single landscape composition parameters had a stronger effect on the persistence of peripheral populations compared to populations in the core, and the scale at which overall habitat loss -landscape structure plus patch characteristics- had the strongest effect was much smaller in the periphery (50 m) compared to the core (500 m). Third, landscape composition parameters determined the persistence of peripheral populations, while in the core it was landscape configuration parameters that affected occupancy the most, which implies possible differences in the characteristics of the landscape that affect dispersal the most in each region. Fourth, my results regarding patch characteristics in each region suggest different patterns of patch habitat use that go in line with the microhabitat selection patterns found, with populations in the core depending on both patch edge and interior, and populations in the periphery being more edge specialist. Finally, these findings allowed me to identify consistencies or differences in the parameters that were most important in processes at variable spatial scales -microhabitat selection vs persistence in the patch- in each region, and to link these patterns with responses at the individual and population level.

Regarding the identification of early warning indicators, I evaluated the effects of landscape structure and patch characteristics resulting from habitat destruction on body condition (BC) , tick load and fluctuating asymmetry (FA; small deviations from symmetry in symmetrical traits) of several metric and meristic traits of *L.viridis* individuals inhabiting core populations. I found that BC increased with the proportion of habitat in the landscape and decreased with the proportion of cropland; FA increased with loss and conversion of habitat, reduction of patch size and increased isolation, and responses were sex and age dependent for some traits; and tick load was positively affected by predictors that can increase the burden of ticks in the landscape through its positive effects on tick's populations or on its host species density. My results suggest that BC and FA can be used as early warning indicators of stress for populations of *L. viridis* facing habitat loss, and that tick load is a trait suitable for monitoring and studying complex ecological interactions among ticks and hosts populations in fragmented landscapes affecting the tick load of lizards. Furthermore, I also found differences in the landscape and patch characteristics parameters that affect persistence vs morphological and physiological traits, suggesting differences in the attributes of habitat loss exerting the strongest pressure at different stages of the population decline process.

In my final synthesis, I linked niche theory with habitat loss, microhabitat selection with populations persistence in the landscape, and effects of habitat loss at early stages with effects at late stages of the population decline process to understand differences in the response and tolerance to habitat loss of *L. viridis* in the core and northern periphery of its distribution range, and set better conservation measures for its protection. Applying niche theory to study effects of habitat loss allows accounting for intraspecific differences in degree of sensitivity, by defining specialization as a mechanistic continuum trait rather than a binary one, which changes across the distribution range of species. This is greatly important to apply adequate conservation measures that account for the specific characteristics of local populations. Furthermore, connecting effects of habitat loss at initial and later stages of the population decline process enables to link spatial distribution patterns of populations with the beginning of a chain of ecological effects that start at the individual level and end up at the population-level response to habitat loss. Therefore, it becomes necessary to identify individual's characteristics that are easily gathered and can be the basis of monitoring programs aimed to avoid populations decline and local extinctions.

My findings are a contribution to the conservation measures applied to protect populations of *L. viridis* in the studied regions, with special novel imputs in the measures to be applied at the landscape scale and the individuals' parameters suitable to be used in possible future monitoring programs. Furthermore, this research highlights the importance of accounting for intraspcific differences in vulnerability to habitat loss, resulting from variable geographicaly-dependent specialization degree of populations, when studying effects of habitat destruction. Finally, this study has conceptual reprecussions on the the spatial and temporal predictions of species distribution models, as well as predictions of range expansion and contraction in the face of synergistic effects between habitat loss and climate change, none of which usually accounts for intraspecific differences in niche size and microhabitat selection.

8. References

Addo-Bediako A, Chown SL, Gaston KJ (2000) Thermal tolerance, climatic variability and latitude. Proceedings of the Royal Society of London Series B: Biological Sciences 267: 739-745.

Ahmadzadeh F, Flecks M, Carretero MA, Böhme W, Ilgaz C, Engler JO, James Harris D, Üzüm N, Rödder D (2013) Rapid lizard radiation lacking niche conservatism: ecological diversification within a complex landscape. Journal of Biogeography 40: 1807-1818.

Alberts AC (1994) Dominance hierarchies in male lizards: Implications for zoo management programs. Zoo Biology 13: 479-490.

Allan BF, Keesing F, Ostfeld RS (2003) Effect of Forest Fragmentation on Lyme Disease Risk. Conservation Biology 17: 267-272.

Almeida-Gomes M, Vieira M, Rocha C, Metzger J, De Coster G (2016) Patch size matters for amphibians in tropical fragmented landscapes. Biological Conservation 195: 89-96.

Amaral MJ, Bicho R, Carretero M, Sanchez-Hernandez J, Faustino A, Soares A, Mann R (2012) The use of a lacertid lizard as a model for reptile ecotoxicology studies: Part 2-Biomarkers of exposure and toxicity among pesticide exposed lizards. Chemosphere 87: 765-774.

Amo L, Fargallo JA, Martínez-Padilla J, Millán J, López P, Martín J (2005) Prevalence and intensity of blood and intestinal parasites in a field population of a Mediterranean lizard, *Lacerta lepida*. Parasitology Research 96: 413-417.

Amo L, López P, Martín J (2004) Prevalence and intensity of haemogregarinid blood parasites in a population of the Iberian rock lizard, *Lacerta monticola*. Parasitology Research 94: 290-293.

Amo L, López P, Martín J (2007a) Habitat deterioration affects antipredatory behavior, body condition, and parasite load of female *Psammodromus algirus* lizards. Canadian Journal of Zoology 85: 743-751.

Amo L, López P, Martín J (2007b) Habitat deterioration affects body condition of lizards: A behavioral approach with *Iberolacerta cyreni* lizards inhabiting ski resorts. Biological Conservation 135: 77 - 85.

Amo L, López P, Martín J (2007c) Refuge use: A conflict between avoiding predation and losing mass in lizards. Physiology & Behavior 90: 334-343.

Andrén H (1994) Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. Oikos 71: 355-366.

Angert AL, Hutchison D, Glossip D, Losos JB (2002) Microhabitat use and thermal biology of the collared lizard (*Crotaphytus collaris collaris*) and the fence lizard (*Sceloporus undulatus hyacinthinus*) in missouri glades. Journal of Herpetology 36: 23-29.

Araújo MB, Ferri-Yáñez F, Bozinovic F, Marquet PA, Valladares F, Chown SL (2013) Heat freezes niche evolution. Ecology Letters 16: 1206-1219.

Araújo MB, Peterson AT (2012) Uses and misuses of bioclimatic envelope modeling. Ecology 93: 1527-1539.

Arnfield AJ (2003) Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and the urban heat island. International Journal of Climatology 23: 1-26.

Arnold EN (1987) Resource partition among lacertid lizards in southern Europe. Journal of Zoology 1: 739-782. d

Arroyo-Rodríguez V, Saldan˜a-Vázquez R, Fahrig L, Santos BA (2017) Does forest fragmentation cause an increase in forest temperature? Ecol Res 32: 81 - 88.

Assmann O (2002) Schutzmaßnahmen für die Smaragdeidechse - *Lacerta viridis* (Laurenti, 1768) bei Passau (BRD, Niederbayern). Mertensiella 13: 251-268.

Augustin NH, Mugglestone MA, Buckland ST (1996) An Autologistic Model for the Spatial Distribution of Wildlife. Journal of Applied Ecology 33: 339-347.

Babocsay G (1997) The niche segregation of three lacertid lizard species (*Lacerta viridis, L. agilis* and *Podarcis taurica*) on sandy grassland in Hungary. Meeting of the Zoological Society of Israel, Tel-Aviv, 48 pp.

Baguette M, Stevens V, Clobert J (2014) The pros and cons of applying the movement ecology paradigm for studying animal dispersal. Movement Ecology 2:13.

Bahn V, O'Conno RJ, Krohn WB (2006) Effect of dispersal at range edges on the structure of species range. Oikos 115: 89 - 96.

Bajer K, Molnár O, Török J, Herczeg G (2012) Temperature, but Not Available Energy, Affects the Expression of a Sexually Selected Ultraviolet (UV) Colour Trait in Male European Green Lizards. PLoS ONE 7: e34359.

Ballesteros-Barrera C, Martínez-Meyer E, Gadsden H (2007) Effects of land-cover transformation and climate change on the distribution of two microendemic lizards, genus *Uma*, of northern Mexico. Journal of Herpetology 41: 733-740.

Băncilă R, Van Gelder I, Rotteveel E, Loman J, Arntzen JW (2010) Fluctuating asymmetry is a function of population isolation in island lizards. Journal of Zoology 282: 266-275.

Banner KM, Higgs MD (2017) Considerations for assessing model averaging of regression coefficients. Ecological Applications 27: 78-93.

Bartón K (2015) MuMIn: Multi-Model Inference.

https://cran.r-project.org/web/packages/MuMIn/index.html, pp.

Bates D, Maechler M, Bolker B, Walker S (2016) lme4: Linear Mixed-Effects Models using 'Eigen' and S4. https://cran.r-project.org/web/packages/lme4/index.html, pp.

Battles AC, Whittle TK, Stehle CM, Johnson MA (2013) Effects of human land use on prey availability and body condition in the green anole lizard, *Anolis carolinensis*. Herpetological Conservation and Biology 8: 16 - 26.

Beasley DAE, Bonisoli-Alquati A, Mousseau TA (2013) The use of fluctuating asymmetry as a measure of environmentally induced developmental instability: A meta-analysis. Ecological Indicators 30: 218-226.

Bell K, Donnelly M (2007) Influence of forest fragmentation on community structure of frogs and lizards in northeastern Costa Rica. Conservation Biology 20: 1750-1760.

Belliure J, Carrascal L (2002) Influence of Heat Transmission Mode on Heating Rates and on the Selection of Patches for Heating in a Mediterranean Lizard. Physiological and biochemical zoology 75: 369-376.

Bender DJ, Contreras TA, Fahrig L (1998) Habitat loss and population decline: A meta-analysis of the patch size effect. Ecology 79: 517-533.

Bender R, Lange S (2001) Adjusting for multiple testing- when and how? Journal of Clinical Epidemiology 54: 343 - 349.

Benedek AM, Sîrbu I (2018) Responses of small mammal communities to environment and agriculture in a rural mosaic landscape. Mammalian Biology 90: 55-65.

Benítez H, Lemic D, Püschel T, Viric Gasparic H, Kos T, Barić B, Bažok R, Pajač Živković I (2018) Fluctuating asymmetry indicates levels of disturbance between agricultural productions: An example in Croatian population of *Pterostichus melas melas* (Coleptera: Carabidae). Zoologischer Anzeiger 276: 42 - 49.

Benson JF, Mahoney PJ, Sikich JA, Serieys LEK, Pollinger JP, Ernest HB, Riley SPD (2016) Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. Proceedings of the Royal Society B: Biological Sciences 283: 20160957.

Berggren Å (2005) Effect of propagule size and landscape structure on morphological differentiation and asymmetry in experimentally introduced roesel's bush-crickets. Conservation Biology 19: 1095-1102.

Bergman J (2019) Scaling from individual physiological measures to population-level demographic change: Case studies and future directions for conservation management. Biological Conservation 238: 108242.

Betts M, Fahrig L, Hadley A, Halstead K, Bowman J, Robinson W, Wiens J, Lindenmayer D (2014) A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. Ecography 37: 517 - 527.

Betts MG, Forbes GJ, Diamond AW (2007) Thresholds in songbird occurrence in relation to landscape structure. Conserv Biol 21: 1046-1058.

Betts MG, Forbes GJ, Diamond AW, Taylor PD (2006) Independent effects of fragmentation on forest songbirds: An organism-based approach. Ecological Applications 16: 1076-1089.

Beutler A, Rudolph BU (2003) Rote Liste gefährdeter Kriechtiere (Reptilia) Bayerns. In: Umweltfragen BSfLu (Ed) Rote Liste gefährdeter Tiere Bayerns. 45 - 47.

Biedermann R (2004) Patch occupancy of two hemipterans sharing a common host plant. Journal of Biogeography 31: 1179-1184.

Blanchet S, Rey O, Etienne R, Lek S, Loot G (2010) Species-specific responses to landscape fragmentation: implications for management strategies. Evolutionary applications 3: 291-304.

Blanco-Fontao B, Fernández-Gil A, Obeso JR, Quevedo M (2010) Diet and habitat selection in Cantabrian Capercaillie (*Tetrao urogallus cantabricus*): ecological differentiation of a rear-edge population. Journal of Ornithology 151: 269-277.

Blanquart F, Kaltz O, Nuismer SL, Gandon S (2013) A practical guide to measuring local adaptation. Ecology Letters 16: 1195-1205.

Blonder B (2015) hypervolume: High-Dimensional Kernel Density Estimation and Geometry Operations. https://cran.r-project.org/web/packages/hypervolume/index.html, pp.

Blonder B, Lamanna C, Violle C, Enquist BJ (2014) The n-dimensional hypervolume. Global Ecology and Biogeography 23: 595-609.

Boakes EH, Isaac NJB, Fuller RA, Mace GM, McGowan PJK (2018) Examining the relationship between local extinction risk and position in range. Conservation Biology 32: 229-239.

Boersma B, Wit JM (1997) Catch-up growth. Endocr Rev 18: 646 - 661.

Bogert CM (1949) Thermoregulation in Reptiles, A Factor in Evolution. Evolution 3: 195-211.

Böhm M, Collen B, Baillie J, Bowles P, Chanson J, Cox N, Hammerson G, Hoffmann M, Livingstone S, Ram M, Rhodin A, Stuart S, Dijk PP, Young B, Afuang L, Aghasyan A, Puntriano C, Ajtic R, Zug G (2013) The Conservation Status of the World's Reptiles. Biological Conservation 157: 372-385.

Böhme M, Schneeweiß N, Fritz U, Moravec J, Majláth I, Majlathova V, Berendonk T (2006) Genetic differentiation and diversity of *Lacerta viridis viridis* (Laurenti, 1768) within the northern part of its range: An investigation using mitochondrial haploypes. Salamandra 42: 29 - 40.

Böhme MU, Schneeweiß N, Fritz U, Schlegel M, Berendonk TU (2007a) Small edge populations at risk: genetic diversity of the green lizard (*Lacerta viridis viridis*) in Germany and implications for conservation management. Conservation Genetics 8: 555-563.

Böhme MU, Fritz U, Kotenko T, Džukić G, Ljubisavljević K, Tzankov N, Berendonk TU (2007b) Phylogeography and cryptic variation within the *Lacerta viridis* complex (Lacertidae, Reptilia). Zoologica Scripta 36: 119-131.

Böhme MU, Moravec J (2011) Conservation genetics of *Lacerta viridis* populations in the Czech Republic (Reptilia: Lacertidae). Acta Soc Zool Bohem 75: 7 – 21.

Böhme W, Rödder D (2014) Amphibien und Reptilien: Verbreitungs- und Verhaltensänderungen aufgrund der Erderwärmung. In: Lozán JL, Grassl, H., Karbe, L. & G. Jendritzky (Ed) Warnsignal Klima: Gefahren für Pflanzen, Tiere und Menschen. Hamburg, 77-81.

Bolaños-García R, Rodríguez-Estrella R, Guzmán-Cornejo C (2018) Ectoparasites associated with a Great Horned Owl nesting (Aves: Strigidae) population in fragmented landscape of Baja California peninsula, Mexico. Acta zoológica mexicana 34:1 - 15.

Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153: 51-68.

Borremans B, Faust C, Manlove KR, Sokolow SH, Lloyd-Smith JO (2019) Cross-species pathogen spillover across ecosystem boundaries: mechanisms and theory. Philosophical Transactions of the Royal Society B: Biological Sciences 374: 20180344.

Bower DS, Brannelly LA, McDonald CA, Webb RJ, Greenspan SE, Vickers M, Gardner MG, Greenlees MJ (2019) A review of the role of parasites in the ecology of reptiles and amphibians. Austral Ecology 44: 433-448.

Boyard C, Vourc'h G, Barnouin J (2008) The relationships between *Ixodes ricinus* and small mammal species at the woodland–pasture interface. Experimental and Applied Acarology 44: 61-76.

Brachet S, Olivieri II, Godelle B, Klein E, Frascaria-Lacoste N, Gouyon PH (1999) Dispersal and metapopulation viability in a heterogeneous landscape. J Theor Biol 198: 479-495.

Braña F, Ji X (2000) Influence of incubation temperature on morphology, locomotor performance, and early growth of hatchling wall lizards (*Podarcis muralis*). Journal of Experimental Zoology 286: 422-433.

Brattstrom BH (1968) Thermal acclimation in Anuran amphibians as a function of latitude and altitude. Comparative Biochemistry and Physiology 24: 93-111.

Brewster C, Beaupre SJ, Wilsson JD (2018) Habitat loss and local extinction: Linking population declines of eastern collared lizards (*Crotaphytus collaris*) to habitat degradation in Ozark Glades. Journal of Herpetology 52: 352 - 360.

Brito JC, Paulo OS, Crespo EG (1998) Distrubution and habitats of schreiber's green lizard (*Lacerta schreiberi*) in Portugal. Herpetological Journal 8: 187-194.

Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. Trends Ecol Evol 23: 453-460.

Brown JH (1984) On the relationship between abundance and distribution of species. Am Nat 124: 255 - 279.

Brown JH, Stevens GCa, Kaufman DM (1996) The geographic range: Size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27: 597-623.

Brusch G, Taylor E, Whitfield S (2015) Turn up the heat: thermal tolerances of lizards at La Selva, Costa Rica. Oecologia 180: 325 - 334.

Bucher R, Entling MH (2011) Contrasting effects of habitat fragmentation, population density, and prey availability on body condition of two orb-weaving spiders. Ecological Entomology 36: 680-685.

Buckley LB (2010) The range implications of lizard traits in changing environments. Global Ecology and Biogeography 19: 452-464.

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: A practical information-theoretic approach Springer-Verlag, New York, pp.

Cadena CD, Loiselle BA (2007) Limits to elevational distributions in two species of emberizine finches: disentangling the role of interspecific competition, autoecology, and geographic variation in the environment. Ecography 30: 491-504.

Cahill AE, Aiello-Lammens ME, Caitlin Fisher-Reid M, Hua X, Karanewsky CJ, Ryu HY, Sbeglia GC, Spagnolo F, Waldron JB, Wiens JJ (2014) Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. Journal of Biogeography 41: 429-442.

Caldwell A, While G, Beeton N, Wapstra E (2015) Potential for thermal tolerance to mediate climate change effects on three members of a cool temperate lizard genus, Niveoscincus. Journal of Thermal Biology 52: 14 - 23.

Carbayo J, Martín J, Civantos E (2019) Habitat type influences parasite load in Algerian Psammodromus (*Psammodromus algirus*) lizards. Canadian Journal of Zoology 97: 172 - 180.

Carrara E, Arroyo-Rodríguez V, Vega-Rivera JH, Schondube JE, de Freitas SM, Fahrig L (2015) Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biological Conservation 184: 117-126.

Castilla AM, Van Damme R, Bauwens D (1999) Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in lacertid lizards. Nat Croat 8: 253 - 274.

Ceballos G, Ehrlich P, Barnosky A, Garcia A, Pringle R, Palmer T (2015) Accelerated Modern Human-Induced Species Losses: Entering the Sixth Mass Extinction. Science Advances 1: e1400253.

Chaplin-Kramer R, de Valpine P, Mills N, Kremen C (2013) Detecting pest control services across spatial and temporal scales. Agriculture, Ecosystems & Environment 181: 206–212.

Chapman CA, Gillespie TR, Goldberg TL (2005) Primates and the Ecology of their Infectious Diseases: How will Anthropogenic Change Affect Host-Parasite Interactions? Evolutionary Anthropology: Issues, News, and Reviews 14: 134-144.

Chardon NI, Pironon S, Peterson ML, Doak DF (2019) Incorporating intraspecific variation into species distribution models improves distribution predictions, but cannot predict species traits for a wide-spread plant species. Ecography 43: 60 - 74.

Charlesworth D, Willis JH (2009) The genetics of inbreeding depression. Nature Reviews Genetics 10: 783-796.

Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical Transactions of the Royal Society B: Biological Sciences 366: 2351-2363.

Chaudhary A, Mooers A (2018) Terrestrial Vertebrate Biodiversity Loss under Future Global Land Use Change Scenarios. Sustainability 10: 2764.

Chefaoui RM, Hortal J, Lobo JM (2005) Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: a case study of Iberian Copris species. Biological Conservation 122: 327-338.

Chevin L-M, Lande R, Mace GM (2010) Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. PLOS Biology 8: e1000357.

Chevin LM, Lande R (2011) Adaptation to marginal habitats by evolution of increased phenotypic plasticity. J Evol Biol 24: 1462-1476.

Chiacchio M, Grimm-Seyfarth A, Henle K, Mihoub J-B (2020) Water availability as a major climatic driver of taxonomic and functional diversity in a desert reptile community. Ecosphere 11(7): e03190.

Chichorro F, Juslén A, Cardoso P (2019) A review of the relation between species traits and extinction risk. Biological Conservation 237: 220-229.

Chown SL, Terblanche JS (2006) Physiological Diversity in Insects: Ecological and Evolutionary Contexts. Advances in insect physiology 33: 50-152.

Cohen J (1988) Statistical power analysis for the behavioral sciences. Academic Press, New York, pp.

Collinge SK, Forman R, T. T. (1998) A Conceptual Model of Land Conversion Processes: Predictions and Evidence from a Microlandscape Experiment with Grassland Insects. Oikos 82: 66-84. doi:10.2307/3546918

Conrad O, Bechtel B, Book M, Dietrich H, Fischer E, Gerlitz L, Wehberg J, Wichmann V, Böhner J (2015) System for Automated Geoscientific Analyses (SAGA) v. 2.1.4, Geosci. Model Dev., 8, 1991-2007.

Cooke SJ, Sack L, Franklin CE, Farrell AP, Beardall J, Wikelski M, Chown SL (2013) What is conservation physiology? Perspectives on an increasingly integrated and essential science. Conservation physiology 1: cot001.

Cote J, Clobert J (2007) Social personalities influence natal dispersal in a lizard. Proceedings of the Royal Society B: Biological Sciences 274: 383-390.

Covaciu-Marcov SD, Cicort-Lucaciu AS, Dobre F, Ferenti S, Birceanu M, Mihut R, Strugariu A (2009) The herpetofauna of the Jiului Gorge National Park, Romania. North-Western Journal of Zoology 5: 1-78.

Cozzi G, Müller CB, Krauss J (2008) How do local habitat management and landscape structure at different spatial scales affect fritillary butterfly distribution on fragmented wetlands? Landscape Ecology 23: 269-283.

Crnobrnja-Isailovic J, I. A, D. B (2005) Fluctuating asymmetry in Podarcis muralis populations from Southern Montenegro: detection of environmental stress in insular populations. Amphibia-Reptilia 26: 149 - 158.

Cunningham HR, Rissler LJ, Buckley LB, Urban MC (2016) Abiotic and biotic constraints across reptile and amphibian ranges. Ecography 39: 1-8.

Cushman SA, Brad M, Adriaensen F, Beier P, Shirley M, Zeller K (2013) Biological corridors and connectivity. In: Macdonald D, Willis K (Eds) Key Topics in Conservation Biology 2. John Wiley and Sons, Oxford.

Davies KF, Margules CR, Lawrence JF (2004) A synergistic effect puts rare, specialized species at greater risk of extinction. Ecology 85: 265-271.

De Coster G, Banks-Leite C, Metzger JP (2015) Atlantic forest bird communities provide different but not fewer functions after habitat loss. Proceedings of the Royal Society B: Biological Sciences 282: 20142844.

Debinski DM, Holt RD (2000) A Survey and Overview of Habitat Fragmentation Experiments. Conservation Biology 14: 342-355.

Delciellos AC, dos Santos de Barros C, Prevedello J, Silva-Ferrerira M, Cerqueira R, Vieira MV (2018) Habitat fragmentation affects individual condition: evidence from small mammals of the Brazilian Atlantic Forest. Journal of Mammalogy 99: 936 - 945.

Delgado García JD, Arévalo JR, Fernández-Palacios JM (2007) Road edge effect on the abundance of the lizard *Gallotia galloti* (Sauria: Lacertidae) in two Canary Islands forests. Biodiversity and Conservation 16: 2949-2963.

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. PNAS 105: 6668 - 6672.

Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W, Venail P, Villéger S, Mouquet N (2010) Defining and measuring ecological specialization. Journal of Applied Ecology 47: 15-25.

Devictor V, Julliard R, Jiguet F (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117: 507-514.

DeVore JL, Shine R, Ducatez S (2020) Urbanization and translocation disrupt the relationship between host density and parasite abundance. Journal of Animal Ecology 00: 1 - 12.

Díaz JA, Bauwens D, Asensio B (1996) A comparative study of the relation between heating rates and ambient temperatures in Lacertid lizards. Physiological Zoology 69: 1359-1383.

Díaz JA, Carbonell R, Virgós E, Santos T, Tellería JL (2000) Effects of forest fragmentation on the distribution of the lizard *Psammodromus algirus*. Animal Conservation 3: 235-240.

Díaz JA, Pérez-Tris J, Tellería JL, Carbonell R, Santos T (2005) Reproductive investment of a lacertid lizard in fragmented habitat. Conservation Biology 19: 1578 - 1585.

Didham RK, Hammond PM, Lawton JH, Eggleton P, Stork NE (1998) Beetle species responses to tropical forest fragmentation. Ecological Monographs 68: 295 -323.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene. Science 345: 401-406.

Dobrowski SZ (2011) A climatic basis for microrefugia: the influence of terrain on climate. Global Change Biology 17: 1022-1035.

Doherty TS, Balouch S, Bell K, Burns TJ, Feldman A, Fist C, Garvey TF, Jessop TS, Meiri S, Driscoll DA (2020) Reptile responses to anthropogenic habitat modification: A global meta-analysis. Global Ecology and Biogeography 29: 1265-1279.

Doherty TS, Fist CN, Driscoll DA (2019) Animal movement varies with resource availability, landscape configuration and body size: a conceptual model and empirical example. Landscape Ecology 34: 603 - 614.

Donald PF, Greenwood JJD (2001) Spatial patterns of range contraction in British breeding birds. Ibis 143: 593-601.

Donihue CM, Brock KM, Foufopoulos J, Herrel A (2016) Feed or fight: testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard. Functional Ecology 30: 566-575.

Dormann CF, Schweiger O, Augenstein I, Bailey D, Billeter R, De Blust G, DeFilippi R, Frenzel M, Hendrickx F, Herzog F, Klotz S, Liira J, Maelfait J-P, Schmidt T, Speelmans M, Van Wingerden WKRE, Zobel M (2007) Effects of landscape structure and land-use intensity on similarity of plant and animal communities. Global Ecology and Biogeography 16: 774-787.

Dray S, Dufour A-B, Thioulouse J (2015) ade4: Analysis of Ecological Data : Exploratory and Euclidean Methods in Environmental Sciences. https://cran.r-project.org/web/packages/ade4/index.html, pp.

Dubois Y, Blouin-Demers G, Shipley B, Thomas D (2009) Thermoregulation and habitat selection in wood turtles *Glyptemys insculpta*: chasing the sun slowly. Journal of Animal Ecology 78: 1023-1032.

Dudek K, Skórka P, Sajkowska ZA, Ekner-Grzyb A, Dudek M, Tryjanowski P (2016) Distribution pattern and number of ticks on lizards. Ticks and Tick-borne Diseases 7: 172-179.

Duggan JM, Schooley RL, Heske EJ (2011) Modeling occupancy dynamics of a rare species, Franklin's ground squirrel, with limited data: are simple connectivity metrics adequate? Landscape Ecology 26: 1477-1490.

Elbing K (2001) Die Smaragdeidechsen: Zwei (Un)gleiche Schwestern. Laurenti-Verlag, Bochum, 143 pp.

Ellis EC, Klein Goldewijk K, Siebert S, Lightman D, Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19: 589-606.

Ellis RD, McWhorter TJ, Maron M (2012) Integrating landscape ecology and conservation physiology. Landscape Ecology 27: 1-12.

EVI Exelis Visual Information Solutions (2012) ENVI version 5.0. Boulder, Colorado.

ESRI (2015) ArcGIS Desktop: Release 10.3.1. Redlands, CA: Environmental Systems Research Institute., pp.

ESRI (2018) ArcGIS Desktop: Release 10.6. Redlands, CA: Environmental Systems Research Institute., pp.

Evans BS, Kilpatrick AM, Hurlbert AH, Marra PP (2017) Dispersal in the Urban Matrix: Assessing the Influence of Landscape Permeability on the Settlement Patterns of Breeding Songbirds. Frontiers in Ecology and Evolution 5: e00063

Ewers RM, Banks-Leite C (2013) Fragmentation Impairs the Microclimate Buffering Effect of Tropical Forests. PLoS ONE 8: e58093.

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81: 117-142.

Eyck H, Buchanan K, Crino O, Jessop T (2019) Effects of developmental stress on animal phenotype and performance: a quantitative review. Biological Reviews 94: 0-000.

Fahrig L (2001) How much habitat is enough? Biological Conservation 100: 65-74.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487-515.

Fahrig L (2007) Non-optimal animal movement in human-altered landscapes. Functional Ecology 21: 1003-1015.

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40: 1649-1663.

Fenner AL, Bull CM (2008) The impact of nematode parasites on the behaviour of an Australian lizard, the gidgee skink Egernia stokesii. Ecological Research 23: 897-903.

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38-49.

Fischer D, Rehak I (2010) The ecology, ethology and variability of the european green lizard *Lacerta viridis*, from a local population along the river Vltava in Central Bohemia. Gazella 37: 50-167.

Fischer J, Lindenmayer D, Cowling A (2004) The challenge of managing multiple species at multiple scales: Reptiles in an Australian grazing landscape. Journal of Applied Ecology 41: 32-44.

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: A synthesis. Global Ecology and Biogeography 16: 265-280.

Fiske I, Chandler R (2011) Unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. . Journal of Statistical Software 43: 1 - 23.

Fitzgerald LA, Walkup D, Chyn K, Buchholtz E, Angeli N, Parker M (2018) The Future for Reptiles: Advances and Challenges in the Anthropocene. In: Dellasala DA, Goldstein MI (Eds) Encyclopedia of the Anthropocene. Elsevier, Oxford, 163-174.

Fletcher JRJ, Ries L, Battin J, Chalfoun AD (2007) The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? Canadian Journal of Zoology 85: 1017-1030.

Florentino B, Ji X (2000) Influence of incubation temperature on morphology, locomotor performance, and early growth of hatchling Wall Lizards (*Podarcis muralis*). Journal of Experimental Zoology 286: 422-433.

Forman RTT (1995) Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, pp.

Foufopoulos J, Kilpatrick AM, Ives Anthony R (2011) Climate Change and Elevated Extinction Rates of Reptiles from Mediterranean Islands. Am Nat 177: 119-129.

Fourcade Y, Ranius T, Öckniger E (2017) Temperature drives abundance fluctuations, but spatial dynamics is constrained by landscape configuration: Implications for climate-driven range shift in a butterfly. J Anim Ecol 86: 1339 - 1351.

Frankham R (2009) Effective population size/adult population size ratios in wildlife: a review. Genetical Research 66: 95-107.

Fras J, Leon V, Busch M (2014) Role of Landscape Scale in the Distribution of Rodents in an Agroecosystem of Argentina. Journal of Agricultural Science 6 (12): 22- 35.

Freeman EA, Moisen G (2008) PresenceAbsence: An R Package for Presence-Absence Model Analysis. Journal of Statistical Software 23: 1 - 31.

Frishkoff L, Hadly E, Daily G (2015) Thermal niche predicts tolerance to habitat conversion in tropical amphibians and reptiles. Global Change Biology 21(11): 3901 - 3916.

Frör E (1986) Erhebung zur Situation der Reptilienbestände im Bereich der Donauhänge zwischen Passau und Jochenstein. Schriftenreihe Bayer Landesamt für Umweltschutz 73: 135 - 158.

Fynn IEM, Campbell J (2019) Forest fragmentation analysis from multiple imaging formats. Journal of Landscape Ecology 12: 1 - 15.

Gadsden H, Ballesteros-Barrera C, Garza O, Castaneda G, Garcia-De La Peña C, Lemos-Espinal J (2012) Effects of land-cover transformation and climate change on the distribution of two endemic lizards, *Crotaphytus antiquus* and *Sceloporus cyanostictus*, of northern Mexico. Journal of Arid Environments 83: 1–9. .

Gallego-Carmona C, Bernal M (2016) Effect of habitat disturbance on the body condition index of the colombian endemic lizard *Anolis antonii* (Squamata: Dactyloidae). South American Journal of Herpetology 11: 183 - 187.

Gangestad, Thornhill (1999) Individual differences in developmental precision and fluctuating asymmetry: A model and its implications. J Evol Biol 12: 402-416.

García-Ramos G, Kirkpatrick M (1997) Genetic Models of Adaptation and Gene Flow in Peripheral Populations. Evolution 51: 21-28.

Gardiner R, Bain G, Hamer R, Jones ME, Johnson CN (2018) Habitat amount and quality, not patch size, determine persistence of a woodland-dependent mammal in an agricultural landscape. Landscape Ecology 33: 1837-1849.

Garmendia A, Arroyo-Rodríguez V, Estrada A, Naranjo E, Stoner K (2013) Landscape and patch attributes impacting medium- and large-sized terrestrial mammals in a fragmented rain forest. Journal of Tropical Ecology 29: 331 - 344.

Garrido M, Pérez-Mellado V (2013) Patterns of parasitism in insular lizards: effects of body size, condition and resource availability. Zoology 116: 106-112.

Gaston K, Fuller R (2008) Commonness, population depletion and conservation biology. Trends Ecol Evol 23: 14-19.

Gaston KJ (2009) Geographic range limits of species. Proceedings of the Royal Society B: Biological Sciences 276: 1391 - 1393.

Gibbons J, Scott D, Ryan T, Buhlmann K, Tuberville T, Metts B, Greene J, Mills T, Leiden Y, Poppy S, Winne C (2000) The Global Decline of Reptiles, Déjà Vu Amphibians. BioScience 50: 653-666.

Gilbert L, Maffey G, Ramsay S, Hester A (2012) The effect of deer Management on the abundance of *Ixodes ricinus* in Scotland. Ecological applications : a publication of the Ecological Society of America 22: 658-667.

Gillespie TR, Chapman CA, Greiner EC (2005) Effects of logging on gastrointestinal parasite infections and infection risk in African primates. Journal of Applied Ecology 42: 699-707.

Gillies CS, St. Clair CC (2008) Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. Proceedings of the National Academy of Sciences 105(50): 19774 - 19779.

Gomez MD, Goijman AP, Coda J, Serafini V, Priotto J (2018) Small mammal responses to farming practices in central Argentinian agroecosystems: The use of hierarchical occupancy models. Austral Ecology 43: 828-838.

Gonçalves-Souza D, Verburg PH, Dobrovolski R (2020) Habitat loss, extinction predictability and conservation efforts in the terrestrial ecoregions. Biological Conservation 246: 108579.

Grigg JW, Buckley LB (2013) Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography. Biology Letters 9: 20121056.

Grimm-Seyfarth A, Mihoub J-B, Henle K (2017) Too hot to die? The effects of vegetation shading on past, present, and future activity budgets of two diurnal skinks from arid Australia. Ecol Evol 7: 6803-6813.

Grimm A, Prieto Ramírez AM, Moulherat S, Reynaud J, Henle K (2014) Life-history trait database of European reptile species. Nature Conservation 9: 45-67.

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol 24: 699-711.

Gu W, Verboom J (2003) Patch-Occupancy Models for Estimating the Risk of Extinction Induced by Habitat Destruction. In: Swihard, R and Moore, J. (Eds) Conserving biodiversity in agricultural landscapes: Model-based planing tools. Purdue University Press.

Guo Q, Taper M, Schoenberger M, Brandle J (2005) Spatial-temporal population dynamics across species range: From centre to margin. Oikos 108: 47 - 57.

Gwiazdowicz DJ, Gdula AK, Kurczewski R, Zawieja B (2020) Factors influencing the level of infestation of Ixodes ricinus (Acari: Ixodidae) on *Lacerta agilis* and *Zootoca vivipara* (Squamata: Lacertidae). Acarologia 60: 390 - 397.

Haila Y (2002) A Conceptual Genealogy of Fragmentation Research: From Island Biogeography to Landscape Ecology. Ecological Applications 12: 321-334.

Hall LS, Krausman PR, Morrison ML (1997) The Habitat Concept and a Plea for Standard Terminology. Wildlife Society Bulletin (1973-2006) 25: 173-182.

Hamer AJ (2016) Accessible habitat delineated by a highway predicts landscape-scale effects of habitat loss in an amphibian community. Landscape Ecology 31: 2259-2274.

Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8: 461-467.

Hanski I (1998) Metapopulation dynamics. Nature 396: 41-49.

Hanski I, Ovaskainen O (2000) The metapopulation capacity of a fragmented landscape. Nature 404: 755 - 758.

Hare KM, Daugherty CH, Cree A (2002) Incubation regime affects juvenile morphology and hatching success, but not sex, of the oviparous lizard *Oligosoma suteri* (Lacertilia: Scincidae). New Zealand Journal of Zoology 29: 221-229.

Hatfield J, Barlow J, Joly C, Lees A, Parruco C, Tobias J, Orme D, Banks-Leite C (2020) Mediation of area and edge effects by adjacent land use. Conservation Biology 34: 395 - 404.

Hatfield JH, Orme CDL, Tobias JA, Banks-Leite C (2018) Trait-based indicators of bird species sensitivity to habitat loss are effective within but not across data sets. Ecological Applications 28: 28-34.

Helle S, Huhta E, Suorsa P, Hakkarainen H (2011) Fluctuating asymmetry as a biomarker of habitat fragmentation in an area-sensitive passerine, the Eurasian treecreeper (*Certhia familiaris*). Ecological Indicators 11: 861-867.

Heltai B, Sály P, Kovács D, Kiss I (2015) Niche segregation of sand lizard (*Lacerta agilis*) and green lizard (*Lacerta viridis*) in an urban semi-natural habitat. Amphibia-Reptilia 36: 389-399.

Helzer CJ, Jelinski DE (1999) The realtive importance of patch area and perimeter-area ratio to grassland breeding birds. Ecological Applications 9: 1448-1458.

Henle K, Andres C, Bernhard D, Grimm A, Stoev P, Tzankov N, Schlegel M (2016) Are species genetically more sensitive to habitat fragmentation on the periphery of their range compared to the core? A case study on the sand lizard (*Lacerta agilis*). Landscape Ecology 32: 131-145.

Henle K, Davies KF, Kleyer M, Margules C, Settele J (2004a) Predictors of Species Sensitivity to Fragmentation. Biodiversity & Conservation 13: 207-251.

Henle K, Dick D, Harpke A, Kühn I, Schweiger O, Settele J (2010) Climate change impacts on European amphibians and reptiles. . In: Europe Co (Ed) Biodiversity and Climate Change: Reports and Guidance Developed under the Bern Convention. 225 - 306.

Henle K, Sarre S, Wiegand K (2004b) The Role of Density Regulation in Extinction Processes and Population Viability Analysis. Biodiversity and Conservation 13: 9-52.

Hirzel AH, Le Lay G (2008) Habitat suitability modelling and niche theory. Journal of Applied Ecology 45: 1372-1381.

Hitchings SP, Beebee TJC (1998) Loss of genetic diversity and fitness in Common Toad (*Bufo bufo*) populations isolated by inimical habitat. J Evol Biol 11: 269-283.

Hoehn M, Sarre SD, Henle K (2007) The tales of two geckos: does dispersal prevent extinction in recently fragmented populations? Molecular Ecology 16: 3299-3312.

Hof C, Levinsky I, Araújo MB, Rahbek C (2011) Rethinking species' ability to cope with rapid climate change. Global Change Biology 17: 2987 - 2990.

Hofmeester T, Sprong H, Jansen P, Prins H, van wieren S (2017) Deer presence rather than abundance determines the population density of the sheep tick, *Ixodes ricinus*, in Dutch forests. Parasites & Vectors 10: 433 - 441.

Hokit G, Branch L (2003) Habitat patch size affects demographics of the Florida Scrub Lizard (*Sceloporus woodi*). Journal of Herpetology 37: 257-265.

Holland GJ, Bennett AF (2010) Habitat fragmentation disrupts the demography of a widespread native mammal. Ecography 33: 841-853.

Holt RD, Barfield M (2009) Trophic interactions and range limits: the diverse roles of predation. Proc Biol Sci 276: 1435-1442.

Holzhauer SIJ, Ekschmitt K, Sander A-C, Dauber J, Wolters V (2006) Effect of historic landscape change on the genetic structure of the bush-cricket *Metrioptera roeseli*. Landscape Ecology 21: 891-899.

House SM, Spellerberg IF (1983) Comparison of *Lacerta agilis* habitats in Britain and Europe. Journal of Herpetology 6: 305 -308.

Huang SP, Porter WP, Tu MC, Chiou CR (2014) Forest cover reduces thermally suitable habitats and affects responses to a warmer climate predicted in a high-elevation lizard. Oecologia 175: 25-35.

Huey RB (1982) Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough HF (Eds) Biology of the Reptilia. Academic Press, London, 25-91.

Huey RB, Hertz PE, Sinervo B (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. Am Nat 161: 357-366.

Hutchinson GE (1957) Concluding remarks. Cold Spring Harbour Symposiumon Quantitative Biology 22: 415–427.

Huyghe K, Van Oystaeyen A, Pasmans F, Tadić Z, Vanhooydonck B, Van Damme R (2010) Seasonal changes in parasite load and a cellular immune response in a colour polymorphic lizard. Oecologia 163: 867-874.

IPR (2010) Plán využití ploch - funkční plochy (územní plán). http://www.geoportalpraha.cz/cs/opendata/21733E1F-21B7-4ABC-B1C2-DC19C0237380.

IUCN (2009) *Lacerta viridis*. The IUCN red list of threatened species. e.T61530A12507156. http://dx.doi.org/10.2305.

IUCN (2020) The IUCN red list of threatened species.

Jackson HB, Fahrig L (2012) What size is a biologically relevant landscape? Landscape Ecology 27: 929-941.

Janin A, Léna J-P, Joly P (2011) Beyond occurrence : Body condition and stress hormone as integrative indicators of habitat availability and fragmentation in the common toad. Biological Conservation 144: 1008-1016.

Janssen I, Zuiderwijk A (2006) Detection probability derived from the national reptile monitoring program in the Netherlands. Monitoring Network of Reptile, Amphibian & Fish Conservation the Netherlands, RAVON. http://eumon.ckff.si/files/porto/3_janssen.pdf, pp.

Jauker B, Krauss J, Jauker F, Steffan-Dewenter I (2013) Linking life history traits to pollinator loss in fragmented calcareous grasslands. Landscape Ecology 28: 107-120.

Joger U, Fritz U, Guicking D, Kalyabina-Hauf S, Nagy ZT, Wink M (2010) Relict populations and endemic clades in palearctic reptiles: Evolutionary history and implications for conservation. In: Habel JC, Assmann T (Eds) Relict Species. Springer Berlin Heidelberg, Berlin, Heidelberg, 119-143 pp.

Kambourova-Ivanova N, Koshev YS, Popgeorgiev G, Rgyov D, Pavlova M, Mollov IA, Nedyalkov N (2012) Effect of Traffic on Mortality of Amphibians, Reptiles, Birds and Mammals on Two Types of Roads Between Pazardzhik and Plovdiv Region (Bulgaria) – Preliminary Results. Acta Zoologica Bulgarica 64: 57 - 67.

Kapos V, Wandelli EV, Camargo JL, Granade GMS (1997) Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. In: Press UoC (Ed) Tropical Forest Remnants: Ecology, Management , and Conservation of Fragmented Communities. Chicago, Ill., USA.

Karell P, Ahola K, Karstinen T, Valkama J, Brommer J (2011) Climate change drives microevolution in a wild bird. Nature communications 2: 208.

Kawecki TJ (2008) Adaptation to Marginal Habitats. Annual Review of Ecology, Evolution, and Systematics 39: 321-342.

Kearney M (2013) Activity restriction and the mechanistic basis for extinctions under climate warming. Ecology Letters 16: 1470-1479.

Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proceedings of the National Academy of Sciences 106(10): 3835-3840.

Keehn JE, Shoemaker KT, Feldman CR (2019) Population-level effects of wind farms on a desert lizard. The Journal of Wildlife Management 83: 145-157.

Keinath DA, Doak DF, Hodges KE, Prugh LR, Fagan W, Sekercioglu CH, Buchart SHM, Kauffman M (2017) A global analysis of traits predicting species sensitivity to habitat fragmentation. Global Ecology and Biogeography 26: 115-127.

Kellner K, Duchamp J, Swihart R (2019) Niche breadth and vertebrate sensitivity to habitat modification: signals from multiple taxa across replicated landscapes. Biodiversity and Conservation 28: 2647-2667.

Kennedy CM, Lonsdorf E, Neel MC, Williams NM, Ricketts TH, Winfree R, Bommarco R, Brittain C, Burley AL, Cariveau D, Carvalheiro LG, Chacoff NP, Cunningham SA, Danforth BN, Dudenhöffer J-H, Elle E, Gaines HR, Garibaldi LA, Gratton C, Holzschuh A, Isaacs R, Javorek SK, Jha S, Klein AM, Krewenka K, Mandelik Y, Mayfield MM, Morandin L, Neame LA, Otieno M, Park M, Potts SG, Rundlöf M, Saez A, Steffan-Dewenter I, Taki H, Viana BF, Westphal C, Wilson JK, Greenleaf SS, Kremen C (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecology Letters 16: 584-599.

Kingsolver JG, Diamond SE, Buckley LB (2013) Heat stress and the fitness consequences of climate change for terrestrial ectotherms. Functional Ecology 27: 1415-1423.

Kirkpatrick M, Barton NH (1997) Evolution of a species' range. Am Nat 150: 1-23.

Koh LP, Sodhi NS, Brook BW (2004) Ecological Correlates of Extinction Proneness in Tropical Butterflies. Conservation Biology 18: 1571-1578.

Komonen A, Grapputo A, Kaitala V, Kotiaho JS, Päivinen J (2004) The role of niche breadth, resource availability and range position on the life history of butterflies. Oikos 105: 41-54.

Komsta L, Novomestky F (2015) moments: Moments, cumulants, skewness, kurtosis and related tests.

https://cran.r- project.org/web/packages/moments/index.html, pp.

Korsós Z (1982) Field observations of two lizard populations (*Lacerta viridis* Laur. and *Lacerta agilis* L.). Vertebrata Hungarica 21: 185-194.

Korsós Z (1983) Comparative niche analysis of two sympatric lizard species (*Lacerta viridis* and *Lacerta agilis*). Vertebrata Hungarica 22: 5-14.

Krasnov BR, Stanko M, Morand S (2007) Host community structure and infestation by Ixodid ticks: repeatability, dilution effect and ecological specialization. Oecologia 154: 185-194.

Krauss J, Steffan-Dewenter I, Tscharntke T (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? Journal of Biogeography 30: 889-900.

Krauss J, Steffan-Dewenter I, Tscharntke T (2004) Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. Oecologia 137: 591-602.

Kühnelt W (1965) Grundriß der Ökologie mit besonderer Berücksichtigung der Tierwelt. Fischer Verlag, Jena, pp.

Kusack JW, Mitchell GW, Evans DR, Cadman MD, Hobson KA (2020) Effects of agricultural intensification on nestling condition and number of young fledged of barn swallows (*Hirundo rustica*). Science of The Total Environment 709: 136195.

Lancaster LT, Dudaniec RY, Hansson B, Svensson EI (2015) Latitudinal shift in thermal niche breadth results from thermal release during a climate-mediated range expansion. Journal of Biogeography 42: 1953-1963.

Lappalainen J, Soininen J (2006) Latitudinal gradients in niche breadth and position—regional patterns in freshwater fish. Naturwissenschaften 93: 246-250.

Larson D (2014) Grassland Fire and Cattle Grazing Regulate Reptile and Amphibian Assembly Among Patches. Environmental management 54: 1434 - 1444.

Laube M, Leppelsack HJ (2007) Individuenspezifisches Raumnutzungs- und Interaktionsverhalten der Östlichen Smaragdeidechse (*Lacerta viridis*) in den Passauer Donauleiten. Zeitschrift für Feldherpetologie 14: 51—62.

Laurance W (2004) Forest-climate interactions in fragmented tropical landscapes. Philosophical transactions of the Royal Society of London Series B, Biological sciences 359: 345-352.

Laurance W (2008) Theory meets reality: How habitat fragmentation research has trascended island biogeography theory. Biological Conservation 141(7): 1731-1744.

Laurance WF, Ferreira LV, Rankin-de Merona JM, Laurance SG (1998) Rain forest fragmentation and the dynamics of amazonian tree communities. Ecology 79: 2032-2040.

Lawrence A, O'Connor K, Haroutounian V, Swei A (2018) Patterns of diversity along a habitat size gradient in a biodiversity hotspot. Ecosphere 9: e02183.

Lawson CL, Bennie J, Hodgson JA, Thomas CD, Wilson RJ (2014) Topographic microclimates drive microhabitat associations at the range margin of a butterfly. Ecography 37: 732 - 740.

Lazić MM, Kaliontzopoulou A, Carretero MA, Crnobrnja-Isailović J (2013) Lizards from urban areas are more asymmetric: Using fluctuating asymmetry to evaluate environmental disturbance. PLoS ONE 8: e84190.

Le Galliard JF, Massot M, Baron J-P, Clobert J (2012) Ecological effects of climate change on European reptiles. In: Brodie JF, Post E, Doak DF (Eds) Wildlife conservation in a changing climate. University of Chicago Press, Chicago, IL., 179-203.

Leamy L, Klingenberg C (2005) The genetics and Evolution of fluctuating asymmetry. Annu Rev Ecol Evol Syst 14: 1-21.

Leary RF, Allendorf FW (1989) Fluctuating asymmetry as an indicator of stress: Implications for conservation biology. Trends Ecol Evol 4: 214-217.

Lecocq T, Harpke A, Ramont P, Schweiger O (2019) Integrating intraspecific differentiation in species distribution models: Consequences on projections of current and future climatically suitable areas of species. Diversity and Distributions 25: 1088 - 1100.

Lecomte J, Clobert J, Massot M, Barbault R (1994) Spatial and behavioural consequences of a density manipulation in the common lizard (*Lacerta vivipara*). Écoscience 1: 300-310.

Ledger KJ, Keenan RM, Sayler KA, Wisely SM (2019) Multi-scale patterns of tick occupancy and abundance across an agricultural landscape in southern Africa. PLoS ONE 14: e0222879.

Lens L, Eggermont H (2008) Fluctuating asymmetry as a putative marker of human-induced stress in avian conservation. Bird Conservation International 18: 125 - 143.

Lesica P, Allendorf FW (1995) When Are Peripheral Populations Valuable for Conservation? Conservation Biology 9: 753-760.

Leung B, Forbes M (1996) Fluctuating asymmetry in relation to stress and fitness: Effects of trait type as revealed by meta-analysis. Écoscience 3: 400-413.

Ljubisavljević K, Tome S, Dzukic G, Kalezic M (2005) Morphological differentiation of an isolated population of the Italian wall lizard (*Podarcis sicula*) of the southeastern Adriatic coast. Biologia - Section Zoology 60: 189-195.

López P, Martín J (2002) Locomotor capacity and dominance in male lizards *Lacerta monticola* : a trade-off between survival and reproductive success? Biological Journal of the Linnean Society 77: 201-209.

Lozano-Jaramillo M, Rico-Guevara A, Cadena CD (2014) Genetic Differentiation, Niche Divergence, and the Origin and Maintenance of the Disjunct Distribution in the Blossomcrown *Anthocephala floriceps* (Trochilidae). PLoS ONE 9: e108345.

Lucas PM, González-Suárez M, Revilla E (2016) Toward multifactorial null models of range contraction in terrestrial vertebrates. Ecography 39: 1100-1108.

MacArthur RH, MacArthur JW (1961) On Bird Species Diversity. Ecology 42: 594-598.

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton, New Jersey: Princeton University Press, pp.

MacKenzie DI, Bailey LL (2004) Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9: 300-318.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Andrew Royle J, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology 83: 2248-2255.

Mackenzie DI, Royle JA (2005) Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42: 1105-1114.

Mangiacotti M, Scali S, Sacchi R, Bassu L, Nulchis V, Corti C (2013) Assessing the Spatial Scale Effect of Anthropogenic Factors on Species Distribution. PLoS ONE 8: e67573.

Mantyka-Pringle C, Martin T, Rhodes J (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Global Change Biology 18: 1239-1252.

Manzer DL, Hannon SJ (2005) Relating grouse nest success and corvid density to habitat: A multi-scale approach. The Journal of Wildlife Management 69: 110-123.

Marchand H, Paillat G, Montuire S, Butet A (2003) Fluctuating asymmetry in bank vole populations (Rodentia, Arvicolinae) reflects stress caused by landscape fragmentation in the Mont-Saint-Michel Bay. Biological Journal of the Linnean Society 80: 37-44.

Maron M, Goulding W, Ellis R, Mohd-Taib FS (2012) Distribution and individual condition reveal a hierarchy of habitat suitability for an area-sensitive passerine. Biodiversity and Conservation 21: 2509 - 2523.

Märtens B, Henle K, Kuhn W, Krug R, Jost K, Grosse WR, Wissel C (1996) Survival of the Sand Lizard (*Lacerta Agilis* Linnaeus, 1758) (Sauria, Lacertidae) in Relation to Habitat Quality and Heterogeneity. In: Settele J, Margules C, Poschlod P, Henle K (Eds) Species Survival in Fragmented Landscapes. Springer Netherlands, Dordrecht, 241-247.

Martensen AC, Ribeiro MC, Banks-Leite C, Prado PI, Metzger JP (2012) Associations of forest cover, fragment area, and connectivity with neotropical understory bird species richness and abundance. Conservation Biology 26: 1100-1111.

Martin AE, Fahrig L (2012) Measuring and selecting scales of effect for landscape predictors in species–habitat models. Ecological Applications 22: 2277-2292.

Martin J, Lopez P (2000) Chemoreception, symmetry and mate choice in lizards. Proceedings: Biological Sciences 267: 1265-1269.

Martin J, Lopez P (2001) Hindlimb asymmetry reduces escape performance in the lizard *Psammodromus algirus*. Physiological and biochemical zoology : PBZ 74: 619-624.

Martin JM, Heske EJ (2005) Juvenile Dispersal of Franklin's Ground Squirrel (*Spermophilus franklinii*) from a Prairie "Island". The American Midland Naturalist 153: 444-449.

Marzahn E, Mayer W, Joger U, Ilgaz Ç, Jablonski D, Kindler C, Kumlutaş Y, Nistri A, Schneeweiss N, Vamberger M, Žagar A, Fritz U (2016) Phylogeography of the *Lacerta viridis* complex: Mitochondrial and nuclear markers provide taxonomic insights. Journal of Zoological Systematics and Evolutionary Research 54: 85-105.

Massot M, Baron JP, Clobert J, Le Galliard JF (2012) Ecological effects of climate change on european reptiles. In: Post E, Doak D, Brodie J (Eds) Wildlife conservation in a changing climate. University of Chicago Press.

Maxwell S, Fuller R, Brooks T, Watson J (2016) Biodiversity: The ravages of guns, nets and bulldozers. Nature 536: 143-145.

Mazerolle MJ (2019) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.2-1. https://cran.r-project.org/package=AICcmodavg.

McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. University of Massachusetts, Amherst.

Meek R (1995) Reptiles, thermoregulation and the environment. Testudo 4(2): 56-78.

Melles SJ, Fortin M-J, Lindsay K, Badzinski D (2011) Expanding northward: influence of climate change, forest connectivity, and population processes on a threatened species' range shift. Global Change Biology 17: 17-31.

Melo GL, Sponchiado J, Cáceres NC, Fahrig L (2017) Testing the habitat amount hypothesis for South American small mammals. Biological Conservation 209: 304-314.

Mendoza H, Rubio A, García-Peña G, Suzan G, Simonetti J (2019) Does land-use change increase the abundance of zoonotic reservoirs? Rodents say yes. European Journal of Wildlife Research 66: 6.

Michael DR, Kay GM, Crane M, Florance D, MacGregor C, Okada S, McBurney L, Blair D, Lindenmayer DB (2015) Ecological niche breadth and microhabitat guild structure in temperate Australian reptiles: Implications for natural resource management in endangered grassy woodland ecosystems. Austral Ecology 40: 651-660.

Michaelides G, Kati V (2009) Diversity patterns and conservation management of the lizard community in a Mediterranean reserve (Cyprus). J Biol Res- Thessalon 12: 211-220.

Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L (2016) What determines the spatial extent of landscape effects on species? Landscape Ecology 31: 1177-1194.

Miller RGJ (1981) Simultaneous statistical inference. McGraw Hill, New York, pp.

Mingo V, Lötters S, Wagner N (2017) The impact of land use intensity and associated pesticide applications on fitness and enzymatic activity in reptiles—A field study. Science of The Total Environment 590-591: 114-124.

Mirc M, Tomasevic Kolarov N, Stamenkovic S, Vukov T (2019) Asymmetry in the common wall lizard *Podarcis muralis* under different levels of urbanization: The effect of trait and FA index selection. Archives of Biological Sciences 71: 33-33.

Miroslav B, Brejšková L, Cuhrová T, Dostál P, Havrda T, Just T, Kafka T, Karel J, Mackovič V, Mach S, Píša V, Řezníček J, Říha M, Šimčíková A, Tvrdý J, Vaculová K, Zelenková K, Ziegler V (2008) Prognóza, koncepce a strategie ochrany přírody a krajiny v Praze. Report for the Department of Development of the Capital City of Prague. Atelier pro urbanismus a územní plánování Zastoupený, Prague., pp.

Mitrovich M, Diffendorfer J, Fisher R (2009) Behavioral Response of the Coachwhip (Masticophis flagellum) to Habitat Fragment Size and Isolation in an Urban Landscape. Journal of Herpetology 43: 646-656.

Mizsei E, Szabolcs M, Szabó L, Boros Z, Mersini K, Roussos SA, Dimaki M, Ioannidis Y, Végvári Z, Lengyel S (2020) Determining priority areas for an Endangered cold-adapted snake on warming mountaintops. Oryx: 1-10.

Møller AP (1995) Developmental stability and ideal despotic distribution of blackbirds in a patchy environment. Oikos 72: 228-234.

Mollov IA (2011) Habitat distribution of the amphibians and reptiles in the city of Plovdiv, Bulgaria. Biharean Biologist 5: 25-31.

Mollov IA, Georgiev DG (2015) Plovdiv. In: Kelcey JG (Ed) Vertebrates and invertabrates of european cities: selected non-avian fauna. Sringer-Verlag, New York.

Mollov IA, Velcheva IG (2010) Spatial Distribution and a Retrospective Analysis of the Herpetofauna in the City of Plovdiv, Bulgaria. Ecología Balkanica 2: 25-38.

Mollov IA, Velcheva IG (2015) Ecological classification of the amphibian and reptilian fauna in the city of Plovdiv. J BioSci Biotechnol: 259-264.

Moore JE, Swihart RK (2005) Modeling patch occupancy by forest rodents: Incorporating detectability and spatial autocorrelation with hierarchically structured data. The Journal of Wildlife Management 69: 933-949.

Morales NS, Fernández IC, Carrasco B, Orchard C (2015) Combining niche modelling, land-use change, and genetic information to assess the conservation status of *Pouteria splendens* populations in central Chile. International Journal of Ecology 2015: 612194.

Morris DW (1996) Coexistence of Specialist and Generalist Rodents Via Habitat Selection. Ecology 77: 22352-22364.

Moser J (1998) Beitrag zur Kenntnis der Verbreitung der Smaragdeidechse in Oberösterreich. Beitr Naturk Oberösterreichs 6: 391-392.

Mugabo M, Marquis O, Perret S, Le Galliard J-F (2011) Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard. Oecologia 166: 949-960.

Muñoz M, Langham G, Brandley M, Rosauer D, Williams S, Moritz C (2016) Basking behavior predicts the evolution of heat tolerance in Australian rainforest lizards. Evolution 70: 2537-2549.

Muñoz MM, Stimola MA, Algar AC, Conover A, Rodriguez AJ, Landestoy MA, Bakken GS, Losos JB (2014) Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. Proceedings of the Royal Society B: Biological Sciences 281: 20132433.

Münsch T, Helbing F, Fartmann T (2019) Habitat quality determines patch occupancy of two specialist Lepidoptera species in well-connected grasslands. Journal of Insect Conservation 23: 247-258.

Murcia C (1995) Edge effects in fragmented forests: Implications for conservation. Trends Ecol Evol 10: 58-62.

Murray MH, Sánchez CA, Becker DJ, Byers KA, Worsley-Tonks KE, Craft ME (2019) City sicker? A meta-analysis of wildlife health and urbanization. Frontiers in Ecology and the Environment 17: 575-583.

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4: 133-142.

Naujokaitis-Lewis IR, Curtis JMR, Tischendorf L, Badzinski D, Lindsay K, Fortin M-J (2013) Uncertainties in coupled species distribution–metapopulation dynamics models for risk assessments under climate change. Diversity and Distributions 19: 541-554.

Navarro-Castilla Á, Barja I, Olea PP, Piñeiro A, Mateo-Tomás P, Silván G, Illera JC (2014) Are degraded habitats from agricultural crops associated with elevated faecal glucocorticoids in a wild population of common vole (Microtus arvalis)? Mammalian Biology 79: 36-43.

Nemitz-Kliemchen M, Andres C, Hofmann S, Prieto-Ramírez AM, Stoev P, Tzankov N, Schaffer S, Bernhard D, Henle K, Schlegel M (2020) Spatial and genetic structure of a *Lacerta viridis* metapopulation in a fragmented landscape in Bulgaria. Global Ecology and Conservation 23: e01104.

Nettmann HK , Rykena S (1984) Lacerta viridis (Laurenti, 1768) - Smaragdeidechse. In: Böhme W (Ed) Handbuch der Reptilien und Amphibien Europas. Aula Verlag, Wiesbaden.

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, Börger L, Bennett DJ, Choimes A, Collen B, Day J, De Palma A, Díaz S, Echeverria-Londoño S, Edgar MJ, Feldman A, Garon M, Harrison MLK, Alhusseini T, Ingram DJ, Itescu Y, Kattge J, Kemp V, Kirkpatrick L, Kleyer M, Correia DLP, Martin CD, Meiri S, Novosolov M, Pan Y, Phillips HRP, Purves DW, Robinson A, Simpson J, Tuck SL, Weiher E, White HJ, Ewers RM, Mace GM, Scharlemann JPW, Purvis A (2015) Global effects of land use on local terrestrial biodiversity. Nature 520: 45-50.

Nezer O, Bar-David S, Gueta T, Carmel Y (2017) High-resolution species-distribution model based on systematic sampling and indirect observations. Biodiversity and Conservation 26: 421-437.

Nisa-Ramiro C, Rodríguez-Ruiz G, López P, da Silva Junior PI, Trefaut-Rodrigues M, Martín J (2019) Chemosensory discrimination of male age by female *Psammodromus algirus* lizards based on femoral secretions and feces. Ethology 125: 802-809.

Nojarov P (2017) Genetic climatic regionalization of the Balkan Peninsula using cluster analysis. Journal of Geographical Sciences 27: 43-61.

Novacek M, Cleland E (2001) The current biodiversity extinction event: Scenarios for mitigation and recovery. Proceedings of the National Academy of Sciences of the United States of America 98: 5466-5470.

Nowakowski A, Watling J, Thompson M, Brusch G, Catenazzi A, Whitfield S, Kurz D, Suárez-Mayorga A, Aponte A, Donnelly M, Todd B (2018) Thermal biology mediates responses of amphibians and reptiles to habitat modification. Ecology Letters 21: 345-355.

Oakleaf JR, Kennedy CM, Baruch-Mordo S, West PC, Gerber JS, Jarvis L, Kiesecker J (2015) A World at Risk: Aggregating Development Trends to Forecast Global Habitat Conversion. PLoS ONE 10: e0138334.

Öckinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, Kuussaari M, Petersen JD, Pöyry J, Settele J, Summerville KS, Bommarco R (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters 13: 969-979.

Oliver T, Hill J, Thomas C, Brereton T, Roy DB (2009) Changes in habitat specificity of species at their climatic range boundaries. Ecology Letters 12: 1091-1102.

Olsson M (1988) Ecology of a Swedish population of the sand lizard (*Lacerta agilis*)-preliminary report. Mertensiella 1: 86-91.

Olsson M, Wapstra E, Madsen T, Ujvari B, Rugfelt C (2005) Costly parasite resistance: a genotype-dependent handicap in sand lizards? Biology Letters 1: 375-377.

Opdam P (1991) Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. Landscape Ecology 5: 93-106.

Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation 117: 285-297.

Overgaard J, Kristensen TN, Mitchell KA, Hoffmann AA (2011) Thermal tolerance in widespread and tropical Drosophila species: does phenotypic plasticity increase with latitude? Am Nat 178(1): 80-96.

Pafilis P, Anastasiou I, Sagonas K, Valakos ED (2013) Grazing by goats on islands affects the populations of an endemic Mediterranean lizard. Journal of Zoology 290: 255-264.

Pafilis P, Maragou P (2013) One more record of *Lacerta viridis* (Laurenti, 1768) from Macedonia. Herpetozoa 26: 101-102.

Pafilis P, Meiri S, Foufopoulos J, Valakos E (2009) Intraspecific competition and high food availability are associated with insular gigantism in a lizard. Naturwissenschaften 96: 1107-1113.

Palmer AR, Strobeck C (1986) Fluctuating asymmetry: Measurement, Analysis, Patterns. Annual Review of Ecology and Systematics 17: 391-421.

Palmer G, Hill JK, Brereton TM, Brooks DR, Chapman JW, Fox R, Oliver TH, Thomas CD (2015) Individualistic sensitivities and exposure to climate change explain variation in species' distribution and abundance changes. Science Advances 1: e1400220.

Pardini R, Bueno AdA, Gardner TA, Prado PI, Metzger JP (2010) Beyond the fragmentation threshold hypothesis: Regime shifts in biodiversity across fragmented landscapes. PLoS ONE 5: e13666.

Pardini R, Nichols L, Püttker T (2017) Biodiversity Response to Habitat Loss and Fragmentation. In: Goldstein MI and DellaSala DA (Eds). Elsevier,. pp: 229-239.

Patterson JW, Davies PMC (1978) Preferred body temperature: Seasonal and sexual differences in the lizard Lacerta vivipara. Journal of Thermal Biology 3: 39-41.

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12: 361-371.

Pedhazur EJ, Schmelkin LP (1991) Meassurement, Design, and Analysis: An Integrated Approach. Lawrence Erlbaum Associates, Hillsdale, NJ., pp.

Peig J, Green AJ (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118: 1883-1891.

Peñalver-Alcázar M, Jiménez-Valverde A, Aragón P (2021) Niche differentiation between deeply divergent phylogenetic lineages of an endemic newt: Implications for Species Distribution Models. Zoology 144: 125852.

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for Global Biodiversity in the 21st Century. Science 330: 1496 - 1501.

Perneger TV (1998) What's wrong with Bonferroni adjustments. BMJ (Clinical research ed) 316: 1236-1238.

Pertoldi C, Kristensen TN, Andersen DH, Loeschcke V (2006) Developmental instability as an estimator of genetic stress. Heredity 96: 122-127.

Peterman WE, Feist SM, Semlitsch RD, Eggert LS (2013) Conservation and management of peripheral populations: Spatial and temporal influences on the genetic structure of wood frog (*Rana sylvatica*) populations. Biological Conservation 158: 351-358.

Petrov B (2007) Amphibians and Reptiles of Bulgaria: Fauna, Vertical Distribution, Zoogeography, and Conservation. In: Fet V, Popov A (Eds) Biogeography and ecology of Bulgaria. Springer, 85-107.

Pilia O (2011) Synergy between habitat fragmentation and climate change: Implications for biodiversity in Alpine ecosystems. Doctoral Thesis, Imperial College London: Imperial College London.

Popgeorgiev GS, Mollov IA (2005) A study of the effects of fires on the populations of the green lizard *Lacerta viridis* (Laurenti, 1768) in eastern Rhodopes. Animalia 41: 95-108.

Poulin J-F, Villard M-A, Edman M, Goulet PJ, Eriksson A-M (2008) Thresholds in nesting habitat requirements of an old forest specialist, the Brown Creeper (Certhia americana), as conservation targets. Biological Conservation 141: 1129-1137.

Powers RP, Jetz W (2019) Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. Nature Climate Change 9: 323-329.

Powney GD, Cham SS, Smallshire D, Isaac NJ (2015) Trait correlates of distribution trends in the Odonata of Britain and Ireland. PeerJ 3: e1410.

Prevedello J, Vieira M (2009) Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation 19: 1205-1223.

Price TD, Kirkpatrick M (2009) Evolutionarily stable range limits set by interspecific competition. Proceedings of the Royal Society B: Biological Sciences 276: 1429 - 1434.

Prieto-Ramirez AM, Pe'er G, Rödder D, Henle K (2018) Realized niche and microhabitat selection of the eastern green lizard (*Lacerta viridis*) at the core and periphery of its distribution range. Ecol Evol 8: 11322-11336.

Prieto-Ramirez AM, Röhler L, Cord AF, Pe'er G, Rödder D, Henle K (2020) Differential effects of habitat loss on occupancy patterns of the eastern green lizard *Lacerta viridis* at the core and periphery of its distribution range. PLoS ONE 15: e0229600.

Pulliam HR (2000) On the relationship between niche and distribution. Ecol Lett 3: 349-361.

Püttker T, Bueno AA, dos Santos de Barros C, Sommer S, Pardini R (2013) Habitat specialization interacts with habitat amount to determine dispersal success of rodents in fragmented landscapes. Journal of Mammalogy 94: 714-726.

Püttker T, Meyer-Lucht Y, Sommer S (2008) Effects of fragmentation on parasite burden (nematodes) of generalist and specialist small mammal species in secondary forest fragments of the coastal Atlantic Forest, Brazil. Ecological Research 23: 207-215.

Quesnelle PE, Lindsay KE, Fahrig L (2014) Low Reproductive Rate Predicts Species Sensitivity to Habitat Loss: A Meta-Analysis of Wetland Vertebrates. PLoS ONE 9: e90926.

Raharivololona B, Ganzhorn J (2009) Gastrointestinal parasite infection of the Gray mouse lemur (Microcebus murinus) in the littoral forest of Mandena, Madagascar: Effects of forest fragmentation and degradation. Madagascar Conservation & Development 4(2): 103 - 111.

Rehák I (2015) Protecting and managing a local population of the European Green lizard *Lacerta viridis* at the Prague Zoo, Czech Republic. Int. Zoo Yb 49: 56-66.

Remm J, Hanski IK, Tuominen S, Selonen V (2017) Multilevel landscape utilization of the Siberian flying squirrel: Scale effects on species habitat use. Ecol Evol 7: 8303-8315.

Renwick AR, Lambin X (2013) Host–parasite interactions in a fragmented landscape. International Journal for Parasitology 43: 27-35.

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43: 223 - 225.

Ries L, Robert J. Fletcher J, Battin J, Sisk TD (2004) Ecological responses to habitat edges: Mechanisms, models, and variability explained. Annual Review of Ecology, Evolution, and Systematics 35: 491-522.

Ripley B, Venables W (2016) nnet: Feed-Forward Neural Networks and Multinomial Log-Linear Models. https://cran.r-project.org/web/packages/nnet/index.html, pp.

Roll U, Feldman A, Novosolov M, Allison A, Bauer AM, Bernard R, Böhm M, Castro-Herrera F, Chirio L, Collen B, Colli GR, Dabool L, Das I, Doan TM, Grismer LL, Hoogmoed M, Itescu Y, Kraus F, LeBreton M, Lewin A, Martins M, Maza E, Meirte D, Nagy ZT, de C. Nogueira C, Pauwels OSG, Pincheira-Donoso D, Powney GD, Sindaco R, Tallowin OJS, Torres-Carvajal O, Trape J-F, Vidan E, Uetz P, Wagner P, Wang Y, Orme CDL, Grenyer R, Meiri S (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. Nature Ecology & Evolution 1: 1677-1682.

Ronce O, Clobert J, Massot M (1998) Natal dispersal and senescence. Proceedings of the National Academy of Sciences 95: 600-605.

Ryberg W, Fitzgerald L (2016) Landscape composition, not connectivity, determines metacommunity structure across multiple scales. Ecography 39: 932 - 941.

Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, Hanski I (1998) Inbreeding and extinction in a butterfly metapopulation. Nature 392: 491-494.

Sagonas K, Valkos ED, Lymberakis P, Pafilis P (2018) Traits of reproduction and feeding of the European Green Lizard, *Lacerta viridis* (Laurenti, 1768), at the southern edge of its distribution. Herpetozoa 30: 115-129.

Sahlean TC, Papeș M, Strugariu A, Gherghel I (2020) Ecological corridors for the amphibians and reptiles in the Natura 2000 sites of Romania. Scientific Reports 10: 19464.

Saint-Girons H, Bradshaw SD (1989) Sédentarité, déplacements et répartition des individus dans une population de *Lacerta viridis* (Laurenti, 1768) (Lacertilia, Lacertidae). Bijdragen tot de Dierkunde 59: 63 - 70.

Sala OE, Stuart Chapin F, Iii, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld Mn, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global Biodiversity Scenarios for the Year 2100. Science 287: 1770 - 1774.

Sánchez CA, Becker DJ, Teitelbaum CS, Barriga P, Brown LM, Majewska AA, Hall RJ, Altizer S (2018) On the relationship between body condition and parasite infection in wildlife: a review and meta-analysis. Ecology Letters 21: 1869-1884.

Santos NJ, Delabie JHC, Gonçalves-Saraiva D, Nieri-Bastos FA, Fernandes-Martins T, Bahia-Labruna M, Oliverira-Carneiro I, Franke CR (2018) Effect of forest cover on ectoparasites of small mammals in the Brazilian atlantic forest. Oecologia Australis 22: 279 -290.

Santos T, Díaz J, Pérez-Tris J, Carbonell R, Tellería J (2008) Habitat quality predicts the distribution of a lizard in fragmented woodlands better than habitat fragmentation. Animal Conservation 11: 46-56.

Sarre S (1996) Habitat fragmentation promotes fluctuating asymmetry but not morphological divergence in two geckos. Researches on Population Ecology 38: 57-64.

Sarre S, Smith GT, Meyers JA (1995) Persistence of two species of gecko (*Oedura reticulata* and *Gehyra variegata*) in remnant habitat. Biological Conservation 71: 25-33.

Sato C, Wood J, Schroder M, Michael D, Osborne W, Green K, Lindenmayer D (2014) Designing for conservation outcomes: The value of remnant habitat for reptiles on ski runs in subalpine landscapes. Landscape Ecology 29: 1225-1236.

Saunders D, Hobbs R, Margules C (1991) Biological Consequences of Ecosystem Fragmentation: A Review. Conservation Biology 5: 18-32.

Savvides P, Poliviou V, Stavrou M, Sfenthourakis S, Pafilis P (2019) Insights into how predator diversity, population density and habitat type may affect defensive behaviour in a Mediterranean lizard. Ethology Ecology & Evolution 31: 12-27.

Scheffers BR, Edwards DP, Diesmos A, Williams SE, Evans TA (2014) Microhabitats reduce animal's exposure to climate extremes. Global Change Biology 20: 495-503.

Schmidtler JF (1986) Orientalische Smaragdeidechsen: 1. Zur Systematik und Verbreitung von *Lacerta viridis* in der Türkei. Salamandra 22: 29 - 46.

Seebacher F, Franklin CE (2012) Determining environmental causes of biological effects: The need for a mechanistic physiological dimension in conservation biology. Philosophical Transactions of the Royal Society B: Biological Sciences 367: 1607-1614.

Segan DB, Murray KA, Watson JEM (2016) A global assessment of current and future biodiversity vulnerability to habitat loss–climate change interactions. Global Ecology and Conservation 5: 12-21.

Selya AS, Rose JS, Dierker LC, Hedeker D, Mermelstein RJ (2012) A Practical Guide to Calculating Cohen's f(2), a Measure of Local Effect Size, from PROC MIXED. Frontiers in psychology 3: 111-111.

Sewell D, Guillera-Arroita G, Griffiths RA, Beebee TJC (2012) When Is a Species Declining? Optimizing Survey Effort to Detect Population Changes in Reptiles. PLoS ONE 7: e43387.

Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. Annual Review of Ecology, Evolution, and Systematics 40: 415-436.

Shamiminoori L, Bull CM (2016) Can we use head scale symmetry in endangered pygmy bluetongue lizards (*Tiliqua adelaidensis*) to alert managers to population condition? 11: 188-198.

Shine R, Harlow PS (1996) Maternal Manipulation of Offspring Phenotypes via Nest-Site Selection in an Oviparous Lizard. Ecology 77: 1808-1817.

Simpson DT, Teague MS, Weeks JK, Kaup BZ, Kerscher O, Leu M (2019) Habitat amount, quality, and fragmentation associated with prevalence of the tick-borne pathogen *Ehrlichia chaffeensis* and occupancy dynamics of its vector, *Amblyomma americanum*. Landscape Ecology 34: 2435-2449.

Sinervo B, Méndez-de-la-Cruz F, Miles D, Heulin B, Bastiaans E, Cruz M, Lara Resendiz R, Martínez-Méndez N, Calderon-Espinosa M, Meza R, Gadsden H, Avila LJ, Morando M, De la Riva I, Victoriano P, Rocha C, Ibargüengoytía N, Puntriano C, Massot M, Sites JJ (2010) Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches. Science 328: 894-899.

Slatyer RA, Hirst M, Sexton JP (2013) Niche breadth predicts geographical range size: a general ecological pattern. Ecology Letters 16: 1104-1114.

Smyth AK, Smee E, Godfrey SS, Crowther M, Phalen D (2014) The use of body condition and haematology to detect widespread threatening processes in sleepy lizards (*Tiliqua rugosa*) in two agricultural environments. Royal Society Open Science 1: 140257.

Soberón J, Peterson A (2011) Ecological niche shifts and environmental space anisotropy: A cautionary note. Revista Mexicana de Biodiversidad 82: 1348-1353.

Soga M, Koike S (2013) Patch isolation only matters for specialist butterflies but patch area affects both specialist and generalist species. Journal of Forest Research 18: 270-278.

Soulé ME (1987) Viable populations for conservation. Cambridge University Press, Cambridge, pp.

Spear SF, Storfer A (2008) Landscape genetic structure of coastal tailed frogs (*Ascaphus truei*) in protected vs. managed forests. Molecular Ecology 17: 4642-4656.

Stellatelli O, Block C, Vega L, Cruz F (2015) Responses of two sympatric sand lizards to exotic forestations in the coastal dunes of Argentina: some implications for conservation. CSIRO Wildlife Research 41: 480-489.

Stow A, Sunnucks P, Briscoe DA, Gardner MG (2001) The impact of habitat fragmentation on dispersal of Cunningham's skink (*Egernia cunninghami*): evidence from allelic and genotypic analyses of microsatellites. Molecular Ecology 10 4: 867-878.

Strijbosch H (2001) Zur unterschiedlichen Habitatwahl von *Lacerta trilineata* und *Lacerta viridis* in Ostgriechenland. Mertensiella 13: 159 - 164.

Strödicke M (1995) Die Smaragdeidechse, *Lacerta viridis* (LAURENTI, 1768), in der Mitte und im Norden der Tschechischen Republik. Herpetozoa 8: 73 - 80.

Strugariu A (2009) The herpetofauna of the Jiului Gorge National Park, Romania. North-Western Journal of Zoology 5: S01 - S78.

Suggitt AJ, Gillingham PK, Hill JK, Huntley B, Kunin WE, Roy DB, Thomas CD (2011) Habitat microclimates drive fine-scale variation in extreme temperatures. Oikos 120: 1-8.

Sumner J, Moritz C, Shine R (1999) Shrinking forest shrinks skink: morphological change in response to rainforest fragmentation in the prickly forest skink (*Gnypetoscincus queenslandiae*). Biological Conservation 91: 159-167.

Sunday JM, Bates AE, Dulvy NK (2010) Global analysis of thermal tolerance and latitude in ectotherms. Proceedings of the Royal Society B. 278: 1823 - 1830.

Suorsa P, Huhta E, Jäntti A, Nikula A, Helle H, Kuitunen M, Koivunen V, Hakkarainen H (2005) Thresholds in selection of breeding habitat by the Eurasian Treecreeper (*Certhia familiaris*). Biological Conservation - BIOL CONSERV 121: 443-452.

Svensson BW (1992) Changes in Occupancy, Niche Breadth and Abundance of Three Gyrinus Species as Their Respective Range Limits Are Approached. Oikos 63: 147-156.

Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biological Reviews 85: 35-53.

Swihart R, Lusk J, Duchamp J, Rizkalla C, Moore J (2006) The roles of landscape context, niche breadth, and range boundaries in predicting species responses to habitat alteration. Diversity and Distributions 12: 277-287.

Swihart RK, Gehring TM, Kolozsvary MB, Nupp TE (2003) Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Diversity and Distributions 9: 1-18.

Taggart P, Leu S, Spiegel O, Godfrey S, Sih A, Bull C (2018) Endure your parasites: sleepy lizard movement is not affected by their ectoparasites. Canadian Journal of Zoology 96(12): 1309 - 1316.

Tallmon DA, Draheim HM, Mills LS, Allendorf FW (2002) Insights into recently fragmented vole populations from combined genetic and demographic data. Molecular Ecology 11: 699-709.

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, pp.

Teixeira C, Hirsch A, Perini H, Young R (2006) Marsupials from space: fluctuating asymmetry, geographical information systems and animal conservation. Proceedings Biological sciences / The Royal Society 273: 1007-1012.

Thakur M, Schättin EW, McShea WJ (2018) Globally common, locally rare: revisiting disregarded genetic diversity for conservation planning of widespread species. Biodiversity and Conservation 27: 3031-3035.

Thamm S, Kalko EKV, Wells K (2009) Ectoparasite infestations of hedgehogs (*Erinaceus europaeus*) are associated with small-scale landscape structures in an urban–suburban environment. EcoHealth 6: 404-413.

Thomas JA, Rose RJ, Clarke RT, Thomas CD, Webb NR (1999) Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. Functional Ecology 13: 55-64.

Thomas JA, Simcox DJ, Wardlaw J, Elmes GW, Hochberg M, Clarke R (1998) Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its Myrmica ant hosts. Journal of Insect Conservation 2: 39-46.

Thompson ME, Halstead BJ, Donnelly MA (2018) Thermal quality influences habitat use of two anole species. Journal of Thermal Biology 75: 54-61.

Thornton D, Branch L, Sunquist M (2010) Passive sampling effects and landscape location alter associations between species traits and response to fragmentation. Ecological Applications - Ecol Appl 21(3): 817 - 829.

Tischendorf L, Grez AA, Zaviezo T, Fahrig L (2005) Mechanisms Affecting Population Density in Fragmented Habitat. Ecology and Society 10(1): 7 - 20.

Tomkins JL, Kotiaho JS (2001) Fluctuating Asymmetry. Encyclopedia of Life Sciences. Macmillan Publishers Ltd, Nature Publishing Group.

Torres LG, Sutton PJH, Thompson DR, Delord K, Weimerskirch H, Sagar PM, Sommer E, Dilley BJ, Ryan PG, Phillips RA (2015) Poor Transferability of Species Distribution

Models for a Pelagic Predator, the Grey Petrel, Indicates Contrasting Habitat Preferences across Ocean Basins. PLoS ONE 10: e0120014.

Tripet F, Richner H (1997) Host Responses to Ectoparasites: Food Compensation by Parent Blue Tits. Oikos 78: 557-561.

Tull JC, Brussard PF (2007) Fluctuating asymmetry as an indicator of environmental stress from off-highway vehicles. The Journal of Wildlife Management 71: 1944-1948.

Turlure C, Van Dyck H, Schtickzelle N, Baguette M (2009) Resource-based habitat definition, niche overlap and conservation of two sympatric glacial relict butterflies. Oikos 118: 950-960.

Turner MG, Gardner RH, O'Neil RV (2001) Landscape Ecology in Theory and Practice. Springer-Verlag, New York, pp.

Uhrin M, Havaš P, Minařík M, Kodejš K, Bugoš I, Danko S, Husák T, Koleska D, Jablonski D (2016) Distribution updates to amphibian and reptile fauna for the Republic of Macedonia. Herpetology Notes 9: 201 - 220.

Unglaub B, Steinfartz S, Kühne D, Haas A, Schmidt B (2018) The relationships between habitat suitability, population size and body condition in a pond-breeding amphibian. Basic and Applied Ecology 27.: 20 - 29.

Urban MC, Richardson JL, Freidenfelds NA (2014) Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. Evolutionary applications 7: 88-103.

Vacheva E, Naumov B, Tzankov N (2020) Diversity and habitat preferences in lizard assemblages (Reptilia: Sauria) from model territories in western bulgaria. Acta Zoologica Bulgarica 72: 385-396.

Václav R, Prokop P, Fekiač V (2007) Expression of breeding coloration in European Green Lizards (*Lacerta viridis*): Variation with morphology and tick infestation. Canadian Journal of Zoology 85: 1199 - 1206.

Van Damme R, Bauwens D, Verheyen RF (1986) Selected body temperatures in the lizard *Lacerta vivipara*: Variation within and between populations. Journal of Thermal Biology 11: 219-222.

van der Mescht L (2011) Ectoparasite assemblage of the four-striped mouse, *Rhabdomys pumilio*: the effect of anthropogenic habitat transformation and temporal variation. Msc. Thesis: University of Stellenbosch.

Van Dongen S (2006) Fluctuating Asymmetry and Developmental Instability in Evolutionary Biology: Past, Present and Future. J Evol Biol 19: 1727-1743.

Van Dongen S, Lens L (2000) The evolutionary potential of developmental instability. J Evol Biol 13: 326-335.

Vasudev D, Fletcher Jr RJ, Goswami VR, Krishnadas M (2015) From dispersal constraints to landscape connectivity: lessons from species distribution modeling. Ecography 38: 967-978.

Verboom J, Schippers P, Cormont A, Sterk M, Vos CC, Opdam PFM (2010) Population dynamics under increasing environmental variability: implications of climate change for ecological network design criteria. Landscape Ecology 25: 1289-1298.

Vergara PM, Armesto JJ (2009) Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. Landscape Ecology 24: 25-38.

Vervust B, Van Dongen S, Grbac I, Van Damme R (2009) Fluctuating asymmetry, physiological performance, and stress in island populations of the italian wall lizard (*Podarcis sicula*). Journal of Herpetology 42: 369-377.

Vignoli L, I M, Luiselli L, Bologna M (2009) Can a large metropolis sustain complex herpetofauna communities? An analysis of green space fragments suitability in Rome. Animal Conservation 12: 456-466.

Villard M-A, Metzger JP (2014) REVIEW: Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology 51: 309-318.

Vucetich JA, Waite TA (2003) Spatial patterns of demography and genetic processes across the species' range: Null hypotheses for landscape conservation genetics. Conservation Genetics 4: 639 - 645.

Waitzmann M, Sandmaier P (1990) Zur Verbreitung, Morphologie und Habitatwahl der Reptilien im Donautal zwischen Passau und Linz (Niederbayern, Oberösterreich). Herpetozoa 3: 25 - 53.

Walkup DK, Leavitt DJ, Fitzgerald LA (2017) Effects of habitat fragmentation on population structure of dune-dwelling lizards. Ecosphere 8: e01729.

Watling JI, Arroyo-Rodríguez V, Pfeifer M, Baeten L, Banks-Leite C, Cisneros LM, Fang R, Hamel-Leigue AC, Lachat T, Leal IR, Lens L, Possingham HP, Raheem DC, Ribeiro DB, Slade EM, Urbina-Cardona JN, Wood EM, Fahrig L (2020) Support for the habitat amount hypothesis from a global synthesis of species density studies. Ecology Letters 23: 674-681.

Watson James EM, Shanahan Danielle F, Di Marco M, Allan J, Laurance William F, Sanderson Eric W, Mackey B, Venter O (2016) Catastrophic declines in wilderness areas undermine global environment targets. Current Biology 26: 2929-2934.

White T, van der Ende J, Nichols TE (2019) Beyond Bonferroni revisited: concerns over inflated false positive research findings in the fields of conservation genetics, biology, and medicine. Conservation Genetics 20: 927-937.

Wiens JA, Stenseth NC, Horne BV, Ims RA (1993) Ecological mechanisms and landscape ecology. Oikos 66: 369-380.

Wikelski M, Cooke SJ (2006) Conservation physiology. Trends Ecol Evol 21: 38-46. doi:10.1016/j.tree.2005.10.018

Williams JW, Jackson ST, Kutzbach JE (2007) Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences 104: 5738.

Wilson MC, Chen X-Y, Corlett RT, Didham RK, Ding P, Holt RD, Holyoak M, Hu G, Hughes AC, Jiang L, Laurance WF, Liu J, Pimm SL, Robinson SK, Russo SE, Si X, Wilcove DS, Wu J, Yu M (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landscape Ecology 31: 219-227.

Winchell KM, Briggs D, Revell LJ (2019) The perils of city life: patterns of injury and fluctuating asymmetry in urban lizards. Biological Journal of the Linnean Society 126: 276-288.

Winter M, Fiedler W, Hochachka WM, Koehncke A, Meiri S, De la Riva I (2016) Patterns and biases in climate change research on amphibians and reptiles: a systematic review. Royal Society Open Science 3: 160158.

With KA (2019) Essentials of Landscape Ecology. Oxford University Press, Oxford, 656 pp.

Wosniack ME, Santos MC, Pie MR, Marques MCM, Raposo EP, Viswanathan GM, Luz MGEd (2014) Unveiling a mechanism for species decline in fragmented habitats: fragmentation induced reduction in encounter rates. Journal of The Royal Society Interface 11: 20130887.

Yackulic CB, Sanderson EW, Uriarte M (2011) Anthropogenic and environmental drivers of modern range loss in large mammals. Proceedings of the National Academy of Sciences 108: 4024-4029.

Yates KL, Bouchet PJ, Caley MJ, Mengersen K, Randin CF, Parnell S, Fielding AH, Bamford AJ, Ban S, Barbosa AM, Dormann CF, Elith J, Embling CB, Ervin GN, Fisher R, Gould S, Graf RF, Gregr EJ, Halpin PN, Heikkinen RK, Heinänen S, Jones AR, Krishnakumar PK, Lauria V, Lozano-Montes H, Mannocci L, Mellin C, Mesgaran MB, Moreno-Amat E, Mormede S, Novaczek E, Oppel S, Ortuño Crespo G, Peterson AT, Rapacciuolo G, Roberts JJ, Ross RE, Scales KL, Schoeman D, Snelgrove P, Sundblad G, Thuiller W, Torres LG, Verbruggen H, Wang L, Wenger S, Whittingham MJ, Zharikov Y, Zurell D, Sequeira AMM (2018) Outstanding Challenges in the Transferability of Ecological Models. Trends Ecol Evol 33: 790-802.

Ye X, Skidmore AK, Wang T (2013) Within-patch habitat quality determines the resilience of specialist species in fragmented landscapes. Landscape Ecology 28: 135-147.

Yurkowski DJ, Ferguson S, Choy ES, Loseto LL, Brown TM, Muir DCG, Semeniuk CAD, Fisk AT (2016) Latitudinal variation in ecological opportunity and intraspecific competition indicates differences in niche variability and diet specialization of Arctic marine predators. Ecol Evol 6: 1666-1678.

Zakharov VM, Zhdanova NP, Kirik EF, Shkil FN (2001) Ontogenesis and population: Evaluation of developmental stability in natural populations. Russian Journal of Developmental Biology 32: 336-351.

Zanette L, Doyle P, Trémont SM (2000) Food shortage in small fragments: evidence from an area-sensitive passerine. Ecology 81: 1654 - 1666.

Zavadil V, Moravec J (2003) Red List of Amphibians and Reptiles of the Czech Republic In: J. Plesník VH, L. Brejšková (Ed) Red List of Threatened Species in the Czech Republic Vertebrates. Příroda, Prague, 1-183.

Zhdanova NP, Zakharov VM (2006) Developmental stability of sand lizard (*Lacerta agilis* L.) under optimal and non-optimal conditions. In: Corti C, Lo Casio P, Biaggini M (Eds) Mainland and insular lizards: A mediterranean perspective. Firenze University Press, Florence.

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1: 3-14.

9. Supporting information

9.1. Supporting information to Chapter 3

Appendix S1: Correlations and variance inflation factor (VIF)

Table S1.1. Correlations and variance inflation factor (VIF) of continuous variables in the dataset used for comparison of microhabitats among regions (all regions included). Spearman rank correlation and Pearson correlation were applied for vegetation structure and abiotic parameters, respectively.

Vegetation structure											
	Spearman Rank Correlation										**VIF**
	Herbs1	Herbs2	Herbs3	Woody plants<2m	Woody plants>2m	Dry leaves	Rocks_ trunks	Bare soil	Way	Branches	
Herbs1	1										2.555
Herbs2	-0.504	1									2.701
Herbs3	-0.297	0.142	1								2.125
Woody plants>2m	0.051	-0.236	-0.259	1							1.490
Woody plants>2m	0.060	-0.145	-0.325	0.187	1						1.409
Dry leaves	0.051	-0.185	-0.177	-0.082	0.157	1					1.463
Rocks_trunks	-0.117	0.082	0.045	-0.192	-0.192	0.064	1				1.281
Bare soil	-0.022	-0.185	-0.179	0.036	0.105	0.134	-0.073	1			1.283
Way	-0.020	-0.081	0.053	0.006	-0.129	-0.153	-0.145	-0.158	1		1.901
Branches	0.227	-0.120	-0.182	-0.131	0.229	0.209	-0.057	0.136	0.107	1	1.302

Abiotic parameters							
	Pearson Correlation						**VIF**
	Temperature	Soil compaction	S-N aspect	W-E aspect	Slope	Radiation	
Temperature	1						1.084
Soil compaction	-0.061	1					1.226
S-N aspect	0.087	-0.075	1				1.079
W-E aspect	0.049	-0.057	-0.031	1			1.027
Slope	0.123	-0.166	-0.218	0.114	1		1.131
Radiation	-0.241	0.408	-0.047	-0.134	-0.186	1	1.302

Table S1.2. Correlations and variance inflation factor (VIF) of continuous variables in the core Plovdiv. Spearman rank correlation and Pearson correlation were applied for vegetation structure and abiotic parameters, respectively. VIF* are values obtained after removing Herbs 2.

Vegetation structure

	Spearman Rank Correlation										VIF	VIF*
	Herbs1	Herbs2	Herbs3	Woody plants<2m	Woody plants>2m	Dry leaves	Rocks_ trunks	Bare soil	Way	Branches		
Herbs1	1										14.039	1.275
Herbs2	-0.481	1									17.740	
Herbs3	-0.238	-0.109	1								8.525	1.347
Woody plants>2m	-0.122	-0.282	-0.222	1							6.721	1.212
Woody plants>2m	-0.038	-0.170	-0.204	-0.141	1						5.212	1.193
Dry leaves	0.023	-0.184	-0.107	-0.031	0.068	1					2.297	1.031
Rocks_trunks	-0.066	-0.089	-0.073	0.008	-0.111	-0.056	1				2.771	1.069
Bare soil	-0.071	-0.176	-0.180	0.207	-0.019	-0.078	-0.056	1			3.340	1.140
Way	-0.178	-0.186	0.017	-0.070	-0.082	-0.009	-0.075	-0.148	1		5.231	1.112
Branches	0.270	-0.055	-0.149	-0.195	0.212	0.033	-0.061	-0.118	-0.011	1	1.188	1.184

Abiotic parameters

	Pearson Correlation						VIF
	Temperature	Soil compaction	S-N aspect	W-E aspect	Slope	Radiation	
Temperature	1						1.057
Soil compaction	0.130	1					1.285
S-N aspect	0.059	0.019	1				1.121
W-E aspect	0.057	0.077	-0.103	1			1.040
Slope	-0.024	-0.001	-0.264	-0.053	1		1.172
Radiation	0.050	0.194	-0.043	-0.039	0.054	1	1.078

Table S1.3. Correlations and variance inflation factor (VIF) of continuous variables in the periphery Passau. Spearman rank correlation and Pearson correlation were applied for vegetation structure and abiotic parameters, respectively.

Vegetation structure

	Spearman Rank Correlation										VIF
	Herbs1	Herbs2	Herbs3	Woody plants<2m	Woody plants>2m	Dry leaves	Rocks_ trunks	Bare soil	Way	Branches	
Herbs1	1										2.271
Herbs2	-0.298	1									2.491
Herbs3	-0.127	0.015	1								2.125
Woody plants>2m	0.141	-0.157	-0.374	1							1.218
Woody plants>2m	0.055	-0.214	-0.313	0.243	1						1.163
Dry leaves	-0.192	-0.279	-0.485	0.227	0.303	1					2.419
Rocks_trunks	-0.320	-0.073	0.080	-0.215	-0.180	0.041	1				1.057
Bare soil	0.029	-0.048	0.106	0.056	-0.044	-0.130	-0.185	1			1.100
Way	-0.080	0.078	0.047	-0.113	0.047	-0.113	-0.153	-0.081	1		1.035
Branches	0.179	-0.204	-0.260	0.227	0.153	0.184	-0.289	-0.073	-0.003	1	1.325

Abiotic parameters

	Pearson Correlation						VIF
	Temperature	Soil compaction	S-N aspect	W-E aspect	Slope	Radiation	
Temperature	1						1.414
Soil compaction	0.131	1					1.179
S-N aspect	0.037	-0.150	1				1.119
W-E aspect	-0.026	-0.135	0.176	1			1.250
Slope	0.151	-0.064	-0.144	0.285	1		1.276
Radiation	-0.224	-0.091	-0.025	-0.102	-0.168	1	1.536

Table S1.4. Correlations and variance inflation factor (VIF) of continuous variables in the periphery Prague. Spearman rank correlation and Pearson correlation were applied for vegetation structure and abiotic parameters, respectively.

Vegetation structure

	Spearman Rank Correlation										**VIF**
	Herbs1	Herbs2	Herbs3	Woody plants<2m	Woody plants>2m	Dry leaves	Rocks_ trunks	Bare soil	Way	Branches	
Herbs1	1										1.770
Herbs2	0.336	1									1.371
Herbs3	-0.140	0.191	1								1.593
Woody plants>2m	-0.040	-0.056	-0.396	1							1.237
Woody plants>2m	-0.170	-0.357	-0.271	0.147	1						1.405
Dry leaves	-0.290	-0.491	-0.399	0.103	0.418	1					2.166
Rocks_trunks	-0.027	0.143	-0.074	-0.080	-0.073	-0.151	1				1.159
Bare soil	-0.164	-0.281	-0.052	-0.047	0.217	0.096	-0.229	1			1.274
Way	-0.090	0.078	0.083	0.082	-0.014	-0.017	-0.187	-0.247	1		1.058
Branches	-0.121	-0.502	-0.378	0.176	0.567	0.568	-0.151	0.094	-0.072	1	1.845

Abiotic parameters

	Pearson Correlation						**VIF**
	Temperature	Soil compaction	S-N aspect	W-E aspect	Slope	Radiation	
Temperature	1						1.107
Soil compaction	0.053	1					1.446
S-N aspect	-0.012	-0.042	1				1.081
W-E aspect	-0.056	-0.166	-0.075	1			1.559
Slope	0.154	-0.032	-0.518	0.029	1		1.909
Radiation	-0.099	0.207	0.104	0.059	-0.320	1	1.681

Appendix S2 – Correction of spatial autocorrelation of residuals (SACR)

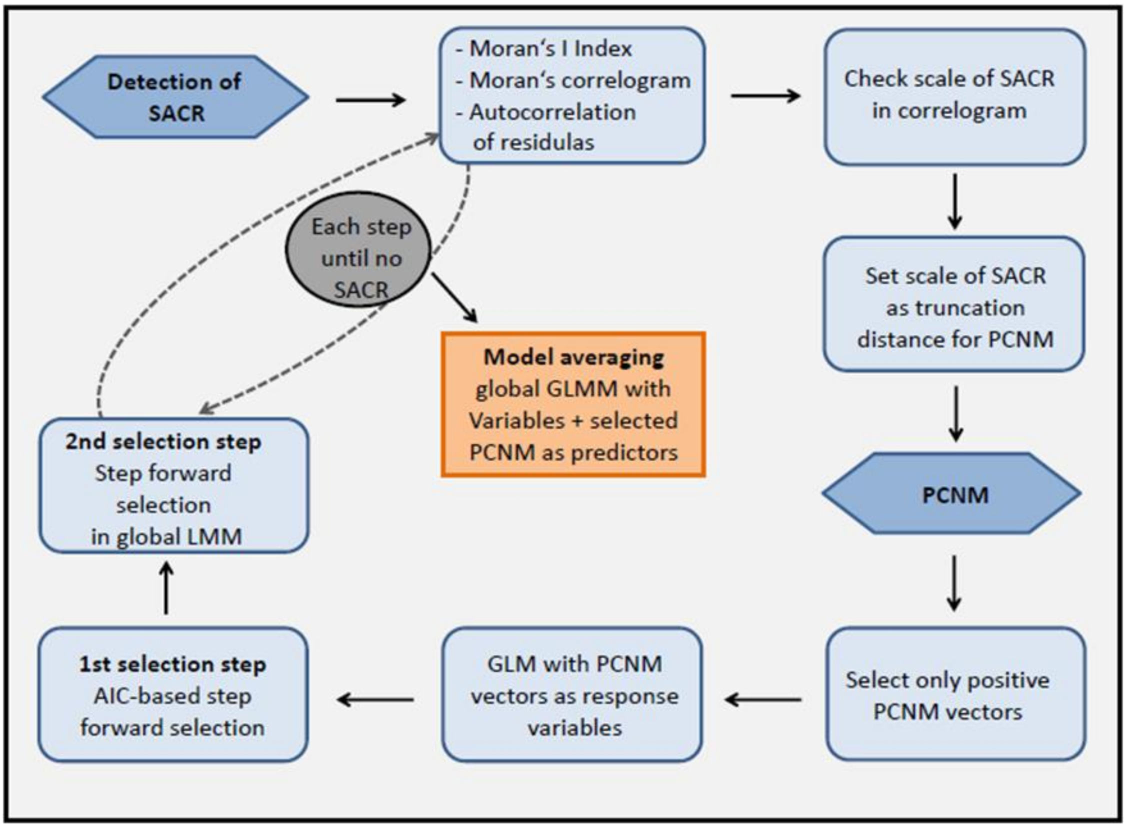


Figure S2.1. Process of detection and correction of spatial autocorrelation of model's residuals (SACR) though principal coordinates of neighbor matrices (PCNM) applied to each global GLMM in the analysis of microhabitat selection. See text for detailed description.

SACR was tested with Moran's index estimated with the 'Moran.I' function in 'ape' package of R, Moran's I correlograms by using 'correlog' function in 'ncf' package, and autocorrelation of residuals with the 'acf' function of the 'nlme' package. For the correlogram the function to build lags was set at 100 m and p-values and correlation directions (positive or negative) were checked to estimate at which scale SACR was present. This study focuses on habitat selection at the micro-scale, therefore the presence of SACR was checked at a maximum scale of 1 km. SACR further than 1 km was assumed to be related with ecological processes occurring at broader scales.

The PCNM analysis was performed with the 'pcnm' function in the Vegan package. Maximum distance of the lag at which SACR was detected in the correlogram, was set as truncation distance for the PCNM. Only positive PCNM were used in further analysis. Because the PCNM analysis usually generates many eigenvectors (72-81 positive eigenvectors in our models), the number of PCNM to be added into the model as predictors was reduced through a two-steps process (Fig. S2.1). The first step was a forward selection based on AIC for binomial GLMs with the global model containing only all positive PCNM as scope (Ficetola and Padoa-Schioppa 2009; Sokol et al. 2013). In the second step, the selected PCNM (7 to 10 in our models) were included one by one into the global GLMM containing all other variables (vegetation structure or abiotic parameters), and step forward selected by testing correction of SACR with Moran's I index, Moran's correlograms and residuals' autocorrealtion at each step (Dray et al. 2006; Griffith and Peres-Neto 2006). Thus, the combination with the smaller number of PCNM that successfully corrected for SACR was finally used for further analysis (Marrot et al. 2015).

For the core area no SACR of model residuals was found in any global model (Table S3.1. Vegetation structure: Moran's I = 0.28; abiotic parameters: Moran'sI = 0.31; combination: Moran's I= 0.31).

For peripheral populations in Passau, SACR was found in the global model of vegetation structure (Moran's I = 1.46e^{-07}) at a scale of ~700 m. A total of 81 positive PCNM were obtained, from which 10 were selected in the first step and three (16, 22, 9) in the second step, correcting successfully for SACR (Moran's I = 0.17). Regarding abiotic parameters in Passau, SACR was also found at a scale of ~700 m (Moran's I = 1.33e^{-15}). A total of 77 PCNM were obtained, from which seven were selected in the first step and four PCNM (22, 44, 6, 1) corrected for SACR in the second step (Moran's I = 0.68). In both sets, all selected PCNM were found to be important for the microhabitat selection after model averaging (Table S3.2). Therefore, when pulling together variables of both sets, the included PCNM already accounted sufficiently for SACR, and no other PCNM analysis was necessary. Only PCNM 22 of the set of vegetation structure was removed given the model could not converge, but all other PCNM still corrected for SACR (Moran's I = 0.75).

In the periphery in Prague, SACR was not detected with Moran's I in any set of variables (vegetation structure: Moran's I = 0.98; abiotic parameters: Moran's I = 0.17). However, in the set of abiotic parameters, SACR was detected by the 'acf' function and the Moran's correlogram at a scale of 600 m. A total of 72 PCNM were obtained, and from those eight were selected in the first step and three (72, 42 and 1) in the second (Table S3.3). In the second step selection was based on reduction of SACR tested with the 'acf' function and Moran's correlograms. In the global model combining most important variables of both sets, no SACR was detected.

References

Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196: 483-493.

Ficetola GF, Padoa-Schioppa E (2009) Human activities alter biogeographical patterns of reptiles on Mediterranean islands. Global Ecology and Biogeography 18: 214-222.

Griffith DA, Peres-Neto PR (2006) Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. Ecology 87: 2603-2613.

Marrot P, Garant D, Charmantier A (2015) Spatial autocorrelation in fitness affects the estimation of natural selection in the wild. Methods in Ecology and Evolution 6: 1474-1483.

Sokol ER, Herbold CW, Lee CK, Cary SC, Barrett JE (2013) Local and regional influences over soil microbial metacommunities in the Transantarctic Mountains. Ecosphere 4: 1-24.

Appendix S3: Individual models of vegetation structure and abiotic parameters for the comparison of microhabitats among regions

Table S3.1. Variables selected through model averaging of multinomial models for comparison of microhabitats among regions. Estimates, standard errors (SE) and relative variable importance (RVI) are shown for individual sets of variables: vegetation structure and abiotic parameters. Estimates and SE correspond to Passau (Pa) and Prague (Pr) in comparison with the core Plovdiv

Variables	Pa		Pr		RVI
	Estimates	SE	Estimates	SE	
Vegetation structure					
Intercept	3.78	1.14	5.86	1.19	
Way	-8.47	3.04	-7.24	2.3	1
Woody plants <2m	-21.31	7.4	-11.88	3.42	1
Woody plants >2m	-9.93	3.09	-14.09	3.7	1
Herbs 1	-5.69	1.53	-6.11	1.43	1
Herbs 3	-3.69	1.47	-10.14	2.69	1
Herbs 2	-3.716	1.33	-9.46	1.92	1
Rocks_trunks	1.22	2.51	0.34	1.56	0.26
Branches	-0.77	2.03	0.09	0.62	0.21
Bare soil	-0.98	2.58	-0.32	1.27	0.17
Abiotic parameters					
Intercept	-4.46	7.27	-14.78	8.38	
Radiation	-0.5	0.09	-0.53	0.1	1
Slope	1.09	0.5	1.83	0.56	1
Soil compaction	-3.35	1.17	-4.16	1.28	1
Temperature	5.33	5.04	12.72	5.82	0.75
S-N aspect	-0.21	0.48	-0.03	0.3	0.25

Appendix S4: Individual models of vegetation structure and abiotic parameters for the analysis of microhabitat selection in each region

Table S4.1. Variables selected in the model averaging of generalized linear mixed model for habitat selection in the core in Plovdiv. Estimates, standard errors (SE) and relative variable importance (RVI) are shown for individual sets of variables: vegetation structure and abiotic parameters.

Variable	Estimate	SE	RVI
Vegetation structure			
(Intercept)	-3.69633	5.78002	
Rocks_trunks	1.77245	4.56812	0.28
Dry leaves	1.38069	4.44620	0.21
Herbs 1	0.17198	0.57128	0.17
Woody plants >2m	0.14448	0.77958	0.09
Way	0.08823	0.62003	0.08
Herbs 3	0.04485	0.41898	0.07
Bare soil	-0.04813	0.63451	0.07
Abiotic parameters			
(Intercept)	15.3877	7.415	
Radiation	0.5275	0.2727	1
Slope	-3.8056	2.3085	1
Soil compaction	-5.7846	1.4432	1
S-N aspect	-3.6429	2.9139	0.74
Temperature	-1.406	3.5887	0.24
W-E aspect	0.1214	0.6582	0.14

Table S4.2. Variables selected in the model averaging of generalized linear mixed model for habitat selection in the periphery in Passau. Estimates, standard errors (SE) and relative variable importance (RVI) are shown for individual sets of variables: vegetation structure and abiotic parameters. PCNM: Principal coordinates of neighbor matrices correcting for spatial autocorrelation.

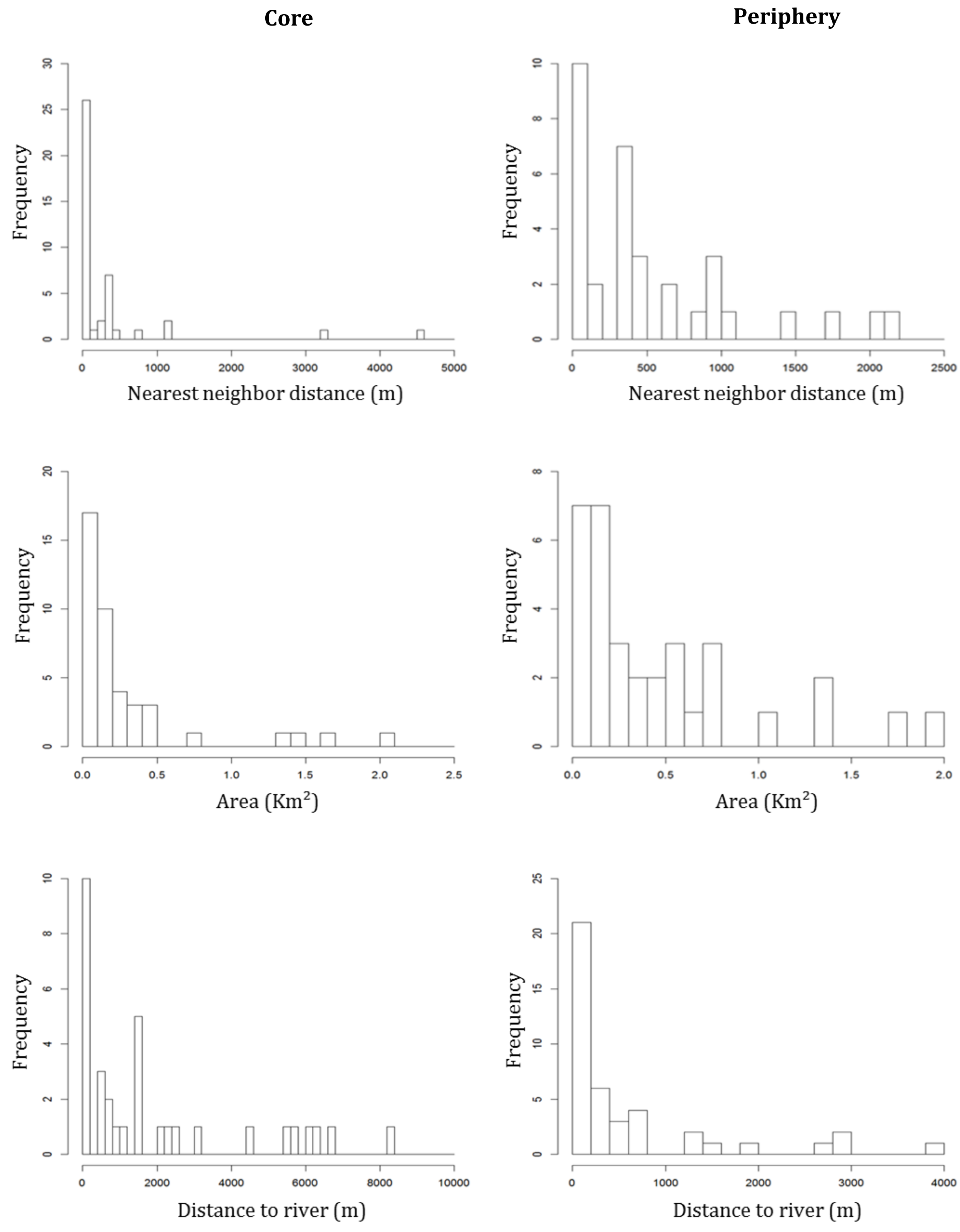
Variable	Estimate	SE	RVI
Vegetation structure			
(Intercept)	-40.284	16.358	
Bare soil	33.719	26.467	1
Branches	-37.81	24.41	1
pcnm16	47.383	23.083	1
pcnm22	238.556	104.436	1
pcnm9	-64.229	34.589	1
Way	58.026	39.074	1
Herbs 3	11.665	6.037	1
Herbs 2	1.2788	2.0666	0.28
Herbs 1	-1.2137	3.63	0.20
Dry leaves	-0.8665	3.71	0.15
Abiotic parameters			
(Intercept)	-2.32E+002	3.23E-003	
pcnm1	4.03E+002	5.98E+001	1
pcnm22	3.66E+002	6.97E+001	1
pcnm44	-1.12E+002	7.31E+002	1
pcnm6	-2.20E+002	5.25E+001	1
Temperature	1.27E+002	3.13E-003	1
S-N aspect	-1.69E+001	3.13E-003	0.81
W-E aspect	2.24E+001	3.13E-003	0.81
Soil compaction	11.694	18.133	0.55
Slope	-1.057	2.98	0.17

Table S4.3. Variables selected in the model averaging of generalized linear mixed model for habitat selection in the periphery in Prague. Estimates, standard errors (SE) and relative variable importance (RVI) are shown for individual sets of variables: vegetation structure and abiotic parameters. PCNM: Principal coordinates of neighbor matrices correcting for spatial autocorrelation.

Variable	Estimate	SE	RVI
Vegetation structure			
(Intercept)	-111.23	78.38	
Way	50.04	51.16	1
Herbs 1	72.74	71.43	1
Herbs 2	1575.42	1826.46	1
Branches	20.88	19.67	0.94
Herbs 3	-317.15	432.45	0.84
Woody plants >2m	28.88	39.67	0.77
Bare soil	61.41	67.36	0.74
Rocks_trunks	127.38	323.9	0.51
Woody plants <2m	-288.39	507.12	0.47
Dry leaves	01.07.62	48.46	0.27
Abiotic parameters			
(Intercept)	-5.2368	5.403	
pcnm1	-13.626	10.2763	1
Slope	1.671	0.7394	0.9
pcnm72	-3.70848	6.41181	0.6
pcnm42	7.32409	12.17195	0.58
Radiation	-0.14635	0.18696	0.56
Soil comp action	-1.97249	2.64025	0.53
S-N aspect	0.07441	0.35289	0.11
Temperature	0.8315	4.06023	0.09
W-E aspect	-0.01027	0.13885	0.02

9.2. Supporting information to Chapter 4

Appendix S1. Distribution of variables representative of habitat configuration in each region



Appendix S2. Location of habitat patches surveyed in each region

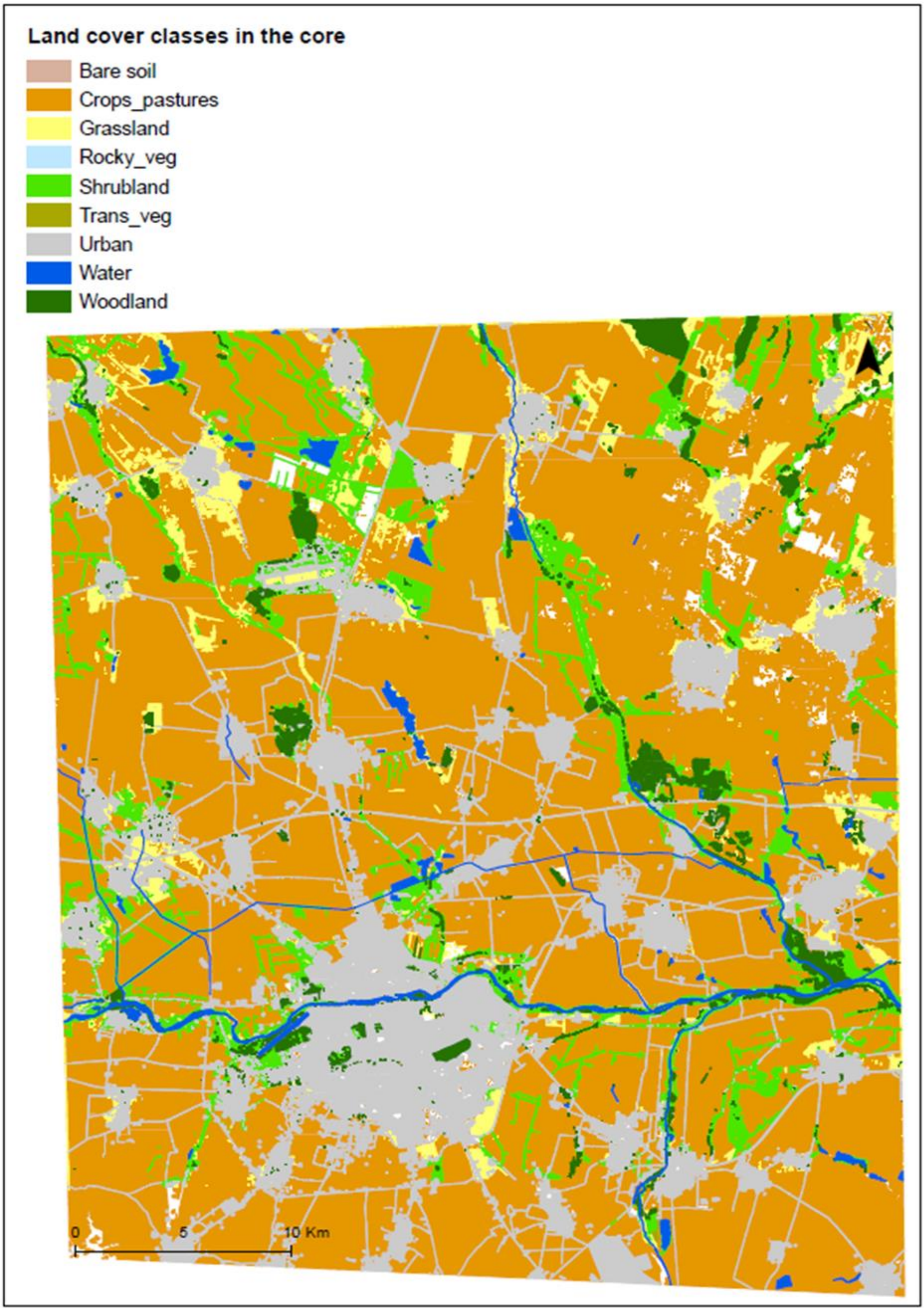
Core

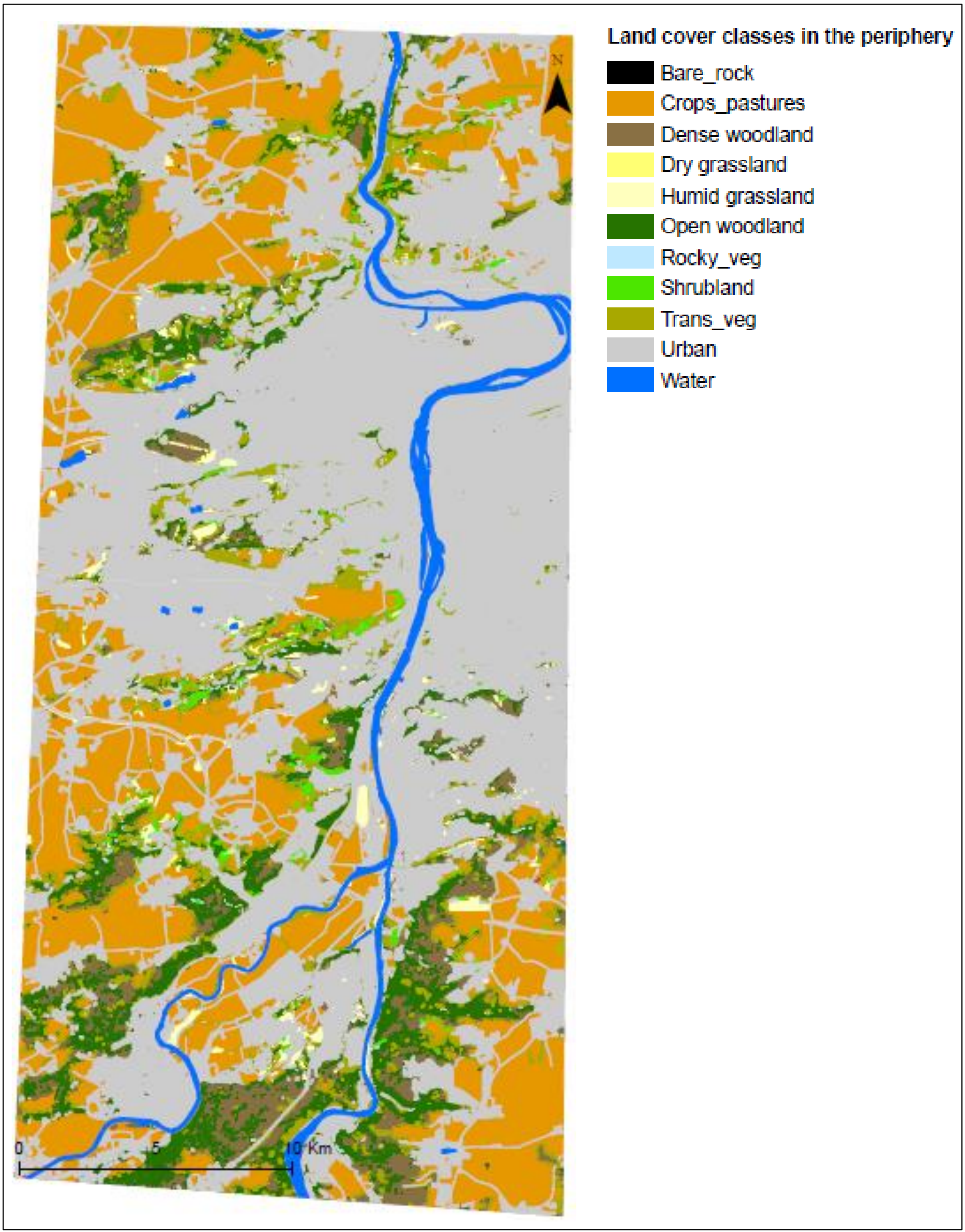
Patch	latitud	longitud
1	42.1543	24.7331
2	42.1447	24.7384
3	42.1367	24.7307
4	42.1424	24.7005
5	42.1558	24.7519
6	42.1530	24.7341
7	42.1457	24.7467
8	42.1639	24.7627
9	42.1616	24.7702
10	42.1612	24.7716
11	42.1597	24.7760
12	42.1622	24.7972
13	42.1560	24.7639
14	42.1486	24.7074
15	42.1529	24.7065
16	42.1585	24.7222
17	42.1587	24.7194
18	42.1573	24.7179
19	42.1611	24.7159
20	42.1684	24.7155
21	42.1762	24.7112
22	42.1813	24.7156
23	42.1641	24.7708
24	42.1904	24.7691
25	42.1951	24.7754
26	42.1986	24.7590
27	42.2315	24.7751
28	42.2190	24.7853
29	42.1248	24.8670
30	42.1510	24.8828
31	42.1520	24.8169
32	42.1246	24.8686
33	42.1936	24.8213
34	42.2123	24.8676
35	42.2286	24.8579
36	42.2246	24.8831
37	42.2060	24.8987
38	42.1997	24.8894
39	42.2262	24.8482
40	42.1984	24.8883
41	42.2119	24.8665
42	42.2387	24.7159

Periphery

Patch	Latitud	Longitud
1	50.1324	14.4002
2	50.1372	14.403
3	50.1179	14.4023
4	50.1469	14.3794
5	49.9542	14.4185
6	49.9616	14.414
7	50.0178	14.4141
8	50.0004	14.3784
9	50.0141	14.3857
10	50.0104	14.3727
11	49.9439	14.4111
12	50.0909	14.3421
13	50.0835	14.3537
14	50.0713	14.3284
15	50.0716	14.3657
16	50.059	14.3456
17	50.0656	14.3339
18	50.0657	14.3806
19	50.0596	14.3901
20	50.0623	14.399
21	49.9877	14.3565
22	49.9857	14.38
23	49.9843	14.3726
24	49.9782	14.4013
25	49.9574	14.4019
26	50.0313	14.3253
27	50.0408	14.371
28	50.0452	14.3938
29	50.0533	14.3861
30	50.0404	14.3997
31	49.9643	14.42
32	49.9553	14.3865
33	50.1452	14.4014

Appendix S3. Maps of classified land cover classes in each region




Land cover classes in the periphery
Bare_rock
Crops_pastures
Dense woodland
Dry grassland
Humid grassland
Open woodland
Rocky_veg
Shrubland
Trans_veg
Urban
Water
N
0
5
10 Km

Appendix S4. Models for detection probability in each region. Variables were included to model only detection probability (p) while maintaining occupancy probability (psi) constant.

Model	AICc	ΔAIC	weight
Core			
p(day+veg_str+area), psi(.)	96.72	0	0.244
p(day+veg_str), psi(.)	96.99	0.27	0.213
p(area), psi(.)	97.6	0.87	0.157
p(day), psi(.)	98.08	1.35	0.124
p(veg_str+area), psi(.)	98.43	1.71	0.104
p(day+area), psi(.)	98.63	1.9	0.094
Periphery			
p(area+veg_str), psi(.)	49.15	0.00	0.28
p(day+area+veg_str), psi(.)	49.53	0.38	0.23
p(.), psi(.)	49.65	0.50	0.22
p(day+veg_str), psi(.)	50.52	1.37	0.14
p(veg_str), psi(.)	50.53	1.37	0.14

Appendix S5. Spearman rank correlations of no scale dependent variables in each region.

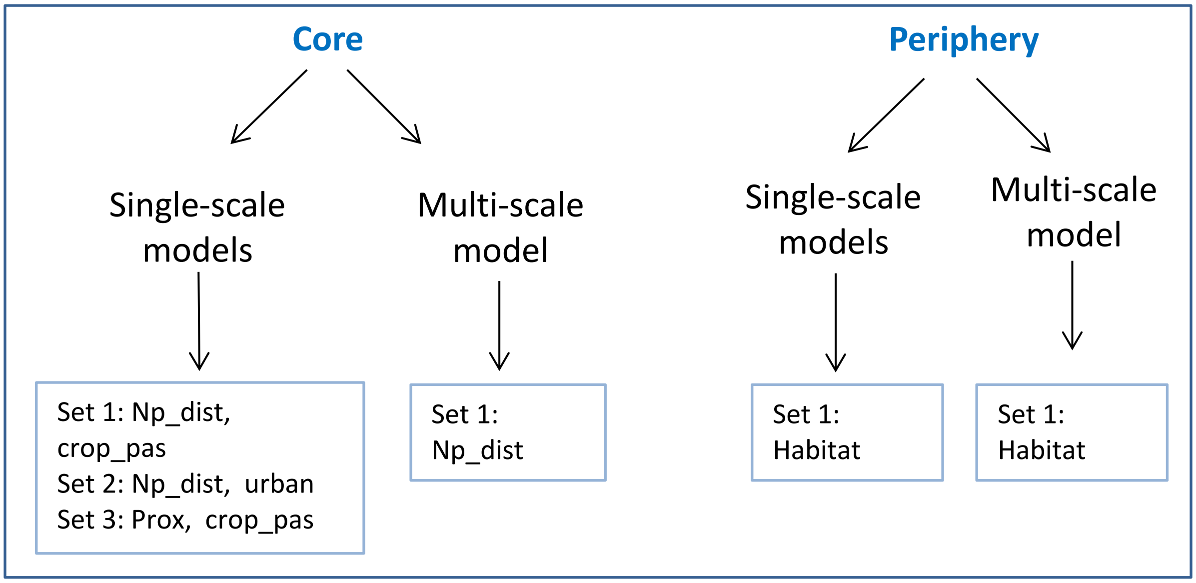
Core

	Area	Perimeter	Per_Area	Shape_index	CAI_5m	CAI_10m	CAI_25m	CAI_51m	CAI_75m	CAI_100m	Veg_str	Radiation	Np_dist	dist_river
Area	1	0.361	-0.839	0.442	0.676	0.660	0.681	0.755	0.763	0.692	0.186	0.333	-0.103	-0.087
Perimeter	0.361	1	0.038	0.249	0.202	0.196	0.213	0.263	0.270	0.175	-0.095	0.233	0.071	0.138
Per_Area	-0.839	0.038	1	-0.091	-0.814	-0.798	-0.794	-0.798	-0.762	-0.699	-0.418	-0.364	0.009	-0.053
Shape_index	0.442	0.249	-0.091	1	-0.312	-0.331	-0.280	-0.126	-0.072	-0.095	-0.477	-0.139	-0.353	-0.573
CAI_5m	0.676	0.202	-0.814	-0.312	1	0.995	0.961	0.897	0.853	0.802	0.573	0.508	0.184	0.348
CAI_10m	0.660	0.196	-0.798	-0.331	0.995	1	0.973	0.909	0.863	0.802	0.582	0.513	0.191	0.354
CAI_25m	0.681	0.213	-0.794	-0.280	0.961	0.973	1	0.955	0.911	0.817	0.550	0.452	0.206	0.344
CAI_51m	0.755	0.263	-0.798	-0.126	0.897	0.909	0.955	1	0.955	0.845	0.441	0.404	0.203	0.283
CAI_75m	0.763	0.270	-0.762	-0.072	0.853	0.863	0.911	0.955	1	0.892	0.347	0.327	0.197	0.229
CAI_100m	0.692	0.175	-0.699	-0.095	0.802	0.802	0.817	0.845	0.892	1	0.307	0.284	0.142	0.138
Veg_str	0.186	-0.095	-0.418	-0.477	0.573	0.582	0.550	0.441	0.347	0.307	1	0.498	0.175	0.333
Radiation	0.333	0.233	-0.364	-0.139	0.508	0.513	0.452	0.404	0.327	0.284	0.498	1	0.410	0.283
np_dist	-0.103	0.071	0.009	-0.353	0.184	0.191	0.206	0.203	0.197	0.142	0.175	0.410	1	0.415
dist_river	-0.087	0.138	-0.053	-0.573	0.348	0.354	0.344	0.283	0.229	0.138	0.333	0.283	0.415	1

Periphery

	Area	Perimeter	Per_area	Shape_index	CAI_5m	CAI_10m	CAI_25m	CAI_50m	CAI_75m	CAI_100m	Veg_str	Radiation	Slope	Np_dist	dist_river	dist_crop
Area	1	0.039	-0.892	0.552	0.064	0.067	0.091	0.046	0.031	-0.040	0.186	0.058	0.223	-0.400	-0.032	-0.221
Perimeter	0.039	1	0.290	-0.028	0.037	0.040	0.067	0.013	0.061	0.096	0.175	0.151	0.103	-0.094	-0.235	-0.094
Per_area	-0.892	0.290	1	-0.332	0.031	0.027	0.015	0.064	0.111	0.202	-0.104	0.041	-0.237	0.317	0.023	0.192
Shape_index	0.552	-0.028	-0.332	1	0.252	0.252	0.280	0.323	0.327	0.302	0.245	0.037	-0.021	-0.358	0.185	-0.257
CAI_5m	0.064	0.037	0.031	0.252	1	0.999	0.979	0.902	0.859	0.796	-0.220	0.111	-0.161	-0.106	0.072	-0.225
CAI_10m	0.067	0.040	0.027	0.252	0.999	1	0.982	0.906	0.864	0.800	-0.206	0.108	-0.157	-0.112	0.071	-0.220
CAI_25m	0.091	0.067	0.015	0.280	0.979	0.982	1	0.958	0.922	0.861	-0.132	0.130	-0.104	-0.165	0.048	-0.189
CAI_50m	0.046	0.013	0.064	0.323	0.902	0.906	0.958	1	0.985	0.936	-0.086	0.173	-0.103	-0.221	0.052	-0.129
CAI_75m	0.031	0.061	0.111	0.327	0.859	0.864	0.922	0.985	1	0.966	-0.066	0.206	-0.095	-0.249	0.032	-0.069
CAI_100m	-0.040	0.096	0.202	0.302	0.796	0.800	0.861	0.936	0.966	1	-0.068	0.249	-0.071	-0.180	0.044	0.022
Veg_str	0.186	0.175	-0.104	0.245	-0.220	-0.206	-0.132	-0.086	-0.066	-0.068	1	-0.048	0.311	-0.100	-0.085	0.075
Radiation	0.058	0.151	0.041	0.037	0.111	0.108	0.130	0.173	0.206	0.249	-0.048	1	-0.265	-0.056	-0.182	0.137
Slope	0.223	0.103	-0.237	-0.021	-0.161	-0.157	-0.104	-0.103	-0.095	-0.071	0.311	-0.265	1	-0.176	-0.235	0.055
np_dist	-0.400	-0.094	0.317	-0.358	-0.106	-0.112	-0.165	-0.221	-0.249	-0.180	-0.100	-0.056	-0.176	1	0.300	0.171
dist_river	-0.032	-0.235	0.023	0.185	0.072	0.071	0.048	0.052	0.032	0.044	-0.085	-0.182	-0.235	0.300	1	0.457
dist_crop	-0.221	-0.094	0.192	-0.257	-0.225	-0.220	-0.189	-0.129	-0.069	0.022	0.075	0.137	0.055	0.171	0.457	1

Appendix S6. Different sets of models ran in each single scale and multiscale models in each region. Each set includes all variables plus the variable or combination of variables indicated.



Appendix S7. Best selected models at small scales from 50m to 250m in the core region.

Scale	R_N^2	PCC	AUC	Kappa$_{0.5}$	Kappa$_{opt}$	Dist_river	Np_dist	Prox	Habitat	Crop_pas	Urban	Area	Perimeter	Shape_index	Veg_str	Radiation
50	0.7	0.88	0.872	0.751	0.8	X		X		X				X	X	X
	0.69	0.904	0.878	0.8	0.8	X		X	X					X	X	X
	0.66	0.857	0.907	0.704	0.755	X		X							X	X
150	0.55	0.833	0.74	0.642	0.642				X							
250	0.64	0.857	0.75	0.695	0.696		X		X	X		X		X	X	

Appendix S8. Conceptual model of habitat configuration and habitat amount effects proposed by Villard and Metzger (2014).

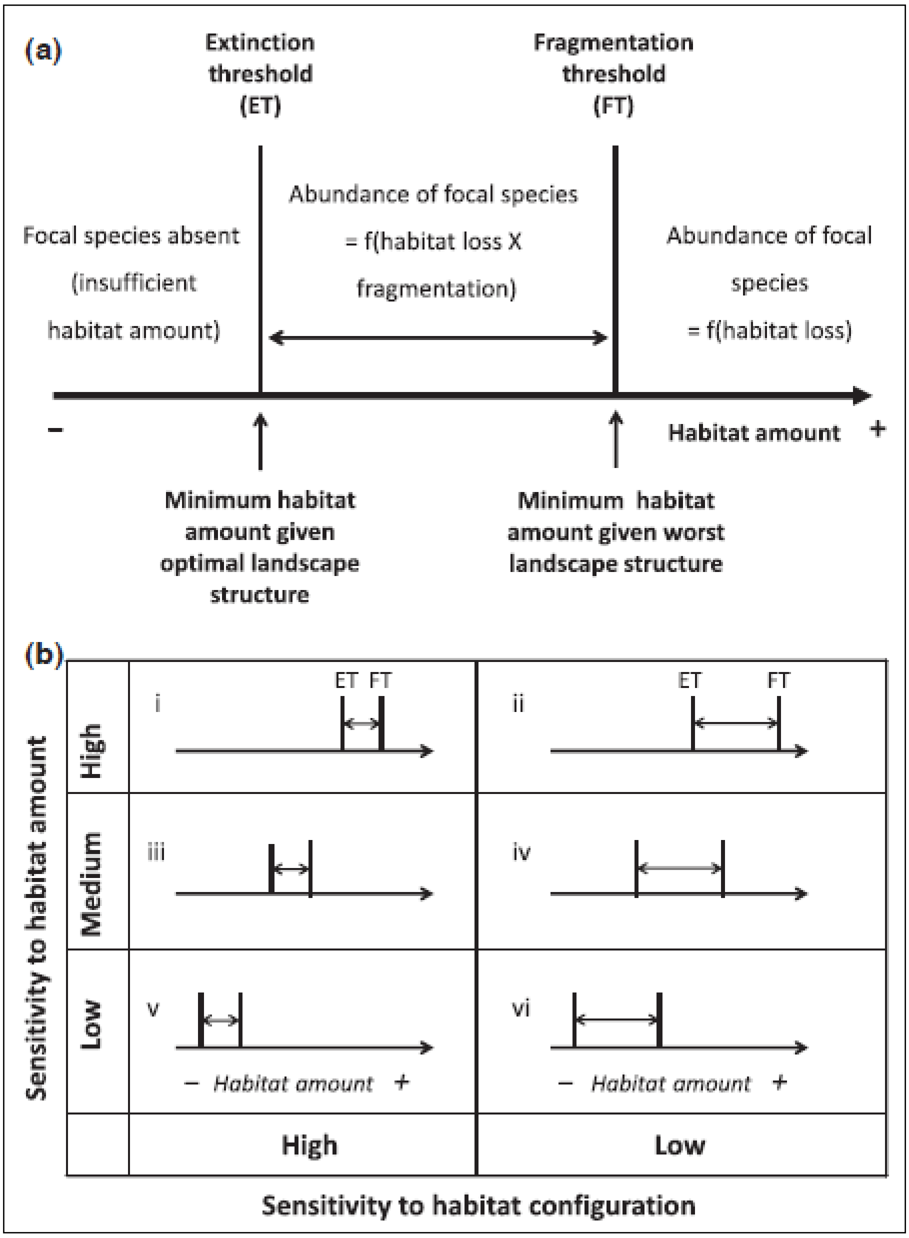


Figure S8.1. Conceptual diagram corresponding to Fig. 6 in Villard and Metzger (2014)

Appendix S9. Individual effects of non-scale and scale dependent variables.

	Core				Periphery			
	Estimate	Error	z	P(>|z|)	Estimate	Error	z	P(>|z|)
Area	0,831	0,663	1,254	0,21	0,611	1,275	0,479	0,632
Perimeter	-1,83	1,561	-1,17	0,242	3,5	2	1,75	0,0794
Per_area	-1,45	0,891	-1,63	0,103	2,24	1,46	1,53	0,1248
Shape_index	3,2	1,789	1,79	0,073	0,094	0,382	0,246	0,806
Isolation	-0,623	0,476	-1,31	0,1903	0,152	0,778	0,196	0,845
Veg_str	15,3	11,6	1,32	0,185	-1,45	8,85	-0,1637	0,87
Radiation	-0,071	0,452	-0,159	0,873	-22,5	26,2	-0,857	0,392

CORE

	Habitat				Crops and pastures				Urban				Proximity index			
Scale	Estimate	Error	z	P(>|z|)	Estimate	Error	z	P(>|z|)	Estimate	Error	z	P(>|z|)	Estimate	Error	z	P(>|z|)
50	5	2,078	2,41	0,0161	-1,88	1,48	-1,27	0,2046	-2,72	1,292	-2,1	0,035	0,195	0,243	0,804	0,422
150	7,4	2,869	2,58	0,0099	-1,72	1,395	-1,24	0,2166	-2,17	1,148	-1,89	0,058	0,257	0,241	1,066	0,286
250	9,99	3,916	2,55	0,0107	-1,83	1,492	-1,22	0,2209	-1,79	1,072	-1,67	0,094	0,289	0,245	1,178	0,239
500	11,56	4,736	2,44	0,0146	-1,75	1,64	-1,07	0,285	-1,642	1,102	-1,49	0,136	0,266	0,244	1,091	0,275
750	13,43	6,012	2,23	0,0255	-1,98	1,82	-1,09	0,277	-1,471	1,141	-1,29	0,197	0,254	0,242	1,048	0,295
1000	14,7	6,584	2,24	0,0252	-2,16	2,01	-1,08	0,282	-1,329	1,145	-1,16	0,245	0,281	0,25	1,125	0,261
1500	17,84	9,99	1,79	0,0742	-1,62	1,96	-0,828	0,408	-1,312	1,175	-1,12	0,264	0,338	0,238	1,42	0,156
2000	26,24	17,26	1,52	0,129	-1,05	1,83	-0,572	0,567	-1,479	1,28	-1,16	0,247	0,349	0,24	1,455	0,145
2500	17,21	8,38	2,05	0,0399	-0,74	1,79	-0,413	0,679	-1,588	1,379	-1,15	0,249	0,353	0,241	1,463	0,144
3000	19,82	9,89	2	0,045	-0,58	1,8	-0,322	0,748	-1,739	1,53	-1,14	0,256	0,356	0,242	1,469	0,142

PERIPHERY

	Habitat				Crops and pastures				Urban				Proximity index			
Scale	Estimate	Error	z	P(>|z|)	Estimate	Error	z	P(>|z|)	Estimate	Error	z	P(>|z|)	Estimate	Error	z	P(>|z|)
50	2	1,912	1,05	0,295	1,7	2,506	0,677	0,498	-0,272	1,289	-0,211	0,833	-8,159	3,36E+004	-0,0002	0,999
150	1,5	1,873	0,802	0,422	2,56	2,71	0,946	0,344	-1,874	1,553	-1,207	0,228	-0,779	0,559	-1,39	0,164
250	2,43	2,285	1,06	0,287	2,26	2,807	0,804	0,421	-2,729	1,768	-1,544	0,123	-0,838	0,554	-1,512	0,13
500	5,31	2,848	1,86	0,062	1,84	2,759	0,668	0,503	-4,95	2,586	-1,913	0,055	-0,686	0,497	-1,382	0,167
750	8,66	4,52	1,92	0,055	1,99	2,647	0,753	0,451	-4,362	2,353	-1,85	0,063	-0,616	0,459	-1,343	0,179
1000	8,37	4,95	1,69	0,091	1,11	2,661	0,417	0,676	-4,712	2,55	-1,849	0,064	-0,554	0,434	-1,277	0,202
1500	18,68	8,12	2,3	0,021	-0,229	2,841	-0,08	0,936	-4,691	2,63	-1,786	0,074	-0,751	0,528	-1,424	0,154
2000	23,75	9,68	2,45	0,014	0,99	3,332	0,297	0,766	-4,87	2,74	-1,778	0,075	-0,832	0,523	-1,592	0,111
2500	32,29	12,57	2,57	0,01	2,25	3,243	0,693	0,488	-5,46	2,93	-1,86	0,062	-0,721	0,48	-1,502	0,133
3000	37,25	15,37	2,42	0,015	3,76	3,39	1,11	0,267	-5,75	3,05	-1,89	0,059	-0,744	0,502	-1,48	0,139

	Dense woodland				Humid grassland			
	Estimate	Error	z	P(>|z|)	Estimate	Error	z	P(>|z|)
50	-0,053	2,293	-0,023	0,982	-20,839	13,853	-1,504	0,133
150	1,22	2,761	0,44	0,659	-14,506	13,76	-1,054	0,292
250	3,39	3,57	0,949	0,342	-14,436	14,572	-0,991	0,322
500	5,55	3,518	1,58	0,115	-24,309	19,676	-1,235	0,217
750	7,09	3,905	1,82	0,069	-37,171	25,54	-1,455	0,146
1000	7,96	4,193	1,9	0,057	-40,32	27,188	-1,483	0,138
1500	8,11	4,293	1,89	0,059	-73,026	37,31	-1,957	0,05
2000	8,51	4,426	1,92	0,054	-69,418	35,239	-1,97	0,048
2500	8,5	4,766	1,78	0,074	-73,266	39,725	-1,844	0,065
3000	7,82	5,14	1,52	0,128	-91,29	42,09	-2,17	0,03

9.3. Supporting information to Chapter 5

Appendix S1. Location of patches where surveys were carried out in the surroundings of Plovdiv, Bulgaria.

Patch	Latitude (°N)	Longitude (°E)
1	42.1424	24.7005
2	42.1560	24.7639
3	42.1622	24.7972
4	42.1510	24.8828
5	42.1246	24.8686
6	42.2286	24.8579
7	42.1498	25.1382

Appendix S2. Calculation of scale parameter through standardize major axis regression (SMA).

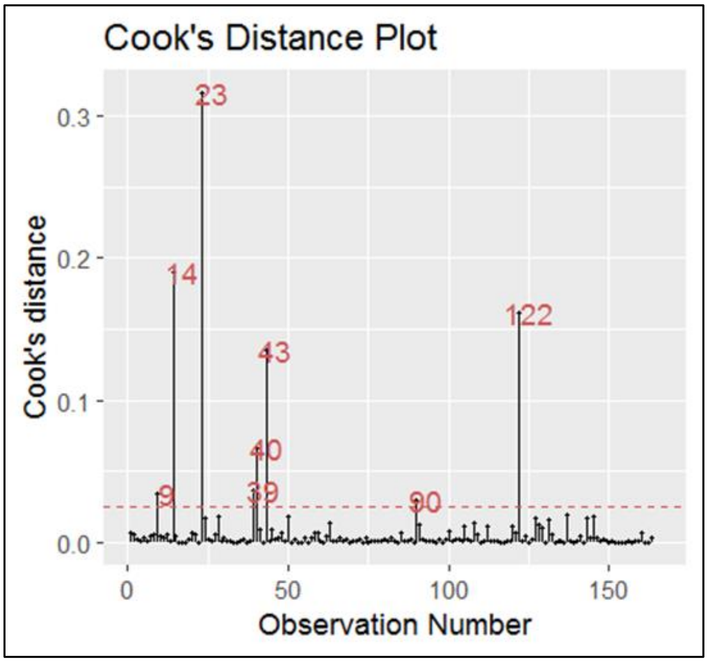


Figure S2.1. Outliers in an initial SMA. Individuals 14, 23, 43, 40 and 122 were removed to perform the definitive SMA.

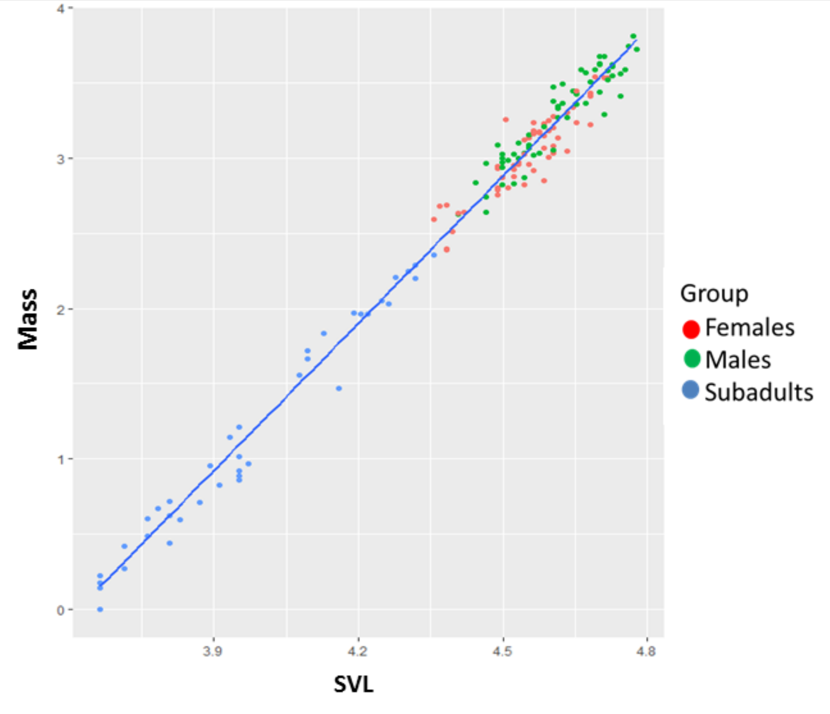
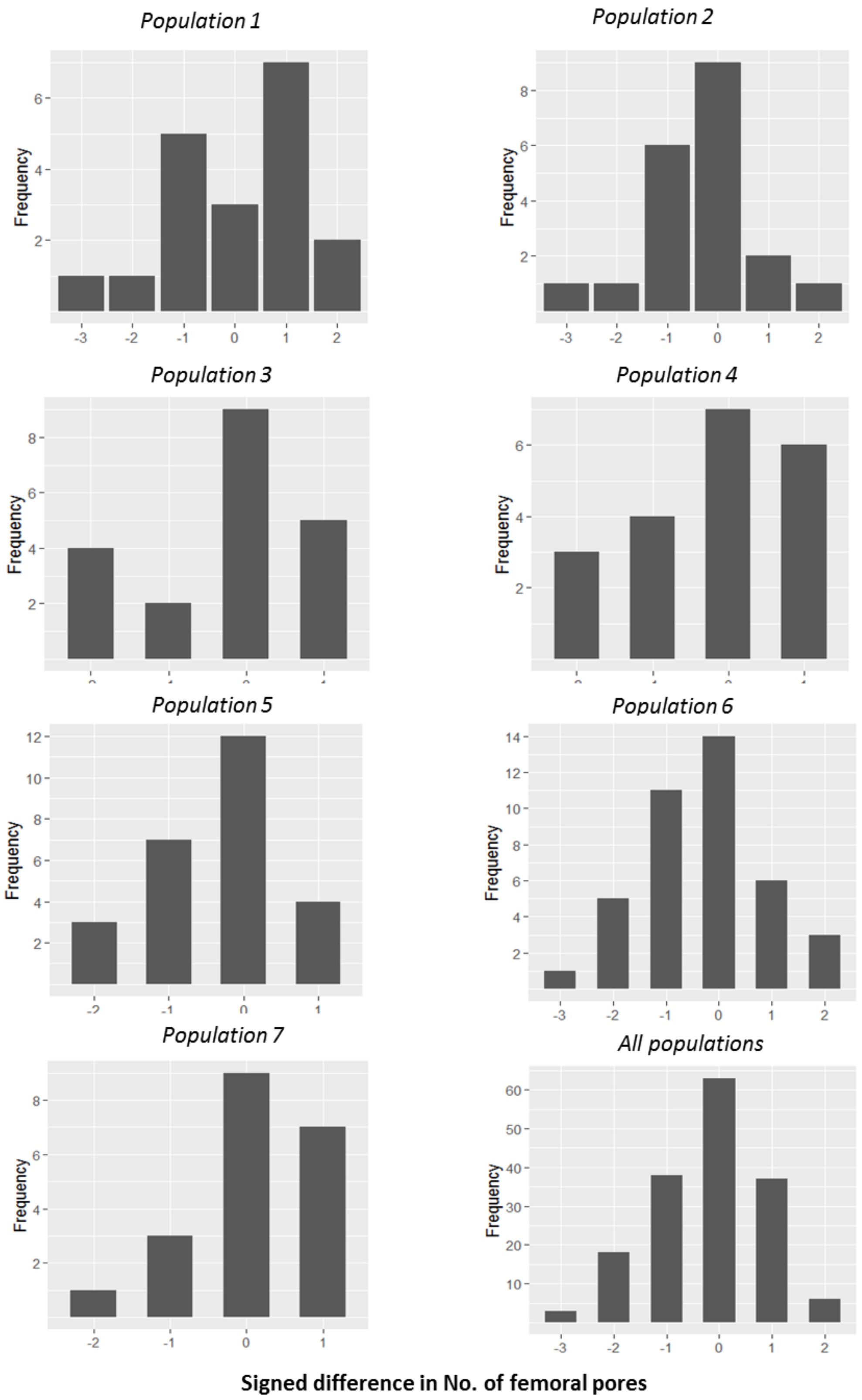


Figure S2.2. Final SMA from which the scale parameter was obtained.

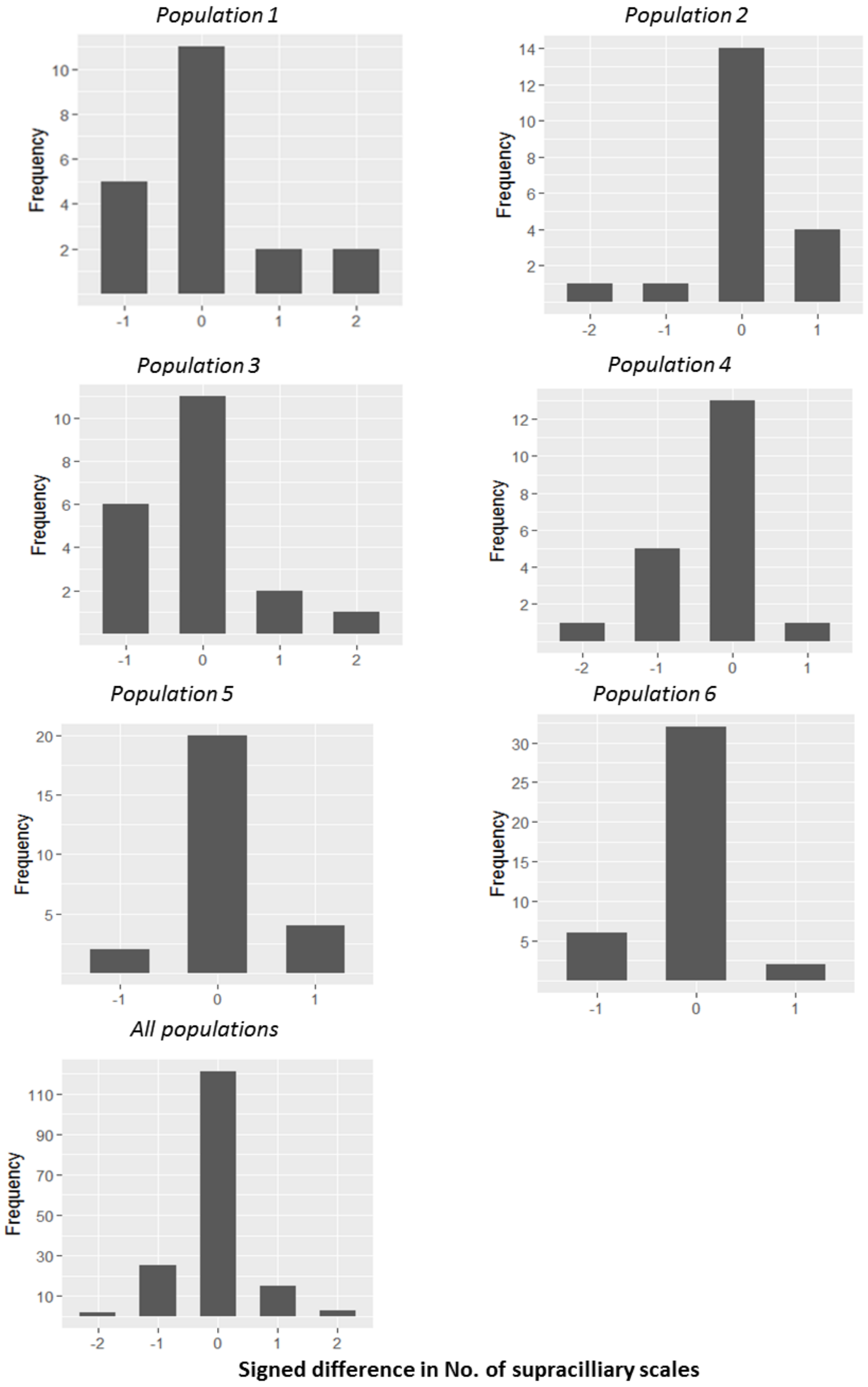
Appendix S3. Antisymmetry and directional asymmetry tests for the two metric traits.

Antisymmetry test (Anscombe Glynn kurtosis test)			**Directional asymmetry test** (D'Agotino skewness test)		
Kurtosis	**Z-value**	**P-value**	**Kurtosis**	**Z-value**	**P-value**
FA Front legs					
3.313	1.016	0.309	0.195	1.044	0.296
FA Hind legs					
2.879	-0.077	0.938	-0.016	-0.088	0.929

Appendix S4. Frequency distribution of signed differences in the number of femoral pores in each population and in all populations.



Appendix S5. Frequency distribution of signed differences in number of supracialliary scales in each population and in all populations. No individuals in population 7 had asymmetry.



Appendix S6. Predictor variables for each patch

Table S6.1. Patch characteristics

Patch	Area (km^2)	Perimeter (km)	Perimeter/Area ratio	Veg. Str.	Isolation (m)
1	0.103	1.508	14.686	1.050	340.714
2	1.653	2.317	1.401	1.056	33.032
3	2.021	1.785	0.883	1.095	20.247
4	0.716	1.479	2.066	1.026	5.328
5	0.398	5.236	13.163	1.001	326.982
6	0.458	1.005	2.193	1.045	7.701
7	2.098	7.332	3.495	-	209.967

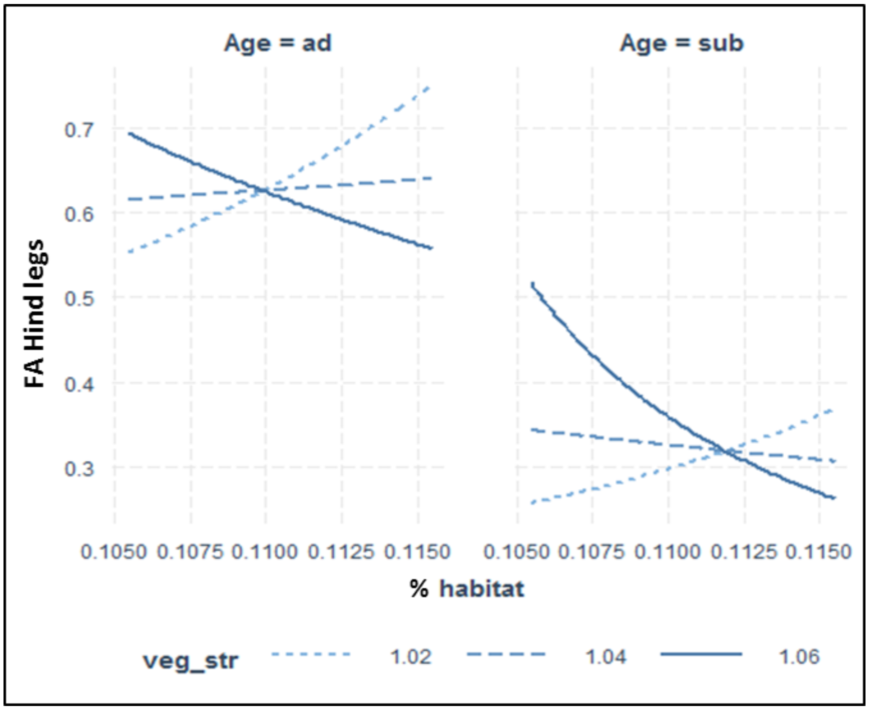
Table S6.2. Landscape composition variables at each scale for each patch.

Patch	50 m	150 m	250 m	500 m	750 m	1 km	1.5 km	2 km	2.5 km	3 km
	Habitat									
1	0.484	0.308	0.181	0.116	0.098	0.079	0.075	0.088	0.110	0.115
2	0.331	0.390	0.370	0.281	0.226	0.197	0.171	0.140	0.121	0.107
3	0.475	0.476	0.463	0.346	0.284	0.243	0.197	0.161	0.132	0.111
4	0.394	0.419	0.318	0.214	0.166	0.137	0.109	0.100	0.104	0.115
5	0.263	0.383	0.410	0.327	0.267	0.199	0.146	0.136	0.114	0.105
6	0.607	0.440	0.320	0.193	0.138	0.119	0.115	0.109	0.113	0.107
	Urban areas									
1	0.000	0.000	0.000	0.010	0.017	0.021	0.053	0.078	0.105	0.147
2	0.048	0.063	0.136	0.233	0.265	0.286	0.340	0.391	0.436	0.474
3	0.353	0.467	0.510	0.659	0.743	0.803	0.869	0.892	0.895	0.909
4	0.255	0.413	0.591	0.783	0.878	0.937	1.010	1.027	0.993	0.937
5	0.372	0.391	0.401	0.409	0.400	0.428	0.491	0.522	0.531	0.542
6	0.338	0.542	0.648	0.776	0.867	0.879	0.817	0.813	0.843	0.871
	Cropland									
1	0.054	0.460	0.678	0.769	0.751	0.807	0.834	0.768	0.706	0.653
2	0.271	0.231	0.260	0.319	0.370	0.392	0.394	0.393	0.382	0.370
3	0.033	0.023	0.020	0.023	0.023	0.021	0.024	0.047	0.073	0.085
4	0.026	0.013	0.015	0.016	0.018	0.019	0.017	0.022	0.037	0.056
5	0.083	0.065	0.078	0.195	0.269	0.294	0.301	0.291	0.303	0.307
6	0.018	0.030	0.049	0.072	0.072	0.083	0.121	0.133	0.111	0.099

Appendix S7. Levene's Test for homogeneity of variance applied to test differences among years.

Trait	Df	F-value	P-value
BCI	1	0.158	0.690
Tick load	1	0.013	0.908
FA Front legs	1	0.27	0.603
FA Hind legs	1	0.016	0.899
FA Femoral pores	1	0.09	0.763
FA Supraciliary scales	1	17.026	$5.8e^{-5}$

Appendix 8. Interactions between proportion of habitat, vegetation structure and age on fluctuating asymmetry of hind legs.



10. Publications

- **Chapter 3**

Prieto-Ramirez AM, Pe'er G, Rödder D, Henle K (2018) Realized niche and microhabitat selection of the eastern green lizard (*Lacerta viridis*) at the core and periphery of its distribution range. Ecology and Evolution, 8, 11322-11336. doi: 10.1002/ece3.4612

- **Chapter 4**

Prieto-Ramirez AM, Röhler L, Cord AF, Pe'er G, Rödder D, Henle K (2020) Differential effects of habitat loss on occupancy patterns of the eastern green lizard *Lacerta viridis* at the core and periphery of its distribution range. PLoS ONE 15 (3): e0229600. https://doi.org/10.1371/journal.pone.0229600

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ORIGINAL RESEARCH

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Realized niche and microhabitat selection of the eastern green lizard (*Lacerta viridis*) at the core and periphery of its distribution range

Ana M. Prieto-Ramirez[1,2] | **Guy Pe'er**[3,4,5] | **Dennis Rödder**[2] | **Klaus Henle**[1]

[1]Department of Conservation Biology, Helmholtz Center for Environmental Research UFZ, Leipzig, Germany
[2]Department of Herpetology, Zoological Research Museum Alexander König ZFMK, Bonn, Germany
[3]Department of Economics and Department of Ecosystem Services, UFZ Leipzig, Leipzig, Germany
[4]German Center for Integrative Biodiversity (iDiv), Halle-Jena-Leipzig, Leipzig, Germany
[5]Universität Leipzig, Leipzig, Germany

Correspondence
Ana M. Prieto-Ramirez, Department of Conservation Biology, Helmholtz Center for Environmental Research UFZ; Department of Herpetology, Zoological Research Museum Alexander König ZFMK, Leipzig, Germany
Email: ana-maria.prieto-ramirez@ufz.de

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Abstract

The available range of habitats and suitable abiotic conditions like temperature and radiation tends to be narrower toward the periphery of the distribution range of species. Peripheral populations of generalist species could then be more specialized and have a smaller and differentiated realized niche (habitat niche in our study) compared to populations at the core. Likewise, patterns of microhabitat selection can differ between periphery and core. In our study, we compared niche size and microhabitat selection among core (Bulgaria) and northern peripheral (Germany, Czech Republic) populations of *Lacerta viridis* and estimated niche differentiation among regions. We collected data on vegetation structure and abiotic parameters at the microhabitat scale in each region. In order to compare niche size among regions and estimate niche differentiation, we built multidimensional niche hypervolumes. We applied generalized linear mixed models and model averaging, accounting for spatial autocorrelation when necessary, to analyze microhabitat differences among regions and microhabitat selection in each region. Peripheral populations were more specialized, having a smaller niche than core ones, and their niche differed from that in the core (Sørensen overlap in all comparisons <0.3). Microhabitats at the periphery had lower radiation and soil compaction and less structured vegetation. Microhabitat selection at the core depended solely on abiotic parameters, while at the periphery it was defined by only vegetation structure (Czech Republic) or a combination of both, vegetation structure, and abiotic factors (Germany). Thus, peripheral populations seem to compensate for overall harsher climatic conditions by responding to different parameters of the microhabitat compared to core populations. We suggest specific conservation measures for *L. virids* in each studied region and point out the general implications of a higher specialization degree of peripheral populations in relation to climate change and habitat fragmentation.

KEYWORDS
Lacerta viridis, mixed models, niche differentiation, niche hypervolume, peripheral populations, spatial autocorrelation

1 | INTRODUCTION

Availability of resources and environmental conditions changes along the distribution range of species, with especially marked differences along the gradients of broadly distributed species (Gaston, 2009; Kirkpatrick & Barton, 1997). These patterns can lead to ecological differences between populations of the same species living either at the core or at the periphery of its distribution range (Brown, Stevens, & Kaufman, 1996). The Kühnelt principle (Kühnelt, 1965) states that the range of colonizable habitats is wider at the core where environmental conditions are optimal, whereas at the periphery conditions are suboptimal and fewer microhabitats are suitable for the species. Therefore, populations at the core should be habitat generalists ("euryoecious"), while populations at the periphery of the species' range can, in comparison, be more specialists ("stenoecious") (Böhme & Rödder, 2014). Under the Hutchinson's concept of ecological niche (Hutchinson, 1957), this suggests that populations living at the periphery of the distribution range will have a smaller locally realized niche breadth compared to generalist core populations. Studies quantifying these differences in animal populations are scarce, but evidence of smaller niche breadth at the periphery compared to the core has been found in a few taxa. For instance, the niche breadth and availability of resources of three invertebrate species, the butterfly *Plebejus argus*, the ant *Myrmica sabuleti*, and the grasshopper *Chorthippus vagans*, were found to decrease toward the northern colder edge of their distribution range (Thomas, Rose, Clarke, Thomas, & Webb, 1999). In vertebrate species, Lappalainen and Soininen (2006) found that the niche breadth of fresh water percid and cyprinid fishes was narrower toward the northern edge of the distribution range, and Yurkowski et al. (2016) demonstrated that niche breadth at the population level decreased with increasing latitude in ringed seals (*Pusa hispida*) and beluga whales (*Delphinapterus leucas*).

Additional to differences in niche breadth, niche differentiation can also be found when comparing core and peripheral populations. Studies investigating niche differentiation in animal species are focused on evolutionary niche divergence among populations across the species' distribution range (Ahmadzadeh et al., 2013; Cadena & Loiselle, 2007), with the niche of relict populations being usually found to be differentiated from that of more central populations (Lozano-Jaramillo, Rico-Guevara, & Cadena, 2014). Many approaches exist for such studies, such as occupancy models with climatic, land cover, or other environmental variables as covariates (Araújo & Peterson, 2012; Chefaoui, Hortal, & Lobo, 2005; Hirzel & Le Lay, 2008), and models that use presence/pseudoabsence data (Morales, Fernández, Carrasco, & Orchard, 2015). These studies are generally done at a macroscale of large regions (often including the whole distribution of a species) and using a coarse spatial resolutions of 1 km^2 or more (Pearson & Dawson, 2003). Such studies are unable to assess the effects of environmental factors that have a much finer spatial variability. There is a lack of studies on animal species testing niche differentiation by using field data at such microhabitat scale that allows deeper insights into intraspecific niche differences between peripheral and core populations, and into the microhabitat selection patterns shaping these differences. Elucidating such differences is important for understanding ecological processes like range shifts under global change, as well as for promoting effective conservation measures for edge populations of threatened species (Lesica & Allendorf, 1995; Peterman, Feist, Semlitsch, & Eggert, 2013).

Given their sensitivity to environmental changes and thermal dependency, reptiles are of particular interest to study niche and microhabitat selection in regions with different ranges of available habitats and climatological regimes (Buckley, 2010; Cunningham, Rissler, Buckley, & Urban, 2016). Moreover, for some taxa like lacertid lizards, there is enough qualitative information about niche differences between core and peripheral populations, like the known differences in the diversity of habitats occupied in core regions of the distribution range compared with the northern periphery (Korsós, 1982; Olsson, 1988). *Lacerta viridis*, for example, is a common species in the Balkan Peninsula in Eastern Europe and Asia Minor (Elbing, 2001) and has its northern distribution range located in Germany and in the Bohemian region of the Czech Republic. In core regions, the species is found in habitats ranging from slopes with rock covering, bushlands, and road edges to mixed forest and pine plantations, including several seminatural and urban habitats (Heltai, Sály, Kovács, & Kiss, ; Covaciu-Marcov et al., 2009; Popgeorgiev & Mollov, 2005). In Germany and Czech Republic, where thermal conditions and other limiting factors like daily hours of sunshine (Frör, 1986; Laube & Leppelsack, 2007) do not provide many suitable habitats for the species, it is scarce and mostly found in open areas and river valleys (Böhme & Moravec, 2011; Böhme, Schneeweiß, Fritz, Schlegel, & Berendonk, 2007). However, despite substantial descriptive evidence suggesting a narrower range of habitats used by northern edge populations, there are no quantitative studies that explicitly quantify and compare the niche between core and peripheral populations, nor any study comparing the factors that determine microhabitat selection in different regions.

In the present study, we compare the specialization degree with respect to realized niche, and microhabitat selection of populations of *L. viridis* (Figure 1) living either at the core (Bulgaria) or at the northern periphery (Germany and Czech Republic) of the species' distribution range (Figure 1).The studied populations in the Czech Republic are relict populations, which are not part of the continuous distribution of the species, and in Germany and the Czech Republic, the species is critically endangered and highly protected according to the EU Habitats Directive and national conservation regulations.. On the other hand, in Bulgaria, *L. viridis* is the most common lizard species (Beutler & Rudolph, 2003; Zavadil & Moravec, 2003). We expected to find (a) smaller realized niches in northern edge populations compared to the core, with a niche differentiation present in populations located around Prague (relicts) but not in those in Passau (which are part of the continuous distribution range); (b) higher preference of *L. viridis* in the periphery for specific vegetation structures at the microhabitat scale, like low and open vegetation, as compensation for overall suboptimal climatic conditions; and (c)

FIGURE 1 Adult male of the eastern green lizard *Lacerta viridis* in Passau, Germany. Photo credits: AMPR

higher influence of vegetation structure in the microhabitat selection in the northern periphery, where the availability of suitable habitats for the species is a limiting factor, while in the core, where the available range of habitats is broader, abiotic parameters will have a higher influence in the microhabitat selection.

2 | MATERIALS AND METHODS

2.1 | Study regions and site selection

The study region at the core of the species' distribution was located in the Thracian Plain of Bulgaria, in the surroundings of Plovdiv (Figure 2a). Bulgaria is the historical and current range core of the species (Popgeorgiev & Mollov, 2005),and in the Thracian Plain are represented most of the habitats in which *L. viridis* is present in central regions, from road edges and open shrublands to mesophilic forest. The study regions at the species' northern periphery were located near Passau (Bavaria, Germany) and in the surroundings of Prague (Bohemia, Czech Republic). From now on, we will use the term *periphery* to refer to the study regions located in the northern periphery. In Passau (Figure 2b), populations are found along the Danube Valley in rocky outcrops in the oak and hornbeam forest and on the southern exposed cliffs, but mostly along an abandoned railroad that runs parallel to the river. Populations of *L. viridis* in the surroundings of Prague (Figure 2c) are relict populations located in open stony areas of the oak forest and on the slopes of the Moldova valley, as well as those of other valleys perpendicular to the Moldova River.

The extent of the areas where the study was carried out in each region was 325 km^2, 288 km^2, and 522 km^2 in Plovdiv, Passau, and Prague, respectively. Based on information available about places where the species has been found and on information about the habitat of *L. viridis* reported in the literature, we identified potential suitable sites into these areas by using satellite maps. Each site represented a portion of habitat potentially holding a population and separated from other sites/populations by structures in the landscape (e.g., agriculture, highways) that do not represent habitat. In order to reduce the effects of probable local processes present in each region, we increased as much as possible the number of sites, by visiting all potentially suitable sites present in the study area in each region. In total, we visited 40, 27 and 33 sites visited in Plovdiv, Passau, and Prague, respectively. Also, to avoid bias in the habitat types visited in each region, at the periphery, we also visited sites with similar vegetation structure to those where *L. viridis* was found in the core (e.g., mixed forest). In Plovdiv, the area of the sites was 0.1–3.91 km^2 and the distance between sites was 5–6,100 m; in Passau, sites had an area of 0.23–4.51 km^2 and were apart from one another 10–800 m; in Prague, sites were 0.3–2.28 km^2 large and the range of distances between was 5–2,171 m.

2.2 | Field survey and data collection

Field surveys took place in Plovdiv and Passau in 2014 and in Prague in 2015. In order to make the surveys comparable among regions, they were carried out in each region starting with the onset of the reproduction season: early April in Plovdiv and early to mid May in the two peripheral regions. Sampling lasted till late May in Plovdiv (core) and till June and July in Passau and Prague. This shift in sampling made average maximum air temperatures per sampling month similar among sites: 18.5 and 23.4°C in Plovidiv, 23.1 and 24.8°C in Passau, and 22.5 and 24.6°C in Prague).

Data were gathered around a total of 363 points, from which 152 were in the core (presence: 102; absence: 50), 117 in the periphery-Pa (33; 84), and 94 in the periphery-Pr (29; 65). In the core region, lizards were found in a variety of habitats from shrublands to mixed forest, in riverbeds as well as far away from any water body. In Passau, the presence of the lizards is restricted to the lower part of the narrow Danube valley, where the habitat is represented by stony areas with low vegetation. Finally, in Prague, lizards were mainly found in the open rocky slopes of the Vltava valley and the valleys of tributary rivers.

We used an occupancy survey design to incorporate detection probability. Following study designs proposed by Mackenzie and Royle (2005) and based on estimates of detection probability for similar species (Janssen & Zuiderwijk, 2006; Sewell, Guillera-Arroita, Griffiths, & Beebee, 2012), the number of visits per site was set to two, one in the morning (9:00–12:00 a.m.) and one in the afternoon (14:00–19:00 p.m.) in accordance with the species' daily activity pattern (Korsós, 1983). The second visit in each population was carried out either on the same day or one day later. Only in two populations in Plovdiv (core) and two in Prague visits were separated by 7 days.

Each visit lasted one hour, and sites were surveyed by means of line transects. Walking speed was standardized at 20 m/min. Thus, one hour visit corresponded to 1,200 m, which were divided into transects of variable lengths (50–400 m). Transects were systematically placed in order to represent the area of the site and all different habitat types present at it. With the use of maps and based on the relative coverage of each habitat type into each site, we calculated the length of each transect and the number of transects that had to be placed in each habitat type. The entire

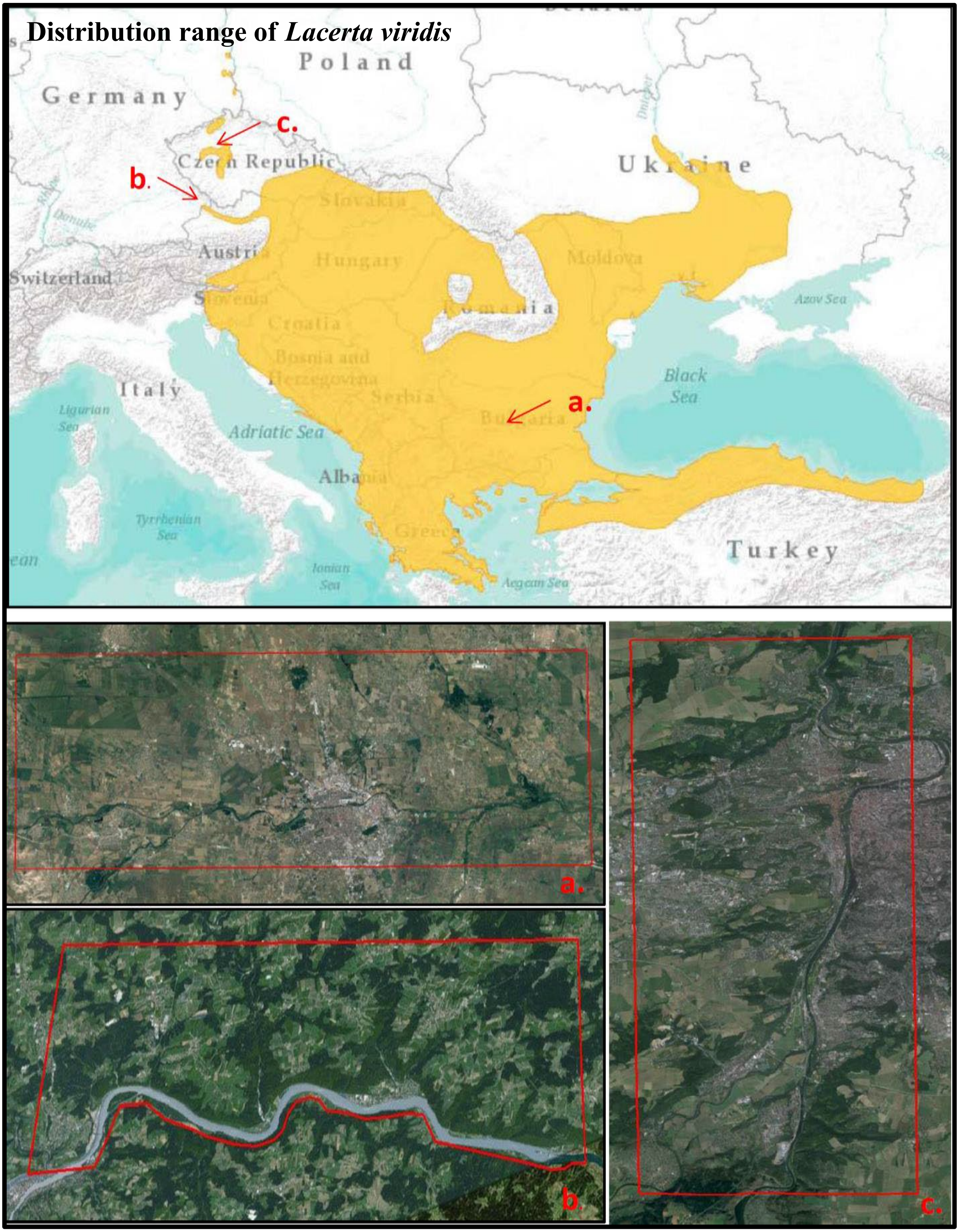

FIGURE 2 Distribution range of *Lacerta viridis* and study sites in the core located in Plovdiv, Bulagria (a), and in two peripheral regions corresponding to Passsau, Germany (b) and Prague, Czech Republic (c)

length of each transect was placed only in one habitat type and did not crossed to another. The number of transects surveyed per site ranged from 3 to 12. To avoid double counting of observed lizards among transects, the minimum distance between transects was 100 m. A width of 2.5 m at each side of the transect was set to carefully inspect visually for *L. viridis*. A metal stake was placed on the specific point where each lizard was seen and coordinates were taken. In a 25-m^2 plot around this point (presence plots), data on vegetation structure and abiotic parameters were recorded. Percentage of vegetation coverage was visually estimated for the following categories: herbs with a height lower than 30 cm (herbs1), between 40 and 80 cm (herbs2) and higher than 90 cm (herbs3); woody plants < 2 m and woody plants > 2 m; dry leaves, rocks and fallen trunks (rocks_trunks), bare soil, way (road edges, dirt tracks, walking paths), and coverage of branches (Branches). Vegetation height was measured with a retractable measure tape. Abiotic parameters included air temperature at 1.5 m height, 10 cm height and ground surface, soil compaction, soil composition, slope, and aspect. Temperatures and soil compaction were measured at three random points (different for each parameter) within each plot and then averaged for the analysis. Soil compaction was measured with a manual penetrometer, and soil composition was qualitatively classified into humus, organic, clay, gravel, or sand. Temperature was measured with a precision digital thermometer (Greisinger GTH 175/PT), exposition was taken with a GPS (Garmin 62S) and slope with a compass (Global system DS 50G).

In order to analyze microhabitat preference of the species, the same data were collected in 25-m^2 plots around random points along each transect, where the lizard was not seen at the time of the survey. These random plots are specific locations that the lizard might use at other time and where it might not be permanently absent, but in order to simplify terminology, from now on we will call them absent plots. Random points were chosen by blindly selecting points along each transect in the GPS. Data gathering in each presence/absence plot took approximately 15 min, which were not accounted for as sampling time, and in consequence one hour of surveying lizards represented 2–4 hr of data sampling. Therefore, due to time constrains, data were gathered around a maximum of three "presence" points per transect per visit in the case more than three lizards were encountered, and a minimum of one random "absence" point per transect. If a lizard was encountered in an already surveyed plot during the second visit, data were not included in the analysis to avoid pseudo-replication.

Additionally, to variables measured in the field, we estimated radiation at each data point and at the specific time range of the study in each region with the "*Potential incoming solar radiation*" tool of the software SAGA. For this purpose, elevation maps with 30-m resolution were obtained from the USGS database. Aspect was transformed into two variables: cosine values, representing the South-North component (S-N aspect), and sine values, representing the West-East component (W-E aspect). S-N aspect values increase from south to north, and W-E aspect values increase from west to east.

2.3 | Data preparation and variable selection

The following procedure was performed for the data set including all regions (see section Comparison of microhabitats among regions), and separately for the individual dataset of each region (see section Microhabitat selection in each region).Vegetation structure data were ARCSIN transformed, tested for correlation with Spearman rank correlation, and assessed for collinearity by estimating the variance inflation factor (VIF). Variables with correlation > 0.6 or VIF > 3 were excluded from analysis (Zuur, Ieno, & Elphick, 2010). In the dataset, including all regions, no correlation or collinearity was found and all variables were retained (Supporting Information Appendix S1, Table S1.1). In Plovdiv, the variable Herbs 2 had a high collinearity (VIF = 17) and was excluded from the analysis of microhabitat selection (see analysis description below). In the other two regions, neither correlation nor collinearity was found (Supporting Information Appendix S1, Table S1.2–S1.4). Therefore, all variables were retained. Continuous abiotic variables were log-transformed and tested for correlation with the Pearson correlation test and also for collinearity with VIF. Variables with correlation >0.6 or VIF > 3 were excluded. Air temperature, temperature at 10 cm height, and temperature at soil surface were correlated ($r > 0.9$) in all study regions; hence for further analysis, only the temperature at the soil surface was used, as lizards' bodies are directly in contact with it, and its influence on microhabitats may be the strongest. No correlation or collinearity was found in other variables (Supporting Information Appendix S1, Table S1.1–S1.4). Correlations between each abiotic continuous variable and the factor soil composition were tested using linear regression. In Plovdiv, soil composition was correlated with soil compaction ($F_{4,136} = 3.75$, $p < 0.01$) and radiation ($F_{4,136} = 10.08$, $p < 0.001$) and therefore removed from the analysis. In Passau and Prague, soil composition was correlated with soil compaction ($F_{2,98} = 3.14$, $p = 0.047$; $F_{3,73} = 4.45$, $p = 0{,}038$). To select between soil compaction and soil composition, we tested the effect of each of the two variables on the presence/absence of the lizard in each region and retained the variable with the strongest effect (Poulin, Villard, Edman, Goulet, & Eriksson, 2008). In all regions, soil composition was least correlated with presence/absence of *L. viridis*, and therefore, for further analysis this variable was removed.

2.4 | Statistical analysis

2.4.1 | Niche size and specialization

To compare realized niches among regions, multidimensional niche hypervolumes were derived with the package "Hypervolume" from R software (Blonder, 2015). All calculations were performed separately for vegetation structure and abiotic parameters in each region. Data were scaled and centered, and principal component analysis (PCA) with the R package "ade4" (Dray, Dufour, & Thioulouse, 2015) was applied to the whole dataset including all points of all regions. This reduction in dimensionality was necessary as the niche hypervolume analysis requires orthogonal axes. Principal components

TABLE 1 Loadings of each variable in the principal components with eigenvalues >1 selected to build the niche hypervolumes for vegetation structure and abiotic parameters

	Principal components					
	PC1	PC2	PC3	PC4	PC5	PC6
Vegetation structure						
Herbs 1	0.19	0.73	−0.37	−0.08	0.09	0.12
Herbs 2	−0.43	−0.32	0.16	−0.24	0.48	0.06
Herbs 3	−0.38	−0.07	−0.28	0.16	−0.38	−0.49
Woody plants <2 m	0.10	0.17	0.64	0.30	−0.14	0.38
Woody plants >2 m	0.20	0.01	0.17	−0.51	0.26	−0.15
Dry leaves	0.50	−0.46	−0.11	0.05	−0.14	0.07
Rocks_trunks	−0.08	−0.25	−0.35	0.46	0.12	0.43
Bare soil	0.17	0.07	0.37	0.41	0.09	−0.58
Way	−0.11	−0.06	0.15	−0.40	−0.70	0.17
Branches	0.53	−0.24	−0.17	−0.12	−0.01	−0.13
Abiotic parameters						
Temperature	−0.34	−0.09	0.72			
Soil compaction	0.37	0.35	0.53			
S-N aspect	0.05	−0.81	0.13			
W-E aspect	−0.25	0.06	−0.43			
Slope	−0.56	0.41	0.06			
Radiation	0.60	0.20	−0.06			

with eigenvalues > 1 were used to construct the hypervolumes of the realized niches in each study region (see Table 1 for variable loadings). Six principal components were selected for vegetation structure (77.05% of total variance) and three for abiotic parameters (62.89% of total variance). We used a fixed bandwidth of 0.5 with 1,000 Monte Carlo samples per data point to calculate the volumes. Hypervolume units are standard deviations (*SD*). Besides the size of each hypervolume, we also estimated the intersection and the union, and for testing niche differentiation, we estimated the Sørensen overlap index for each comparison, which is an index measuring the similarity among two samples with values varying from 0 for low overlap to 1 for complete overlap (Blonder, Lamanna, Violle, & Enquist, 2014).

2.4.2 | Comparison of microhabitats among regions

For comparing microhabitats among regions, a multinomial logistic regression was run using the "*multinom*" function of the "nnet" R package (Ripley & Venables, 2016), with "region" as response variable. Analysis was first done separately for vegetation structure and abiotic parameters. After fitting a global model with all variables of either vegetation structure or abiotic parameters, all possible models with a reduced number of parameters were generated with the "*dredge*" function of the "MuMIn" R package (Bartón, 2015). Model comparison was based on Akaike's information criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002). All models with ΔAICc<2 relative to the best model were selected, and parameters were estimated by averaging across these models with the "*model.avg*" function of "MuMIn" package. Relative variable importance (RVI) was calculated by summing the Akaike weights of each variable across the selected models. Variables with RVI > 0.6 were considered important (Kennedy et al., 2013). Important variables of both sets of variables, vegetation structure and abiotic parameters, were then combined in a third global model. Again, all possible models were generated and those with ΔAICc < 2 were averaged. We selected the approach of analyzing vegetation structure and abiotic parameters separately, and then combine most important variables of both averaged models in order to avoid overfitting of the global model, which is a common risk in mixed models that tends to overweight the variables averaged through the best models (Grueber, Nakagawa, Laws, & Jamieson, 2011).

2.4.3 | Microhabitat selection in each region

We applied generalized linear mixed models GLMM, with plot presence/absence as response variable, site occupancy (i.e., the presence or absence of the lizard in each visited site) as random factor and variables of vegetation structure or abiotic parameters as fixed factors. Analyses were initially done separately for vegetation structure and abiotic parameters. For each region, a full model containing all variables, either of vegetation structure or of abiotic parameters, was fitted using the "*glmer*" function of the "lme4" R package (Bates, Maechler, Bolker, & Walker, 2016) with a logit link function and binomial error distribution. We tested for spatial autocorrelation of residuals (SACR) and when present, we applied principle coordinates of neighbor matrices (PCNM) (See "Detection and correction of spatial autocorrelation"). We then proceeded as described in Comparison of microhabitats among regions to generate all possible models,

TABLE 2 Comparison among the realized niche size in Plovdiv (Pl), Passau (Pa), and Prague (Pr)

Comparison	Volume 1	Volume 2	Intersection	Union	Sørensen overlap
Vegetation structure					
Pl–Pa	90.89	28.85	6.69	113.05	0.11
Pl–Pr	90.89	27.03	5.93	111.98	0.10
Pa–Pr	28.85	27.03	2.38	53.50	0.08
Abiotic parameters					
Pl–Pa	32.89	20.97	10.16	47.70	0.37
Pl–Pr	32.89	23.24	4.29	51.84	0.15
Pa–Pr	20.97	23.24	6.32	37.89	0.28

Note. Volume 1 and 2 correspond to the first and second region mentioned in the name of each comparison.

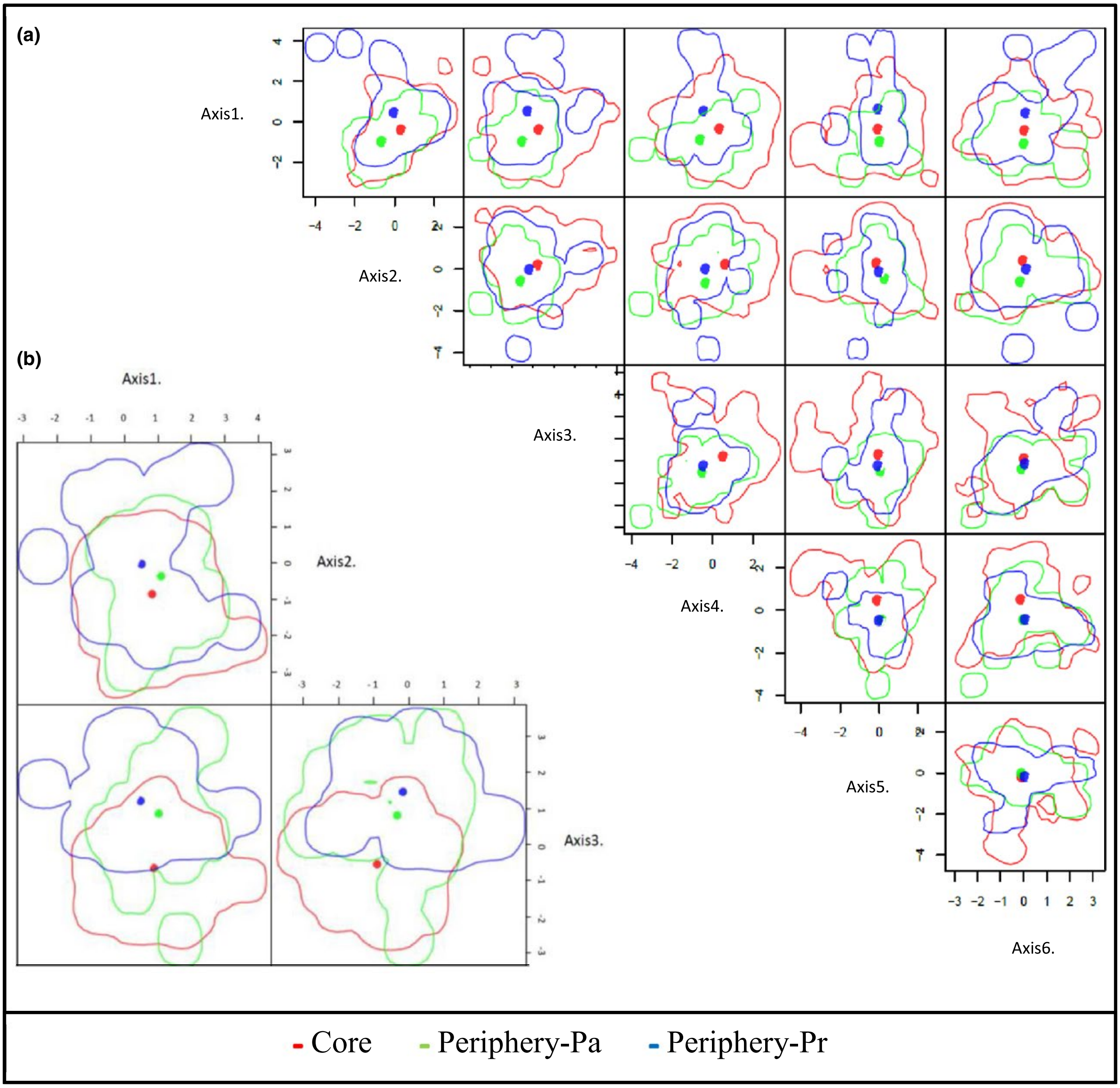

FIGURE 3 Two dimension (2D) representation of the multidimensional niche hypervolumes of realized niches for vegetation structure (a, 6 dimensions) and abiotic parameters (b, 3 dimensions) in the core of the distribution range of *L. viridis* (core, red), in the periphery in Passau (periphery-Pa, green) and in the periphery in Prague (periphery-Pr, blue). Dimensionality of each niche hypervolume corresponds to the number of principal components with eigenvalue >1

averaged through those with ΔAICc < 2 and combine the most important variables of both the vegetation structure and abiotic parameters averaged models. We checked again for VIF and for SACR, and the process of model averaging was repeated to obtain the final model that includes the most important variables among vegetation structure and abiotic factors. For each final model, we report conditional R^2 corresponding to the variance explained by fixed factors and random term together, and marginal R^2 representing the variance explained by fixed factors only (Nakagawa & Schielzeth, 2013).

2.4.4 | Detection and correction of spatial autocorrelation

All global models (vegetation structure, abiotic parameters, or combinations thereof) of microhabitat selection in each region were tested for spatial autocorrelation of model residuals (SACR) by estimating Moran's I index, calculating Moran's I-based correlograms and computing autocorrelation of residuals. Correction for SACR was done by means of principal coordinates of neighbor matrices (PCNM). PCNM are a type of Moran's eigenvector maps and consist of calculating spatial eigenvectors based on a matrix of truncated distances. The obtained PCNM vectors can then be added into the model as fixed terms to account for SACR (Borcard & Legendre, 2002) (Supporting Information Appendix S2).

3 | RESULTS

3.1 | Niche size and specialization

The realized niche of vegetation structure was largest in the core, followed by the periphery-Pa and the periphery-Pr (Table 2, Figure 3a). The realized niche of vegetation structure was found to differ in both peripheral regions from the niche in the core with the same degree of differentiation (Sørensen overlap = 0.1). Percentages of intersected niche volume ranged between 21.93%–23.18% for the peripheries and 6.5%–7.36% for the core. Between peripheral regions, there was also differentiation (Sørensen overlap = 0.08) and low percentages of overlapped niche volumes (8.24% for periphery-Pa and 8.80% for periphery-Pr).

The realized niche based on abiotic parameters was also largest in the core, but in this case, it was followed by that in the periphery-Pr and the smallest abiotic niche was in the periphery-Pa (Table 2, Figure 3b). In both peripheral regions, it differed from that in the core, with the lowest overlap found between the Periphery-Pr and the core (Sørensen overlap = 0.15), with 18.45% of the niche in periphery-Pr intersecting with 13.04% of the niche in the core. Between periphery-Pa and core (Sørensen overlap = 0.37) intersected volumes were 48.45% and 30.89%, respectively. The comparison between peripheries also showed niche differentiation (Sørensen overlap = 0.28), and 30.13% of the niche of Periphery-Pa overlapped with 27.19% of the niche in Periphery-Pr.

3.2 | Comparison of microhabitats among regions

With the multinomial logistic regression (Table 3), we found that the most important variables differentiating microhabitats used among regions were radiation, soil compaction, Herbs1, Herbs2, Herbs3, woody plants<2 m, woody plants>2 m, and Way (RVI = 1). In both peripheral regions, radiation and soil compaction were lower compared to the core region. Also, herbs and woody plants had a lower proportion in microhabitats used in peripheral regions compared to the core region. When comparing between peripheral regions microhabitats used in periphery-Pr had an even lower radiation and proportion of herbs and woody plants<2 m, but higher soil compaction and woody plants>2 m.

TABLE 3 Parameter estimates with 95% confidence interval (LCL and UCL) from averaged models of the multinomial logistic regression for the comparison among realized niches in Plovdiv (Pl), Passau (Pa), and Prague (Pr)

		Pl versus Pa			Pl versus Pr			Pa versus Pr		
	RVI	Estimate (SE)	LCL	UCL	Estimate(SE)	LCL	UCL	Estimate (SE)	LCL	UCL
Intercept		14.15 (4.24)	−12.90	26.80	16.56 (4.59)	−23.26	31.80	2.4 (2.60)	−18.15	12.74
Radiation	1	−0.61 (0.14)	−0.96	−0.33	−0.66 (0.15)	−1.01	−0.35	−0.04 (0.09)	−0.21	0.14
Soil compaction	1	−5.57 (1.77)	−10.20	−2.01	−5.40 (1.85)	−10.45	−1.85	0.16 (1.17)	−2.42	2.33
Way	1	−16.09 (5.79)	−28.07	−5.05	−15.28 (6.54)	−27.95	−3.09	0.81 (5.05)	−8.57	10.65
Woody plants <2 m	1	−38.38 (12.93)	−67.98	−12.76	−26.11 (11.94)	−51.32	0.34	12.35 (9.47)	−4.68	34.45
Woody plants >2 m	1	−13.81 (6.65)	−28.48	−0.88	−27.78 (9.43)	−46.30	−8.34	−13.96 (7.75)	−27.73	2.41
Herbs 1	1	−7.71 (2.52)	−13.43	−2.13	−8.46 (2.48)	−14.42	−2.75	−0.74 (1.85)	−4.54	2.93
Herbs 3	1	−0.22 (2.36)	−5.27	4,592	−9.90 (4.29)	−17.94	−1.11	−9.68 (4.11)	−17.23	−1.15
Herbs 2	1	−6.38 (2.91)	−12.90	−0.67	−12.83 (3.28)	−20.00	−6.30	−6.44 (2.14)	−10.64	−2.08
Temperature	0.51	5.77 (7.85)	−3.44	26.28	9.21 (10.86)	1.91	34.53	3.45 (5.22)	−4.07	17.73
Slope	0.47	0.36 (0.58)	−0.51	2.04	0.78 (0.99)	0.10	3.21	0.42 (0.6)	−0.25	2.03

Note. Estimates and confidence intervals correspond to Pa and Pr in comparison to Pl, and to Pr in comparison with Pa. Most important variables are those with relative variable importance RVI > 0.6.

TABLE 4 Microhabitat selection of green lizards in the core (Plovdiv) and in the periphery (Passau, Prague). Table shows the most important variables (relative variable importance RVI > 0.6) among vegetation structure and abiotic factors resulting from model averaging of selected models (ΔAIC < 2)

Variable	Estimate	SE	RVI
Plovdiv			
Intercept	15.3877	7.415	
Radiation	0.5275	0.2727	1
Slope	−3.8056	2.3085	1
Soil compaction	−5.7846	1.4432	1
S-N aspect	−3.6429	2.9139	0.74
Temperature	−1.406	3.5887	0.24
W-E aspect	0.1214	0.6582	0.14
Passau			
Intercept	−1.03e03	6.02e−03	
Branches	−2.91e02	2.89e01	1
S-N aspect	−5.44e01	6.02e03	1
pcnm1	4.48e02	6.02e−03	1
pcnm44	−2.13e+02	4.14e02	1
W-E aspect	4.97e01	6.02e−03	1
Temperature	6.54e02	6.02e−03	1
pcnm6	−4.91e02	6.02e−03	0.9
pcnm9	−60.13	395.32	0.21
pcnm22	−22.36	1,341.55	0.12
Way	7.664	22.18	0.11
Herbs 3	1.24	96.80	0.11
Bare soil	−6.25	18.25	0.10
pcnm16	−0.39	146.65	0.10
Prague			
Intercept	−4.27	5.08	
pcnm1	−72.84	96.15	1
Herbs 1	4.88	3.79	1
Herbs 2	85.42	54.62	1
Slope	27.15	364.24	0.57
Way	72.81	1,027.02	0.57
Herbs 3	−792.12	14,232.53	0.43
Branches	12.87	378.09	0.22
Bare soil	55.08	1,421.35	0.22

Note. In the core, none of the vegetation parameters was retained in the global model. PCNM: Principal coordinates of neighbor matrices correcting for spatial autocorrelation.

Most of the populations in Prague were found on rocky slopes of the valley, with sparse vegetation and scarce trees. Given the rocky substrate of slopes inhabited by *L. viridis* in Prague, the soil compaction was higher in Prague compared to Passau (Supporting Information Appendix S3, Table S3.1 for model selection and model averaging separately for vegetation structure and abiotic parameters).

3.3 | Microhabitat selection in each region

Results of model averaging of the GLMMs based on abiotic and vegetation parameters as potential predictors are shown in Table 4. Microhabitat selection in the core region was affected only by abiotic parameters. The most important variables found were radiation, slope, soil compaction (RVI = 1), and S-N aspect (RVI = 0.74), with radiation having a positive effect on the presence/absence of *L. viridis*, and slope, soil compaction, and S-N aspect having a negative effect. A high proportion of the variance was explained by our model, with the larger part being explained by the random intercept (conditional $R^2 = 0.93$; marginal $R^2 = 0.20$). The inclusion of random intercepts can enormously improve the explanatory capacity of models, and a high conditional R^2 value is a very common output in GLMM that intend to find the best set of variables to explain the data (Nakagawa & Schielzeth, 2013) (Supporting Information Appendix S4, Table S4.1 for model selection and model averaging separately for vegetation structure and abiotic parameters).

The most important variables affecting microhabitat selection in the periphery-Pa were a combination of vegetation structure and abiotic parameters: Branches, S-N aspect, W-E aspects, and temperature (RVI = 1) *Lacerta viridis* in the periphery-Pa avoided locations with high coverage of branches and selected places with an eastern and southern aspect where temperatures are higher. The model explained most of the variance, with fixed factors explaining almost half of it (conditional $R^2 = 0.99$; marginal R^2-marginal = 0.43) (Supporting Information Appendix S4, Table S4.2 for model selection and model averaging separately for vegetation structure and abiotic parameters).

Microhabitat selection in the periphery-Pr was affected only by vegetation structure variables. *Lacerta viridis* in the periphery-Pr selected places with low structure principally composed by low vegetation (RVI Herbs2, Herbs1 = 1). Most of the variance in the model was explained by fixed factors (conditional $R^2 = 0.61$; marginal R^2-marginal = 0.60) with a very small proportion being explained by the random intercept (Supporting Information Appendix S4, Table S4.3 for model selection and model averaging separately for vegetation structure and abiotic parameters).

4 | DISCUSSION

We hypothesized that the microhabitat niche is smaller at the periphery of the distribution of our study species, *L. viridis*, compared to the core and that there should be a higher preference for specific vegetation structures at the microhabitat scale at the periphery. We further hypothesized that in the core, where availability of suitable habitats does not represent a limiting factor, abiotic parameters will determine microhabitat selection. All hypotheses were met in line with Kühnelt's principle (Kühnelt, 1965), which states that the range of colonizable habitats is wider at the core where environmental conditions are optimal, whereas at the periphery conditions are suboptimal and fewer microhabitats are suitable for the species. The niche of vegetation structure and abiotic parameters was smaller in the periphery and was differentiated from the niche in the core. In the periphery, *L. viridis* compensated for the overall lower suitability of environmental conditions by selecting microhabitats with specific vegetation structures that allow it to take advantage of sufficiently suitable conditions. As expected, only abiotic parameters determined microhabitat selection at the core, whereas at the periphery in Prague, only variables of the vegetation structure influenced microhabitat selection. However, in the periphery in Passau, a combination of abiotic and vegetation structure parameters determined microhabitat selection.

Smaller niche size and niche differentiation in the periphery can be the result of either different thermoregulatory behavior, phenotypic plasticity or local adaptation (genotypic changes) to conditions that lay near the limits of suitability. On the one hand, thermoregulatory behavior can allow individuals at the northern (and upper altitudinal) periphery to meet their thermal requirements by stringent selection of optimal habitats, which therefore often determines the peripheral limits of the distribution of ectotherms (Henle et al., 2010; Huang, Porter, Tu, & Chiou, 2014). In the core region, thermal condition should be more benign, thus allowing ectotherms to reach their thermal requirements in a larger number of different habitats. This is the basic idea behind Kühnelt's principle of regional stenoecy (Kühnelt, 1965) and has been shown qualitatively in various lizard species (Böhme & Rödder, 2014). Furthermore, thermoregulatory behavior might avoid selective pressures to act upon physiological traits and is sometimes regarded as the most plausible mechanism to explain patterns of niche differentiation when data relies on realized niche (Araújo et al., 2013; Bogert, 1949; Grigg & Buckley, 2013; Huey, Hertz, & Sinervo, 2003).

On the other hand, thermoregulatory behavior in lizards is more often found to be determinant near the hot extremes of species' niches, where individuals avoid heat by retreating into burrows or staying under shadow, compared to near the colder limits of the niche (Muñoz et al., 2014). Moreover, for peripheral populations that are not connected with the distribution range of the species (relict populations), in which immigration from more central populations cannot contribute to population persistence, pressure for adaptation is stronger and therefore phenotypic plasticity and local adaptation (genotypical changes) can be more plausible mechanisms shaping smaller niche size and niche differentiation (Blanquart, Kaltz, Nuismer, & Gandon, 2013; Chevin, Lande, & Mace, 2010; García-Ramos & Kirkpatrick, 1997). Under this scenario, the selective pressure of environmental conditions can result in adjustments of the thermal physiology, like changes in heat and cooling rates, and critical thermal limits, with the range of selected body temperatures (SBT) at the periphery being different and narrower in comparison with core (Brattstrom, 1968; Castilla, Damme, & Bauwens, 1999; Henle et al., 2010; Huey, 1982). For instance, the STB of the common lizard *Lacerta vivipara* differs between locations, with populations in southern latitudes having a higher STB compared with those located at higher latitudes (Patterson & Davies, 1978; Van Damme, Bauwens, & Verheyen, 1986). The lack of connectedness with the continuous distribution range is indeed the case of the populations in Prague, which are regarded as relicts, have overall small size, and are genetically differentiated from other peripheral (but not relict) populations (Böhme & Moravec, 2011). Additionally, there is evidence in several ectotherm taxa that the expression of the potential phenotypic plasticity of a species is higher near its lower thermal limit, which for several taxa have a strong relation with high latitudes (Chown & Terblanche, 2006; Overgaard, Kristensen, Mitchell, & Hoffmann, 2011).

One possible selective pressure acting upon populations in colder northern peripheral regions can be radiation. Contrary to expectation, radiation had a positive effect on the presence of the lizards in the core area but no effect in the peripheral areas. As a consequence, this variable strongly differentiated microhabitats among regions, being lower in both peripheral regions in comparison with the core. Most importantly, the niches of *L. viridis* in peripheral regions were characterized by lower vegetation height than the niche in the core, where higher temperatures can compensate for increased shading by higher vegetation. Thermal conditions and other limiting factors like daily hours of sunshine (Frör, 1986; Laube & Leppelsack, 2007) presumably do not allow such a compensation at the periphery.

In Passau and Plovdiv, selected microhabitats additionally seem to reflect the response to abiotic parameters shaped also by topography. In Plovdiv, the effects of slope and S-N aspect were six to ten orders of magnitude stronger than the effect of radiation and were negative. This can be explained by the absence of the lizard in the two rocky hills included among the sites we visited in Plovdiv. In the Passau region, the Danube valley is narrow and is characterized by rocky cliffs, above which the habitat changes dramatically into dense mixed forest and oak forest with high coverage of branches. Despite higher radiation values above the cliffs in comparison with the valley ($z = -3.501$, $p < 0.01$) and the relative abundance of forest edges and clearings with potentially suitable vegetation structures, *L. viridis* seems unable to cope with unfavorable microclimatic conditions in the forest to colonize those areas. Similar observations were made for the Taiwanese lizards *Takydromus hsuehshanensis* (Huang et al., 2014). On the other hand, the rocky open valley has a southeastern aspect, with higher temperatures and suitable microclimate for *L. viridis*. Then, in Passau, it can be more difficult for *L. viridis* to compensate for overall climatic conditions (e.g., lower radiation) by just selecting suitable vegetation structures, because topography confines lizards mostly to the lower part of the valley and they lack accessibility to alternative localities with suitable microclimate.

In all three regions studied other lizard species are also present, *Lacerta agilis* in Passau and Prague, *and Lacerta trilineata* and *Podarcis tauricus* in Plovdiv. Although interspecific interactions, like competition, can have an influence in the niche and microhabitat selection of species, we think that in the regions of our study the possible effect of these interactions, if present, will be very low. Theory predicts that in peripheral populations in higher (colder) latitudes individuals are more limited by climatic conditions, while biotic interactions like predation and competition are more important at low latitudinal peripheries (Cahill et al., 2014; Holt & Barfield, 2009; Price & Kirkpatrick, 2009). In Passau and Prague, *Lacerta agilis* occupies much more humid and covered environments than those inhabited by *L. viridis*, which at this part of its distribution range, as our results showed, tends to occupy drier opener places. Evenmore, in Passau, each species occupies completely different habitats and does not occur synoptically (Waitzmann & Sandmaier, 1990). Nevertheless, an influence of the interaction of both species on the niche of *L. viridis* can be expected in southern regions, where the habitat of both species overlaps (Korsós, 1982), due to the trend of *L. viridis* to inhabit more covered areas toward lower latitudinal regions. However, even in this region, analyses at a finer scale have demonstrated significant niche segregation (Babocsay, 1997; Heltai et al., 2015) that allows the coexistence of both species in the same habitat.

In the core region, the habitats used by *Lacerta trilineata*, *Podarcis tauricus*, and *L. virdis* have an overlap in the driest and least covered portion of the niche of *L. viridis* (Mollov, 2011), which corresponds to the most covered and humid habitats inhabited by the other two species. Therefore, an effect of the interaction with other species on the microhabitat selection of *L. viridis* in this region might be possible but only in a reduced portion of its niche and would have shifted the niche toward the conditions in the periphery if the niche would be indeed suppressed. Analyses at the microhabitat scale in another core region, Hungry also suggest coexistence through niche segregation (Babocsay, 1997). Moreover, the differentiation of habitats between *L. trilineata* and *Podarcis tauricus*, and *L. viridis* becomes stronger toward the southern parts of the distribution range of *L. virids*, like in Greece, where *L. viridis* occupies even more covered habitats (Strijbosch, 2001).

4.1 | Implications for conservation

Our findings have several implications for the management and conservation of core versus peripheral populations of species. Management measures applied for the protection of peripheral populations of *L. viridis* should address the high specialization degree of the species in these regions, their microhabitat selection and their need to compensate for less suitable climatic conditions. In Prague and in Passau, maintenance of low vegetation in sites where the species already occurs is important for the species' viability, as it will allow individuals to compensate for low radiation. In Passau, management measures are already installed in the lower parts of the valley (below the cliff; O. Aßmann, pers. comm.). However, we suggest that similar measures should be considered in the upper border of the cliff, in order to increase the potentially suitable area for the species. Also, corridors, for example, along forest tracks or powerlines could facilitate connections between suitable habitats below and above the cliffs. We are not aware that measures for maintaining open vegetation are applied around Prague and would recommend considering them for the long-term viability of *L. viridis*.

In Plovdiv (Bulgaria), where our core study area was located, it is the diversity of habitats and their vegetation structures that matters most for the species. In the core, abiotic conditions suitable for *L. viridis* are met in a wide range of habitat types, including those with high vegetation and branches coverage. Landscape heterogeneity is altogether known to be important for the viability of many species (Brachet et al., 1999), and in the case of the populations of *L. viridis* in the core it is the presence of habitats with different vegetation structures that could represent the highest benefits. This can be considered, for instance, in Natura 2000 planning or in agri-environmental measures employed so that they also protect scrubland habitats in the region.

In two of the studied regions, Plovdiv and Prague, the species' habitat was severely fragmented. Recently, Henle et al. (2016) found that peripheral populations of a related lizard species, *Lacerta agilis*, had a higher specialization degree, lower genetic diversity, and were more sensitive to habitat fragmentation compared to those located in the center. A similar pattern of lower genetic diversity and higher sensitivity to fragmentation caused by the narrower niche is likely to occur also in northern peripheral populations of *L. viridis*. Thus, besides protection of high quality habitats, reestablishing connectivity is an important complementary conservation need.

4.2 | Limitations and outlook

As in many ecological studies dealing with the quantification of spatial ecological patterns, the risk of local processes influencing the geographical correlation with the parameter under study is always present, and in our study, the inclusion of more regions would have allowed a broader generalization of our results. However, we tried as much as possible to counteract this risk by taking data in less plots per site but increasing the number of sites per region. Most importantly, we defined the spatial scale to which the patterns of niche size are related (Chase & Myers, 2011). To do so, we selected regions that had to fulfill two preconditions closely related to processes that occur at a biogeographical scale: (a) to have contrasting ranges of habitat availability representative of different parts of the distribution range (broad in the core and narrow in the northern peripheries) and (b) to have clearly different climatic regimes. Both premises were fulfilled by all three regions in our study. Local processes due to the particularities of each location, like the topography in Passau and Plovdiv, or the disconnectedness in Prague, are of course still present, but their effects might probably be more related with mechanisms (e.g., local adaptation) acting at a rather local scale, than with differences in niche size and microhabitat selection per sé, which might more strongly respond to a spatial gradient of habitat availability and climatic regimes at a larger spatial scale.

Although our study only includes high latitudinal peripheries of the species' range and the core and lacks data from other locations along the distribution range of the species, we consider this a valuable input given the many empirical gaps in studying species' range limits, namely, a detailed analysis of the factors affecting species at the core versus periphery (Sexton, McIntyre, Angert, & Rice, 2009). As a next step, it is important to investigate whether limitations in other regions also lead to changes in niche and microhabitat selection compared to the core. The peripheral regions in our study one a relict (Prague) and the other at the tip of a narrow extension of the distribution range of the species (Passau) might not fully represent the northern periphery. In other northern edges, located at the border of the contiguous distribution range, habitat availability might not be broader and climatic conditions might be as limiting as in Passau and Prague, but the persistence of populations might depend more on immigration than on adaptation to specific conditions. Hence, niche would still be smaller compared to the core but probably less differentiated. On the other hand, in low latitudinal regions, interactions with other lizards' species might have a more important role in restricting the niche than it does in northern peripheries (Cahill et al., 2014).However, the study of the niche and microhabitat selection of several species must be carefully addressed at the proper spatial scales in order to correctly quantify possible overlaps or segregation among species (Heltai et al., 2015), and its effects in the intraspecific comparison of the niche of populations at peripheries with the core.

Other regions not included in our study that could also represent cold range edges are those located at high altitudes. High altitudinal populations of *L. viridis* are located in the central and southern parts of the species' range, in the Balkan Peninsula from southern Rumania to northern Anatolia (Pafilis & Maragou, 2013; Schmidtler, 1986; Uhrin et al., 2016). Although this regions are characterized either as subtropical or transitional subtropical-temperate climatic zones (Nojarov, 2017), it is possible that climatic conditions at high altitudes, as well as an expected narrower range of habitats available, have the same effect on the niche size of *L. viridis* as the conditions in temperate peripheries. This can be specially possible in the Carpathians in south Rumania, where there is a more continental climatic regime with less oceanic and subtropical influence, and where some mountainous populations of *L. viridis* have been reported (Strugariu, 2009). As these regions are surrounded by the contiguous distribution range of the species, and therefore, might strongly depend on immigration, compared with the peripheral regions that we visited, niche differentiation might be lower.

Finally, a higher specialization degree is already known to be linked with a higher sensitivity to habitat fragmentation and climate change at the species level (Henle, Davies, Kleyer, Margules, & Settele, 2004; Lancaster, Dudaniec, Hansson, & Svensson, 2015; Vergara & Armesto, 2009). In the same way, peripheral populations may be more specialized than core populations and be stronger affected by these two processes (Cahill et al., 2014; Hampe & Petit, 2005; Henle et al., 2016). Therefore, the identification of differences in niche and microhabitat selection at fine scales in various locations across the distribution range of single species would significantly improve predictions of species distributions under different scenarios of climate change and habitat fragmentation. This would be enormously valuable to prioritize the application of conservation measures at the population level and at regional and local scales.

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CONFLICT OF INTEREST

None declared.

AUTHORS CONTRIBUTIONS

AMPR and KH conceived the idea; all authors designed the field surveys and defined the data analysis approach; AMPR conducted the field work, analyzed the data, and wrote the manuscript; all other authors provided manuscript reviews and editorial advice.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0bg620m.

ORCID

Ana M. Prieto-Ramirez http://orcid.org/0000-0001-7633-3192

REFERENCES

Ahmadzadeh, F., Flecks, M., Carretero, M. A., Böhme, W., Ilgaz, C., Engler, J. O., ... Rödder, D. (2013). Rapid lizard radiation lacking niche conservatism: Ecological diversification within a complex landscape. *Journal of Biogeography*, *40*, 1807–1818. https://doi.org/10.1111/jbi.12121

Araújo, M. B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P. A., Valladares, F., & Chown, S. L. (2013). Heat freezes niche evolution. *Ecology Letters*, *16*, 1206–1219. https://doi.org/10.1111/ele.12155

Araújo, M. B., & Peterson, A. T. (2012). Uses and misuses of bioclimatic envelope modeling. *Ecology*, *93*, 1527–1539. https://doi.org/10.1890/11-1930.1

Babocsay, G. (1997) The niche segregation of three lacertid lizard species (Lacerta viridis, L. agilis and Podarcis taurica) on sandy grassland in Hungary. In: Meeting of the Zoological Society of Israel, p. 48, Tel-Aviv.

Bartón, K. (2015). MuMIn: Multi-Model Inference. https://cran.r-project.org/web/packages/MuMIn/index.html.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2016). lme4: Linear Mixed-Effects Models using 'Eigen' and S4. https://cran.r-project.org/web/packages/lme4/index.html .

Beutler, A., & Rudolph, B. U. (2003). Rote Liste gefährdeter Lurche (Amphibia) Bayerns. In Bayerisches Landesamt für Umwelt (Eds.), *Schriftenreihe Bayerisches Landesamt für Umweltschutz* (Vol. *166*, pp. 48–51).

Blanquart, F., Kaltz, O., Nuismer, S. L., & Gandon, S. (2013). A practical guide to measuring local adaptation. *Ecology Letters*, *16*, 1195–1205. https://doi.org/10.1111/ele.12150

Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The n-dimensional hypervolume. *Global Ecology and Biogeography*, *23*, 595–609.

Blonder, B. (2015). hypervolume: High-Dimensional Kernel Density Estimation and Geometry Operations. https://cran.r-project.org/web/packages/hypervolume/index.html .

Bogert, C. M. (1949). Thermoregulation in reptiles, a factor in evolution. *Evolution*, *3*, 195–211. https://doi.org/10.1111/j.1558-5646.1949.tb00021.x

Böhme, M. U., & Moravec, J. (2011). Conservation genetics of Lacerta viridis populations in the Czech Republic (Reptilia: Lacertidae). *Acta Societatis Zoologicae Bohemicae*, *75*, 7–21.

Böhme, W., & Rödder, D. (2014). Amphibien und Reptilien: Verbreitungs- und Verhaltensänderungen aufgrund der Erderwärmung. In J. L. Lozán, H. Grassl, L. Karbe, & G. Jendritzky (Eds.), *Warnsignal Klima: Gefahren für Pflanzen, Tiere und Menschen* (2nd edn., pp. 77–81). Hamburg, Germany. Retrieved from www.warnsignale.uni-hamburg.de.

Böhme, M. U., Schneeweiß, N., Fritz, U., Schlegel, M., & Berendonk, T. U. (2007). Small edge populations at risk: Genetic diversity of the green lizard (Lacerta viridis viridis) in Germany and implications for conservation management. *Conservation Genetics*, *8*, 555–563. https://doi.org/10.1007/s10592-006-9191-0

Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, *153*, 51–68. https://doi.org/10.1016/S0304-3800(01)00501-4

Brachet, S., Olivieri, I. I., Godelle, B., Klein, E., Frascaria-Lacoste, N., & Gouyon, P. H. (1999). Dispersal and metapopulation viability in a heterogeneous landscape. *Journal of Theoretical Biology*, *198*, 479–495. https://doi.org/10.1006/jtbi.1999.0926

Brattstrom, B. H. (1968). Thermal acclimation in anuran amphibians as a function of latitude and altitude. *Comparative Biochemistry and Physiology*, *24*, 93–111.

Brown, J. H., Stevens, G. C. A., & Kaufman, D. M. (1996). The Geographic Range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, *27*, 597–623. https://doi.org/10.1146/annurev.ecolsys.27.1.597

Buckley, L. B. (2010). The range implications of lizard traits in changing environments. *Global Ecology and Biogeography*, *19*, 452–464. https://doi.org/10.1111/j.1466-8238.2010.00538.x

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. (2nd ed.). New York, NY: Springer-Verlag.

Cadena, C. D., & Loiselle, B. A. (2007). Limits to elevational distributions in two species of emberizine finches: Disentangling the role of interspecific competition, autoecology, and geographic variation in the environment. *Ecography*, *30*, 491–504.

Cahill, A. E., Aiello-Lammens, M. E., Caitlin Fisher-Reid, M., Hua, X., Karanewsky, C. J., Ryu, H. Y., … Wiens, J. J. (2014). Causes of warm-edge range limits: Systematic review, proximate factors and implications for climate change. *Journal of Biogeography*, *41*, 429–442.

Castilla, A. M., Van Damme, R., & Bauwens, D. (1999). Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in lacertid lizards. *Natura Croatica*, *8*, 253–274.

Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2351–2363. https://doi.org/10.1098/rstb.2011.0063

Chefaoui, R. M., Hortal, J., & Lobo, J. M. (2005). Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: A case study of Iberian Copris species. *Biological Conservation*, *122*, 327–338. https://doi.org/10.1016/j.biocon.2004.08.005

Chevin, L.-M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLOS Biology*, *8*, e1000357. https://doi.org/10.1371/journal.pbio.1000357

Chown, S. L., & Terblanche, J. S. (2006). Physiological diversity in insects: Ecological and evolutionary contexts. *Advances in Insect Physiology*, *33*, 50–152.

Covaciu-Marcov, S. D., Cicort-Lucaciu, A. S., Dobre, F., Ferenti, S., Birceanu, M., Mihut, R., & Strugariu, A. (2009). The herpetofauna of the Jiului Gorge National Park, Romania. *North-Western Journal of Zoology*, *5*, 1–78.

Cunningham, H. R., Rissler, L. J., Buckley, L. B., & Urban, M. C. (2016). Abiotic and biotic constraints across reptile and amphibian ranges. *Ecography*, *39*, 1–8. https://doi.org/10.1111/ecog.01369

Dray, S., Dufour, A.-B., & Thioulouse, J. (2015). ade4: Analysis of Ecological Data : Exploratory and Euclidean Methods in Environmental Sciences. https://cran.r-project.org/web/packages/ade4/index.html.

Elbing, K. (2001). *Die Smaragdeidechsen: Zwei (Un)gleiche Schwestern*. Bochum, Germany: Laurenti-Verlag.

Frör, E. (1986). Erhebung zur Situation der Reptilienbestände im Bereich der Donauhänge zwischen Passau und Jochenstein. *Schriftenreihe Bayer. Landesamt Für Umweltschutz*, *73*, 135–158.

García-Ramos, G., & Kirkpatrick, M. (1997). Genetic models of adaptation and gene flow in peripheral populations. *Evolution*, *51*, 21–28. https://doi.org/10.1111/j.1558-5646.1997.tb02384.x

Gaston, K. J. (2009). Geographic range limits of species. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 1391. https://doi.org/10.1098/rspb.2009.0100

Grigg, J. W., & Buckley, L. B. (2013). Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography. *Biology Letters*, *9*, 20121056. https://doi.org/10.1098/rsbl.2012.1056

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology*, *24*, 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, *8*, 461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x

Heltai, B., Sály, P., Kovács, D., & Kiss, I. (2015). Niche segregation of sand lizard (*Lacerta agilis*) and green lizard (*Lacerta viridis*) in an urban semi-natural habitat. *Amphibia-Reptilia*, *36*, 389–399.

Henle, K., Andres, C., Bernhard, D., Grimm, A., Stoev, P., Tzankov, N., & Schlegel, M. (2016). Are species genetically more sensitive to habitat fragmentation on the periphery of their range compared to the core? A case study on the sand lizard (Lacerta agilis). *Landscape Ecology*, *32*, 131–145. https://doi.org/10.1007/s10980-016-0418-2

Henle, K., Davies, K. F., Kleyer, M., Margules, C., & Settele, J. (2004). Predictors of species sensitivity to fragmentation. *Biodiversity & Conservation*, *13*, 207–251. https://doi.org/10.1023/B:BIOC.0000004319.91643.9e

Henle, K., Dick, D., Harpke, A., Kühn, I., Schweiger, O., & Settele, J. (2010). Climate change impacts on European amphibians and reptiles. In Council of Europe (Eds.), Biodiversity and Climate Change: Reports and Guidance Developed under the Bern COnvention, Vol. I. *Nature and Environment*, *156*, 225–306.

Hirzel, A. H., & Le Lay, G. (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, *45*, 1372–1381. https://doi.org/10.1111/j.1365-2664.2008.01524.x

Holt, R. D., & Barfield, M. (2009). Trophic interactions and range limits: The diverse roles of predation. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*, 1435–1442. https://doi.org/10.1098/rspb.2008.1536

Huang, S. P., Porter, W. P., Tu, M. C., & Chiou, C. R. (2014). Forest cover reduces thermally suitable habitats and affects responses to a warmer climate predicted in a hiogh-elevational lizard. *Oecologia*, *175*(1), 25–35.

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In C. Gans, & H. F. Pough (Eds.), *Biology of the reptilia* (pp. 25–91). London, UK: Academic Press.

Huey, R. B., Hertz, P. E., & Sinervo, B. (2003). Behavioral drive versus behavioral inertia in evolution: A null model approach. *American Naturalist*, *161*, 357–366. https://doi.org/10.1086/346135

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbour Symposiumon Quantitative Biology*, *22*, 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Janssen, I., & Zuiderwijk, A. (2006). Detection probability derived from the national reptile monitoring program in the Netherlands. In. Monitoring Network of Reptile, Amphibian & Fish Conservation the Netherlands, RAVON, http://eumon.ckff.si/files/porto/3_janssen.pdf.

Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., … Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, *16*, 584–599. https://doi.org/10.1111/ele.12082

Kirkpatrick, M., & Barton, N. H. (1997). Evolution of a species' range. *American Naturalist*, *150*, 1–23. https://doi.org/10.1086/286054

Korsós, Z. (1982). Field observations of two lizard populations (*Lacerta viridis* Laur. and *Lacerta agilis* L.). *Vertebrata Hungarica*, *21*, 185–194.

Korsós, Z. (1983). Comparative niche analysis of two sympatric lizard species (*Lacerta viridis* and *Lacerta agilis*). *Vertebrata Hungarica*, *22*, 5–14.

Kühnelt, W. (1965). *Grundriß der Ökologie mit besonderer Berücksichtigung der Tierwelt*. Jena, Germany: Fischer Verlag.

Lancaster, L. T., Dudaniec, R. Y., Hansson, B., & Svensson, E. I. (2015). Latitudinal shift in thermal niche breadth results from thermal release during a climate-mediated range expansion. *Journal of Biogeography*, *42*, 1953–1963. https://doi.org/10.1111/jbi.12553

Lappalainen, J., & Soininen, J. (2006). Latitudinal gradients in niche breadth and position—Regional patterns in freshwater fish. *Naturwissenschaften*, *93*, 246–250. https://doi.org/10.1007/s00114-006-0093-2

Laube, M., & Leppelsack, H. J. (2007). Individuenspezifisches Raumnutzungs- und Interaktionsverhalten der Östlichen Smaragdeidechse (Lacerta viridis) in den Passauer Donauleiten. *Zeitschrift Für Feldherpetologie*, *14*, 51–62.

Lesica, P., & Allendorf, F. W. (1995). When are peripheral populations valuable for conservation? *Conservation Biology*, *9*, 753–760. https://doi.org/10.1046/j.1523-1739.1995.09040753.x

Lozano-Jaramillo, M., Rico-Guevara, A., & Cadena, C. D. (2014). Genetic differentiation, niche divergence, and the origin and maintenance of the disjunct distribution in the Blossomcrown Anthocephala floriceps (Trochilidae). *PLoS ONE*, *9*, e108345.

Mackenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology*, *42*, 1105–1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x

Mollov, I. A. (2011). Habitat distribution of the amphibians and reptiles in the city of Plovdiv, Bulgaria. *Biharean Biologist*, *5*, 25–31.

Morales, N. S., Fernández, I. C., Carrasco, B., & Orchard, C. (2015). Combining niche modelling, land-use change, and genetic information to assess the conservation status of pouteria splendens populations in Central Chile. *International Journal of Ecology*, *2015*, 12.

Muñoz, M. M., Stimola, M. A., Algar, A. C., Conover, A., Rodriguez, A. J., Landestoy, M. A., … Losos, J. B. (2014). Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. *Proceedings of the Royal Society B: Biological Sciences*, *281*.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142.

Nojarov, P. (2017). Genetic climatic regionalization of the Balkan Peninsula using cluster analysis. *Journal of Geographical Sciences*, *27*, 43–61. https://doi.org/10.1007/s11442-017-1363-y

Olsson, M. (1988). Ecology of a Swedish population of the sand lizard (*Lacerta agilis*)- preliminary report. *Mertensiella*, *1*, 86–91.

Overgaard, J., Kristensen, T. N., Mitchell, K. A., & Hoffmann, A. A. (2011). Thermal tolerance in widespread and tropical drosophila species: does phenotypic plasticity increase with latitude? *The American Naturalist*, *178*, S80–S96.

Pafilis, P., & Maragou, P. (2013). One more record of *Lacerta viridis* (Laurenti, 1768) from Macedonia. *Herpetozoa*, *26*, 101–102.

Patterson, J. W., & Davies, P. M. C. (1978). Preferred body temperature: Seasonal and sexual differences in the lizard Lacerta vivipara. *Journal of Thermal Biology*, *3*, 39–41. https://doi.org/10.1016/0306-4565(78)90034-7

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, *12*, 361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

Peterman, W. E., Feist, S. M., Semlitsch, R. D., & Eggert, L. S. (2013). Conservation and management of peripheral populations: Spatial and temporal influences on the genetic structure of wood frog (Rana sylvatica) populations. *Biological Conservation*, *158*, 351–358. https://doi.org/10.1016/j.biocon.2012.07.028

Popgeorgiev, G. S., & Mollov, I. A. (2005). A study of the effects of fires on the populations of the green lizard *Lacerta viridis* (Laurenti, 1768) in eastern Rhodopes. *Animalia*, *41*, 95–108.

Poulin, J.-F., Villard, M.-A., Edman, M., Goulet, P. J., & Eriksson, A.-M. (2008). Thresholds in nesting habitat requirements of an old forest specialist, the Brown Creeper (Certhia americana), as conservation targets. *Biological Conservation*, *141*, 1129–1137. https://doi.org/10.1016/j.biocon.2008.02.012

Price, T. D., & Kirkpatrick, M. (2009). Evolutionarily stable range limits set by interspecific competition. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 1429. https://doi.org/10.1098/rspb.2008.1199

Ripley, B., & Venables, W. (2016). nnet: Feed-Forward Neural Networks and Multinomial Log-Linear Models. https://cran.r-project.org/web/packages/nnet/index.html.

Schmidtler, J. F. (1986). Orientalische Smaragdeidechsen: 1. Zur Systematik und Verbreitung von Lacerta viridis in der Türkei. *Salamandra*, *22*, 29–46.

Sewell, D., Guillera-Arroita, G., Griffiths, R. A., & Beebee, T. J. C. (2012). When is a species declining? optimizing survey effort to detect population changes in reptiles. *PLOS ONE*, *7*, e43387.

Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Strijbosch, H. (2001). Zur unterschiedlichen Habitatwahl von *Lacerta trilineata* und *Lacerta viridis* in Ostgriechenland. *Mertensiella*, *13*, 159–164.

Strugariu, A. (2009). The herpetofauna of the Jiului Gorge National Park, Romania. *North-Western Journal of Zoology*, *5*, S01–S78.

Thomas, J. A., Rose, R. J., Clarke, R. T., Thomas, C. D., & Webb, N. R. (1999). Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology*, *13*, 55–64. https://doi.org/10.1046/j.1365-2435.1999.00008.x

Uhrin, M., Havaš, P., Minařík, M., Kodejš, K., Bugoš, I., Danko, S., … Jablonski, D. (2016). Distribution updates to amphibian and reptile fauna for the Republic of Macedonia. *Herpetology Notes*, *9*, 201–220.

Van Damme, R., Bauwens, D., & Verheyen, R. F. (1986). Selected body temperatures in the lizard Lacerta vivipara: Variation within and between populations. *Journal of Thermal Biology*, *11*, 219–222. https://doi.org/10.1016/0306-4565(86)90006-9

Vergara, P. M., & Armesto, J. J. (2009). Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. *Landscape Ecology*, *24*, 25–38. https://doi.org/10.1007/s10980-008-9275-y

Waitzmann, M., & Sandmaier, P. (1990). Zur Verbreitung, Morphologie und Habitatwahl der Reptilien im Donautal zwischen Passau und Linz (Niederbayern, Oberösterreich). *Herpetozoa*, *3*, 25–53.

Yurkowski, D. J., Ferguson, S., Choy, E. S., Loseto, L. L., Brown, T. M., Muir, D. C. G., … Fisk, A. T. (2016). Latitudinal variation in ecological opportunity and intraspecific competition indicates differences in niche variability and diet specialization of Arctic marine predators. *Ecology and Evolution*, *6*, 1666–1678. https://doi.org/10.1002/ece3.1980

Zavadil, V., & Moravec, J. (2003). Red list of amphibians and reptiles of the Czech Republic. In V. H. J. Plesník, & L. Brejšková (Ed.), *Red list of threatened species in the Czech Republic vertebrates* (pp. 1–183). Prague, Czech Republic: Příroda.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

SUPPORTING INFORMATION

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RESEARCH ARTICLE

Differential effects of habitat loss on occupancy patterns of the eastern green lizard *Lacerta viridis* at the core and periphery of its distribution range

Ana María Prieto-Ramirez[1]*, **Leonie Röhler**[2], **Anna F. Cord**[2], **Guy Pe'er**[3,4,5], **Dennis Rödder**[6], **Klaus Henle**[1]

1 Department of Conservation Biology, Helmholtz Center for Environmental Research–UFZ, Leipzig, Germany, **2** Department of Landscape Ecology, Helmholtz Center for Environmental Research–UFZ, Leipzig, Germany, **3** German Center for Integrative Biodiversity Research (iDiv) Jena-Halle-Leipzig, Leipzig, Germany, **4** Department of Economics and Department Ecosystem Services, Helmholtz Center for Environmental Research–UFZ, Leipzig, Germany, **5** University of Leipzig, Leipzig, Germany, **6** Department of Herpetology, Zoological Research Museum Alexander Koenig ZFMK, Bonn, Germany

* ana-maria.prieto-ramire@ufz.de

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Data Availability Statement: Data are available at: https://github.com/anaprieto1/Occupancy-of-Lacerta-viridis-.

Abstract

The effects of habitat loss on the distribution of populations are often linked with species specialization degree. Specialist species can be more affected by changes in landscape structure and local patch characteristics compared to generalist species. Moreover, the spatial scale at which different land covers (eg. habitat, cropland, urban areas) affect specialist species can be smaller. Specialization is usually assumed as a constant trait along the distribution range of species. However, for several taxa, there is evidence of higher specialization degree in peripheral populations compared with populations in the core. Hence, peripheral populations should have a higher sensitivity to habitat loss, and strongest effects should be found at a smaller spatial scale. To test these expectations, we implemented a patch-landscape approach at different spatial scales, and compared effects of landscape structure and patch characteristics on occupancy probability among northern peripheral, more specialized populations (Czech Republic) and core populations (Bulgaria) of the eastern green lizard *Lacerta viridis*. We found that landscape structure and patch characteristics affect differently the occupancy probability of *Lacerta viridis* in each region. Strongest effects of habitat loss were found at a spatial scale of 150m around patches in the periphery, but at a scale of 500m in the core. In the periphery occupancy probability of populations was principally affected by landscape composition, and the effect of habitat quality was stronger compared to core populations. In the core, persistence of populations was mainly explained by characteristics of the spatial configuration of habitat patches. We discuss possible ecological mechanisms behind the relationship between sensitivity to habitat loss, populations' specialization degree and position in the distribution range, and suggest conservation measures for *L. viridis*.

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Introduction

Anthropogenic land-use changes lead to the loss of natural and semi-natural habitats, resulting in reduced overall amount of habitat available, fragmentation into smaller patches and increasing isolation among these patches due to land-use intensification forming a matrix of inhospitable land. These processes alter landscape composition and configuration: as patch area decreases, patch isolation increases, and spatial relations between landscape elements (e.g. habitat, non-habitat areas, and topographic features like rivers) are altered. The ecological consequences for species, at the landscape scale, include reduced functional connectivity and reduced viability [1], leading to declining trends in abundance and distribution.

The effects of modified landscape structure on the distribution of natural populations have been widely studied and linked with species-specific traits [2–4]. In particular, habitat specialization is one of the main traits shaping species' response to habitat loss [5, 6]. Specialist species are known to be more sensitive to changes in patch size [7–9], isolation [10–12], habitat quality [13], and overall amount of habitat in the landscape [14, 15], whereas generalist species can typically better cope with reduced patch size and overall reduce in the amount of habitat [16].

Differential responses to habitat loss between generalist and specialist species have also been linked to the 'scale of effect' of different parameters. We define the 'scale of effect' as the extent of area at which the strongest effect of a given factor on an ecological response is found [17]. It has become a central topic in ecology in the past years, with particular focus onto the question how landscape composition influences species' distribution. The scale of effect of habitat amount on species' distribution has been shown to be smaller for specialist than for generalist species across different taxa such as butterflies [18], birds [14, 16] and rodents [19]. Similarly, the scale of effect of other landscape composition variables is usually expected to be smaller for specialist species [20].

Studies on the effects of habitat loss that consider species' specialization usually assume species to be characterized by the same trait along their distribution range. However, the degree of specialization can change across the distribution range of a given species, resulting in intraspecific differences among populations. The Kühnelt principle [21] states that the range of colonizable habitats is wider at the core of the distribution range where environmental conditions are optimal, whereas at the periphery conditions are suboptimal and fewer microhabitats are suitable for the species. Therefore, populations at the core should be habitat generalists ("euryoecious"), while populations at the periphery of the species' range can be, in comparison, more specialized ("stenoecious") [22]. Accordingly, it has been found in lizards [23, 24], birds [25] and insects [26] that individuals in peripheral populations have narrower realized niches than those living in the core of the distribution range. However, in spite of existing evidence, most studies on habitat loss carried out at broad scales, involving the total or partial extent of the distribution range of a species, have overlooked this variability, and therefore, the possible differential effects on distribution patterns. Consequently, conservation measures applied at local scales–especially in the periphery–might not be adequate enough to protect threatened populations if the measures were derived from analyses of habitat loss effects in other parts of the distribution range.

Here we investigated the effects of habitat loss and fragmentation on the occupancy patterns of core and northern peripheral populations of the eastern green lizard *Lacerta viridis*. Recently, it has been found that northern peripheral populations of *L. viridis* (Germany, Czech Republic) have a higher specialization degree compared to core populations (Bulgaria) [24]. In the periphery, populations have narrower niches and can only persist in habitats with comparably lower vegetation structure that allow them to compensate for suboptimal overall climatic conditions (e.g. lower radiation). In the core, populations have a broader range of available habitats and select for microhabitats with higher vegetation structure. The higher specialization degree of *L. viridis* populations in the northern periphery suggests that these populations might also have a higher sensitivity to habitat loss and fragmentation compared to generalist populations living in the core of the distribution range.

In this study, we implemented a patch-landscape approach to evaluate the occupancy patterns of populations of *L. viridis* in Bulgaria (core) and in the Czech Republic (periphery). Our main objectives were to find out which are the most relevant spatial scales affecting patch occupancy in each region and which parameters of the landscape structure and patch characteristics have the strongest effect. We expected to find at the intraspecific level the same patterns of the effects of habitat loss reported at the species level. We hypothesized that: 1) the relevant scale(s) at which occupancy is best explained should be smaller at the periphery compared to the core; 2) the proportion of different land-cover types will have a smaller scale of effect at the periphery compared to the core; and 3) peripheral populations are more sensitive to isolation, area and reduced habitat quality compared to core generalist population.

Methods

Study areas

The study regions were located in the northern periphery and in the core of the distribution range of *L. viridis* (Fig 1). The study region at the species' periphery was located in the surroundings of Prague (Bohemia, Czech Republic), where populations are located in open stony areas within open oak forest and along the cliffs of the Moldova valley, as well as those of other valleys perpendicular to the Moldova river valley (Pr; Fig 1B). The core region was located in the Thracian Plain of Bulgaria, in the surroundings of Plovdiv (Core; Fig 1C). The region is an alluvial plain dominated by the banks of the Maritsa River and its tributary rivers. Here *L. viridis* inhabits diverse natural and semi-natural habitats, from road edges and open shrubland to mesophilic forest [27]. In both study regions habitat of *L. viridis* has been lost due to agricultural expansion and intensification, as well as by (semi-)urban development. We selected landscapes in both regions with similar configuration and composition characteristics that could ensure enough levels of comparability. Both landscapes had low percentages of habitat (11.2% in the core and 13.1% in the periphery) and similar habitat configuration in terms of ranges of patch area and isolation (S1 Appendix).

Field survey

Field surveys were carried out in Plovdiv in 2014 and in Prague in 2015. *L. viridis* is active from beginning of April to beginning of October in Bulgaria, and from late May to beginning of September in the Czech Republic. Therefore, in order to make surveys comparable, data collection was carried out earlier in the core than in the periphery: From beginning of April to late May in the core, and from mid-May to late July in the periphery. The difference in sampling times made average maximum air temperatures per sampling month relatively similar among regions (Core: 18.5–23.4˚C; periphery: 22.5–– 24.6˚C).

Based on literature about the habitat requirements of *L. viridis*, and available information about places where the species has been found in each region (pers.com: Plovdiv: Tzankov, N; Prague: Moravic, J; Chamlar, J.), we identified patches of habitat to be surveyed in each region using satellite maps available in Google earth. We visited 42 patches in the core and 33 in the periphery (see S2 Appendix for locations). All polygons corresponding to the edges of the surveyed patches in both regions were manually digitalized using ArcMap [29].

Occupancy surveys and analysis were designed following the protocol proposed by Mackenzie and Royle [30], prescribing a specific number of visits depending on the probability of

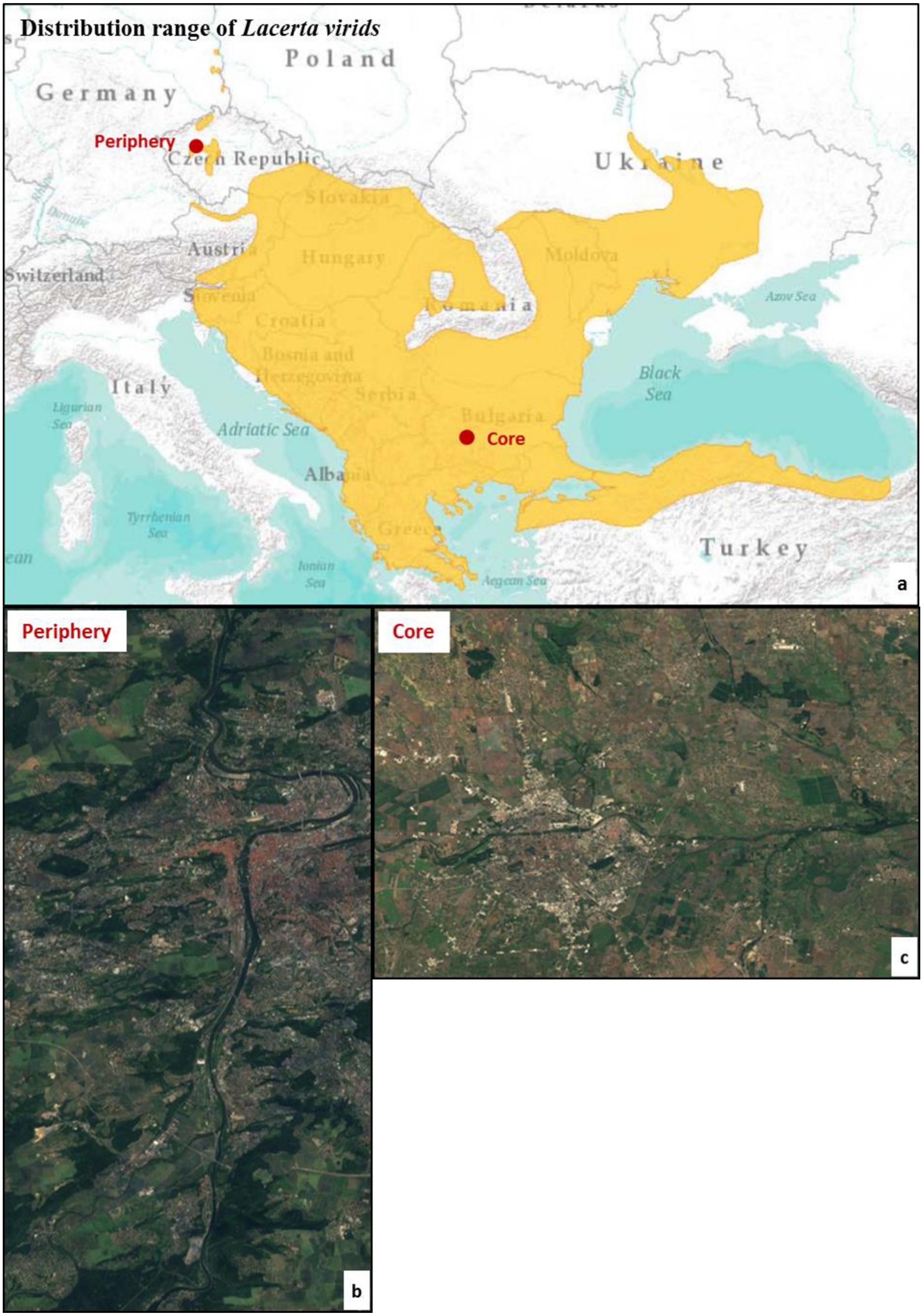
Distribution range of *Lacerta virids*
Poland
Germany
Periphery
Czech Republic
Ukraine
Slovakia
Austria
Hungary
Moldova
Switzerland
Slovenia
Romania
Azov Sea
Croatia
Bosnia and Herzegovina
Italy
Serbia
Black Sea
Ligurian Sea
Adriatic Sea
Bulgaria
Core
Albania
Tyrrhenian Sea
Greece
Turkey
Ionian Sea
Aegean Sea
a
Periphery
Core
c
b

Fig 1. Distribution range of *Lacerta viridis* (a) and location of the study sites. In the periphery (b) the study site is located in the surroundings of Prague and has an extent of 522 km^2 (location: top-left 50.17˚N, 14.29; top-right 50.16˚N, 14.46˚E; bottom-left 49.92˚N, 14.27˚E; bottom-right 49.92˚N, 14.45˚E). The study site in the core region (c) corresponds to the surroundings of Plovdiv and has an extent of 325 km^2 (location: top-left 42.26˚N, 24.68˚E; top-right 42.24˚N, 24.93˚E; bottom-left 42.12˚N, 24.66˚E; bottom-right 42.10˚N, 24.91˚E). Images source: a: IUCN, *Lacerta viridis* distribution range [28]; b and c: Sentinel-2 cloudless 2016 by EOX IT Services GmbH CCBY 4.0 license.

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detection of the species. Based on estimates of detection probability for similar species [31, 32], the number of surveys per patch was set to two, one in the morning (9:00–12:00 a.m.) and one in the afternoon (14:00–19:00 p.m.) of the same day or one day later, in accordance with the species' daily activity pattern [33].

Surveys lasted one hour each, walking along predetermined line transects. With a standard walking speed of 20 m/min, which is slow enough to search and detect lizards, a one hour survey corresponds to a total length of 1200m, which were subsequently divided into transects. As most patches had a heterogenous compostion, the number and length of transects varied depending on the number of different habitat types into each patch and the proportion of area of the patch covered by each habitat type. Nevertheless, all the transects in a patch always summed up 1200 m to assure one hour visit. Satellite imagery was used to define the relative coverage of each habitat type within each patch. Transect lengths varied between 50–400 m. Transects were located at least 100 m of each other, and the total length of each transect was placed in only one habitat type. The number of transects surveyed per patch ranged from three to 12. During transect walking, a width of 2.5 m was scanned at each side of the transect to visually search for *L. viridis*. As surveys were based on visual identification of lizards, and no collection of biological material or handling of animals was required, no permits were necessary for carrying out this study.

Land cover classification

To calculate landscape composition variables around each patch (see section "Calculating patch variables and landscape structures" below), we generated land-cover maps for the two study sites. Land cover classes in each region are described in Table 1. Based on reported literature, we define habitat types as the different vegetation structures used by *L. viridis* in each region. Relevant habitat types in the core were: woodland, shrubland, rocky outcrop vegetation (rocky_veg), grassland, transitional vegetation (trans_veg) and open ground and river beds (bare soil). Habitat types in the periphery were: open woodland (openwood), shrubland, rocky outcrop vegetation, dry grassland (dry_grass) and transitional vegetation. Natural or semi-natural areas that are non-habitat in the periphery were dense woodland (densewood) and humid grassland (humid_grass). In both regions, urban areas (urban), and crops and pastures (crop_-pas) were defined as other non-habitat land-cover classes (S3 Appendix).

To obtain the land cover classified map in the core, a supervised Mahalanobis Distance classification of cloud free, atmospherically and topographically corrected Rapid Eye satellite imagery (acquired on May 8th, 2014; 5m resolution), in combination with information derived from the Copernicus Land Monitoring Service (incl. Urban Atlas 2012, Imperviousness Degree–IMD 2012 and Tree Cover Density–TCD 2012; 20m resolution) was performed. Training (polygon) data for the target classes were generated based on land cover information collected during the field survey and complemented by data digitized based on the RapidEye imagery. Post-processing included a majority analysis (except for the class urban) with a kernel size of 3x3 to remove isolated cropland pixels mapped within (semi-)natural vegetation cover. The final map had an overall accuracy of 91.1%. All processing and analyses were performed in ArcGIS 10.6 [34] and ENVI 5.0 [35]

Table 1. Land cover classes conforming the classified maps of both, core and periphery, regions.

Land cover class	Variable name	Description	Region	Habitat
Bare soil	Bare_soil	Open ground corresponding to not paved ways in the interior of patches and sandy, not vegetated river beds	Core, Periphery	Yes
Rocky outcrop vegetation	Rocky_veg	Rock outcrops and its associated grasses and herbs	Periphery	Yes
Grassland	Grass	Dry and mesic grasslands	Core	Yes
Dry_grassland	Dry_grass	Broad leaved dry grassland, termophilus herbs, ecotones at the edge of forest and shrubs	Periphery	Yes
Humid grassland	Humid_grass	Perennial grasses in wetlands, wet meadows, moor grasses and river bed grasslands and herbs	Periphery	No
Shrubland	Shrubland	Shrubs and scrubs areas	Core, Periphery	Yes
Transitional vegetation	Trans_veg	Transitional woodlands with cover density <30%	Core, Periphery	Yes
Woodland	Woodland	Woodland with crown cover density >30%	Core	Yes
Open woodland	Openwood	Woodland with crown cover density between 30%– 75%	Periphery	Yes
Dense woodland	Densewood	Woodland with crown cover density between 75% and 100%	Periphery	No
Crops and Pastures	Crop_pas	Areas used for agricultural activities, either cultivation or pasture purposes	Core, Periphery	No
Urban area	Urban	Continuous and discontinuous urban fabric, road networks	Core, Periphery	No

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Classification of land cover classes in the periphery was achieved by reclassifying the most recent vegetation community and land-use map [36] available from the Prague Institute for Planning and Development (Institut plánování a rozvoje hl. m. Prahy, IPR). This is a vector map with 5m resolution with 66 classes: 10 corresponding to different urban land uses, two to agriculture and pastures, and 52 representing different vegetation communities. In a first step we reclassified the vegetation communities that correspond to dry_grass, humid_grass, shrubland, rocky_veg and woodland. In a second step, woodland was reclassified as openwood, densewood and trans_veg based on tree cover density (TCD) data available from CORINE. Areas in the northern and southern edges of that study site were unfortunately not covered by the IPR maps. Therefore, for these areas we produced a land cover map based on the Urban Atlas 2012 and TCD information, and when necessary, manually digitalized the different classes by using orthophotos available from the IPR webpage.

Calculating patch variables and landscape structures

To evaluate the possible differential effects of habitat loss in the core and periphery, we applied a patch-landscape approach and analyzed the influence of variables representative of landscape structure and patch characteristics on occupancy. We differentiated between four types of variables: landscape configuration, landscape composition, patch geometry and patch habitat quality. Variables defining the landscape configuration around each patch included distance to river (dist_river), distance to urban areas (dist_urban) and distance to crops and pastures (dist_crop), and two measures of isolation, the edge-to-edge Euclidean distance to the nearest patch (np_dist) and proximity index (prox).The proximity index (Gustafson and Parker, 1994) is a scale dependent measure of isolation and is calculated as the sum of the ratios patch area / distance to the focal patch for all patches that fall, at least partially, into the buffer of a given distance around the focal patch.

Variables related to landscape composition were calculated at different buffer-distances (hereafter, "scales") around each patch in each region. The different scales were selected based on reported dispersal distances for *L. viridis* [37–39]. Scales selected were: 50m, 150m, 250m, 500m, 750m, 1km, 1.5km, 2km, 2.5km and 3km. At each scale, we calculated the proportion of urban, crop_pas and habitat (the sum of all habitat types).

Patch geometry variables included area, perimeter, perimeter to area ratio (Per_area) and shape index (Shape_index). Patch habitat quality was defined based on the most important parameters found for this species [24, 40–42]: vegetation structure, radiation and slope. Vegetation structure was calculated based on available information at the microhabitat scale. At each single transect in each patch, percentage of vegetation coverage was taken in at least one plot of 25 m^2. Vegetation coverage classes included herbs < 30 cm, herbs between 40 and 80 cm, herbs > 90 cm, woody plants < 2 m, woody plants > 2 m, dry leaves, rocks and fallen trunks, bare soil, and branches coverage. Plots correspond either to the area around the specific point where a lizard was detected or to the area around random points blindly selected in the GPS along each transect. For each plot we calculated the foliage height diversity' index (FHD; [43]), which is a modification of the Shannon index applied to vegetation structure. Because most of the patches had a heterogeneous habitat composition, the plots of a single patch might belong to different habitat types. Therefore, we averaged the FHD values of the plots belonging to the same habitat type across patches to obtain the averaged FHD of each habitat type. Vegetation structure (Veg_str) of each patch was then calculated as the sum of the FDH of each habitat type weighted by the area that each specific habitat type occupied within the patch. To calculate the topographic slope we used software SAGA [43] to derive slope maps from digital elevation models (DEMs) with 30m resolution available from the U.S Geological Survey. We averaged pixel values corresponding to each patch. We calculated radiation from the DEMs with the 'Potential incoming solar radiation' module of SAGA [44]. Radiation value of each patch hence corresponded to the average annual radiation during the 5 years preceding the field work in each region, calculated from April to September, from 8am to 6pm and with a temporal resolution of 10 days and two hours. All other calculation procedures were carried out with ArcMap version 10.3.1 [28], except for shape_index and prox which were calculated with FRAGSTATS version 4 [45].

Statistical analysis

To evaluate the occupancy patterns of populations of *L. viridis*, we applied the occupancy model proposed by MacKenzie and Bailey [46] as implemented in the package 'Unmarked' [47] in the software R [48]. This model calculates the probability of occupancy (*p*) by correcting for the probability that an individual will actually be detected (*psi*). The first step was to fit a detection probability model to be used in all subsequent steps. For this, we tested the effect of vegetation structure, day of survey and patch area on detection probability. As previously shown, vegetation structure can affect the detectability by reducing the visibility for the observer. Day influences lizards' activity, given it is determined by annual seasonality, increasing with the advance of the spring and starting to decrease at the beginning of the summer in the core, and at mid-summer in the periphery. Higher activity can increase the encounter rate and, therefore, the probability of detection. Finally, big patches can be expected to hold large populations, which might increase the probability of detecting a lizard. Thus, to find out the model that better explained detection probability, we built models with constant *p* and with all possible variable combinations among vegetation structure, day of survey and patch area as predictors of detection. Then, we compared models based on AIC and selected those with $\Delta AICc < 2$ [49]. The model including the three variables was the best in the core, and the second best model in the periphery ($\Delta AIC = 0.38$) (S4 Appendix). Consequently, all three variables were used as predictors of detection probability in all subsequent analysis in both regions.

In order to find out which were the relevant scales at which occupancy is explained in each region we tested whether occupancy patterns are explained at single scale(s) or simultaneously at multiple scales. Single-scale models included all composition variables measured at the same scale, plus configuration and patch variables, and multi-scale models included each composition variable at its scale of effect, together with configuration and patch variables. Therefore, before building multi-scale models we needed to find out which was the scale of effect of each composition variable -percentage of habitat, crops_pastures and urban- in each region. For this purpose, we fitted univariate models with each of these variables at each scale as predictor of occupancy (*p*) and selected the scale with the highest Nagelkerke R^2 (RN^2) as the scale of effect. In cases when the highest RN^2 value was present in several scales, the smallest scale was selected. For proximity index (prox), which is a scale-dependent configuration variable, the same procedure was applied to find its scale of effect in each region.

Then, to avoid collinearity among variables included in the same model, we applied a Spearman rank correlation test (S5 Appendix) to each single-scale and multi-scale dataset. Among correlated variables ($rs > 0.60$) we selected the one with the strongest effect on occupancy probability. Additionally, we calculated the variance inflation factor (vif) of selected covariates, and retained those with vif<10. In both regions we found strong collinearity among some variables that might have an important ecological role on occupancy. Therefore, in order to avoid skipping relevant variables from the analysis due to collinearity, we run several sets of single-scale and multi-scale models in each region (S6 Appendix). Each set included all non-correlated variables, and only one from the pair of correlated variables. In the core, Np_dist was correlated with prox at all scales, as well as crop_pas with urban. Both, Crop_pas and urban, might exert strong pressure on the occupancy, and proxy is a scale dependent measure of isolation that might have different explanatory power compared to Np_dist. Therefore, we run four sets of single-scale models for this region: Np_dist and crop_pas, Np_dist and urban, prox and crop_pas, or prox and urban. For the multi-scale model in the core, crop_pas was not correlated with urban; thus, both variables could be simultaneously included and only two multi-scale models were fitted, one with np_dist and one with prox. In the periphery, habitat was negatively correlated with urban at all scales, as well as in the multi-scale dataset. Therefore, for this region we fitted two single-scale models at each scale and two multi-scale models, one with habitat and the other with urban.

After having found the best model for detection probability, the scale of effect of composition based variables and prox to be used in multi-scale models, and having tested for collinearity among variables, we could then proceed with building single-scale and multi-scale global models. All global models were tested for Spatial Autocorrelation of Residuals ('SAC') to avoid underlying spatial processes to affect our results. For this, we calculated Global Moran's I and when significant SAC was found, an autocovariate parameter was calculated by means of principal components of neighbor matrices (PCNM) and added to the global model [50]. Goodness-of-fit test and overdispersion parameter (c-hat) were estimated by applying the parametric bootstrap procedure proposed by MacKenzie and Bailey [51] and implemented in the 'AICcModavg' package of R [52].

Finally, to find out the best model(s) explaining occupancy patterns in each region, we generated all possible models starting from each single-scale and multi-scale global model, with the function *dredge* of MuMiN package in R [53]. Then, we selected the models with $\Delta AIC < 2$ [49]. Selected models were evaluated based on indicators that can be derived from a confusion matrix, which contains observed and predicted presence/absence (1/0) values of a given model [54]. We calculated the percent correctly classified (PCC), the area under the receiver operator characteristic curve (AUC) and Kappa statistics. All indicators have values ranging from 0 to 1. Kappa measures the agreement between the observed presence/absence values and those expected by chance, and can be calculated at different thresholds used to translate predicted probabilities into 0/1 values. We calculated two Kappa measures, one at threshold of 0.5 (Kappa0.5) and another one at the optimized threshold (Kappaopt), where the optimized threshold was determined by calculating Kappa at each threshold from 0 to 1 at intervals of 0.01. All indicators were calculated with the 'PresenceAbsence' package of R [55]. Additionally, we also calculated the RN^2 of each selected model. We then selected the models with the highest value for most of the model indicators, and compared among all the single-scale models, and with the multi-scale models. Lastly, we determined which variables influenced the most occupancy patterns in each region, and whether the multi-scale models outperformed the single-scale models.

Results

A total of 172 lizards were detected in both regions, 135 in the core and 37 in the Periphery. From 42 patches visited in the core, lizards were detected in 17 patches in both surveys and in 7 patches in one survey, for a total of 24 patches occupied. In the periphery, 7 out of 33 patches were occupied, and lizards were detected in 5 patches in both surveys and in 2 patches in one survey.

Scales at which occupancy is explained in each region

The effect of composition-based variables (urban, crop_pas, habitat) and the proximity index (prox) on occupancy probability as single variables is shown in Fig 2. At all scales, the effect of urban, crop_pas and prox was higher in the periphery (Fig 2A) compared to the core (Fig 2B). At the core, crop_pas and prox showed a low, almost constant effect across scales, and the effect of urban at its scale of effect (50m) was just slightly higher compared to the other scales. By contrast, in the periphery the difference among scales was much more marked for these variables. Here, the scale of effect of urban was found at 500m, and the effects of crop_pas and prox at 1000m and 2000m, respectively, but their effects did not change considerably across scales. The effect of habitat at small scales (<500m) was similar between regions, but increased with scale in the periphery, reaching its maximum at 2000m, and decreased with scale in the core. The effect of natural covers that do not represent habitat in the periphery was strongest at large scales (Fig 2C). The effect of densewood showed a tendency to increase with scale up to 2000m, after which a slight decrease in the effect is found. A tendency to increase with scale was observed for humid_grass after 250m, reaching its peak at the scale of 3000m.

Although the scale of effect of individual composition-based variables was larger in the periphery compared to the core, when combining effects of multiple variables, representing not only landscape composition but also landscape configuration and patch characteristics, we found that the response of the species to habitat loss occurs at a much smaller spatial scale in the periphery relative to the core; (Table 2, Table 3). Specifically, the top single scale models explaining occupancy probability in the core were in the range of 500 m and higher (see S7 Appendix for best models selected at small scales), while in the periphery the best SS models were found already at 150 m.

Most important variables at single scales

We found differences between regions regarding the variables that consistently had an effect on the occupancy probability across scales in SS models. In the core, most important variables were those defining landscape configuration and patch geometric characteristics (Table 2). Dist_river appeared consistently in all SS models, as well as a measure of isolation, either np_dist or prox. Perimeter and shape_index were also included in most models across scales.

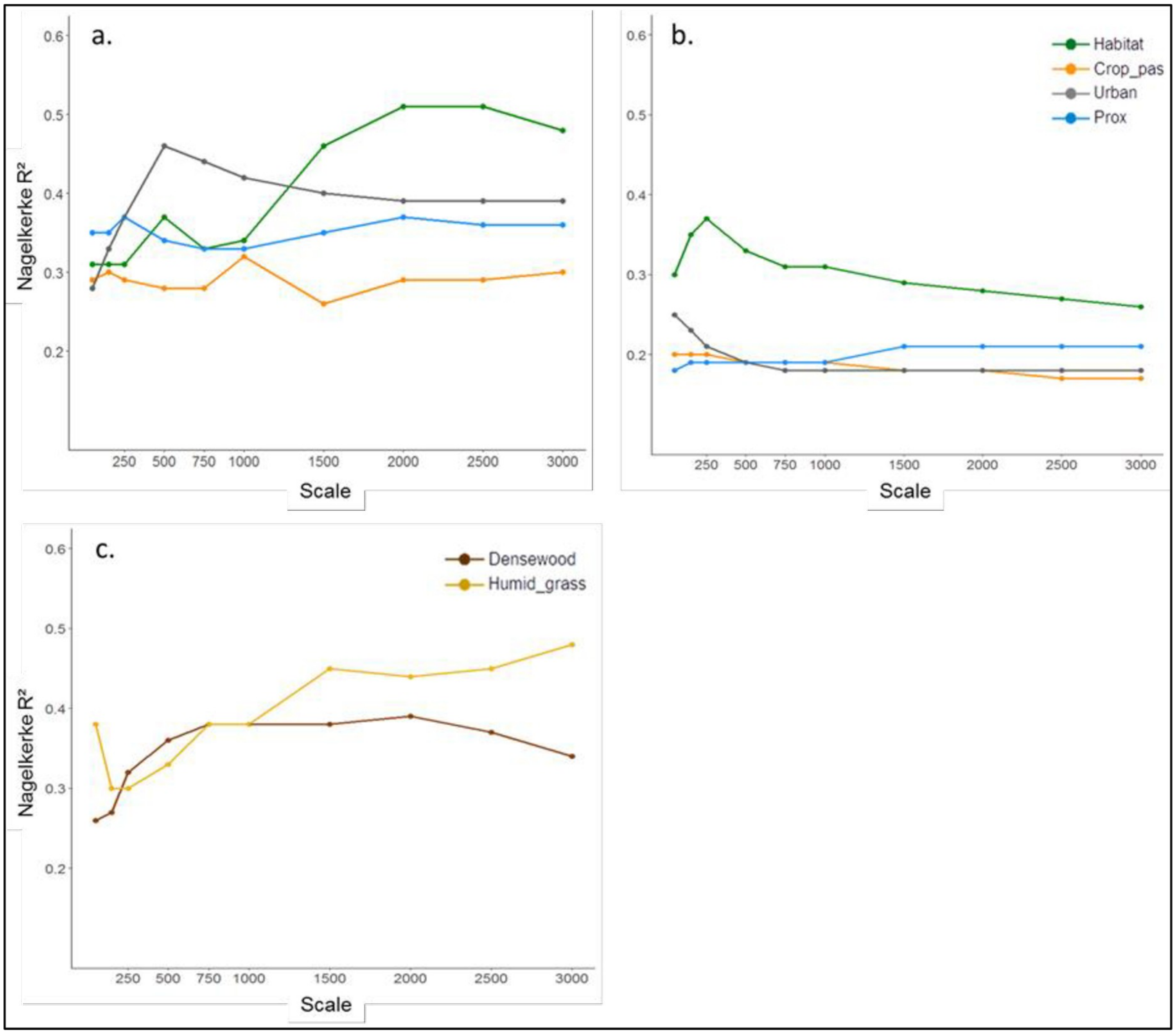

Fig 2. Effect of composition based variables and proximity index through spatial scales in the periphery (a, c) and in the core (b).

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Area was not as commonly included as the variables mentioned above but was present in half of the SS models (15 out of 31), principally in models from 500m to 2000m. In the core, occupancy probability across single scales increased with isolation and perimeter and decreased with distance to the river, patch area and shape index. Although all indices across single scales had very close values, the best model was found at 750 m, which additionally included habitat, a variable that appeared only in few SS models. Prediction curves of the best model in the core showed that occupancy probability starts to decrease with a distance of 150m from the river, and reaches a value of 1 already with 10m distance from nearest patch and 20% of habitat coverage (Fig 3). Comparably, in the periphery, a combination of variables related to landscape composition, patch geometry and habitat quality defined the occupancy probability across single scales (Table 3). Densewood and crop_pas had a positive effect on occupancy and were present in the majority of SS models, as well as perimeter and slope. As in the core, area appeared in half of the SS models (13 out of 25), and was concentrated in scales above 500m, having a negative effect on occupancy probability. In the periphery, almost all indices had the same value across SS models. Based on the prediction curves, occupancy was above 0.5 when

Table 2. Multiscale (ms) and single scale selected models at the core region.

Scale	RN^2	PCC	AUC	Kappa0,5	Kappaopt	Dist_river	Np_dist	Prox	Habitat	Crop_pas	Urban	Area	Perimeter	Shape_index	Veg_str	Radiation
ms	0.4	0.761	0.824	0.513	0.559				+							
	0.43	0.761	0.821	0.513	0.559				+							
	0.33	0.761	0.821	0.513	0.513				+							
	0.37	0.761	0.824	0.513	0.513				+							
500	0.7	0.928	0.902	0.851	0.851	-		-			-		+	-	+	-
	0.7	0.928	0.902	0.851	0.851	-		-		+		-	+	-	+	
750	0.68	**0.952**	**0.918**	**0.901**	**0.901**	-	+		+				+			
	0.62	0.928	0.878	0.851	0.851	-	+		+			+	+			
1000	0.69	0.928	0.871	0.851	0.851	-	+				-	-	+	-		
	0.69	0.928	0.8855	0.851	0.851	-	+				-	-	+	-		
	0.7	0.928	0.902	0.851		-	+					-	+	-		-
1500	0.69	0.92	0.895	0.851	0.851	-	+					+	+	-		
	0.68	0.928	0.868	0.851	0.851	-	+				-	-	+	-		
	0.7	0.928	0.902	0.851	0.851	-	+					-	+	-		-
	0.66	0.928	0.895	0.851	0.851	-	+		+				+	-		
2000	0.69	0.92	0.895	0.851	0.851	-	+					-	+	-		
	0.67	0.928	0.895	0.851	0.851	-	+				-	-	+	-		
	0.7	0.928	0.902	0.851		-	+					-	+	-		-
	0.7	0.928	0.902	0.851	0.851	-	+		+				+	-		-
	0.67	0.928	0.895	0.851	0.851	-	+		+				+	-		
	0.67	0.928	0.902	0.851	0.851	-		-	+				+		+	-
2500	0.69	0.928	0.891	0.851	0.851	-	+		+							
	0.69	0.928	0.898	0.851	0.851	-			+							-
	0.67	0.928	0.895	0.851	0.851	-		-			-		+	-		
	0.7	0.928	0.895	0.851	0.851	-		-			-	-	+	-	+	
	0.69	0.928	0.895	0.851	0.851	-		-		+			+	-		
	0.64	0.928	0.895	0.851	0.851	-		-		+			+	-		
	0.63	0.928	0.895	0.851	0.851	-		-		+			+	-		
	0.66	0.928	0.855	0.851	0.851	-			-	+		-	+	-		
3000	0.7	0.92	0.899	0.851	0.851	-	+				-	-	+	-		
	0.69	0.928	0.902	0.851	0.851	-	+				-		+	-		
	0.69	0.928	0.895	0.851	0.851	-	+					-	+	-		
	0.69	0.928	0.895	0.851	0.851	-		-			-		+	-		
	0.68	0.928	0.895	0.851	0.851	-		-			-		+	-		
	0.68	0.928	0.895	0.851	0.851	-		-	+	+			+	-		

Only variables explaining occupancy probability are presented, and the direction of their effects is shown as positive (+) or negative (-). Models with the same set of variables represent models with different combinations of the three variables explaining detection probability. In bold is signalized the model with the highest values for most of the model performance indicators.

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the proportion of densewood was between 0.4 and 0.6 and the proportion of crop_pas between 0.3 and 0.7 (Fig 4).

Other variables had a lower representativeness across single scales in each region. In the core, the effects of composition-focused variables were mostly concentrated at larger scales. Urban was present in most of the models at 1000m and 3000m and crop_pas appeared in very few models, from which the majority belonged to the 2500m scale. Habitat also had a low representativeness in SS models in the core with most of them being at the 2000m and 2500m scales. Thus, habitat was not very consistent in explaining occupancy probability across scales

Table 3. Multiscale (ms) and single scale selected models in the periphery region.

Scale	RN^2	PCC	AUC	Kappa0,5	Kappaopt	Dist_river	Np_dist	Prox	Habitat	Densewood	Humid_grass	Crop_pas	Urban	Area	Perimeter	Shape_index	Veg_str	Slope
Ms	0.86	1	1	1	1		+	-		+				-	+			+
	0.83	1	1	1	1	+				+	-		-		+		-	
	0.79	1	1	1	1		+			+	-				+		-	
50	0.83	0.939	0.928	0.835	0.835				+		-	+			+		-	
150	0.85	1	1	1	1					+		+			+		-	+
	0.88	1	1	1						+		+			+		-	+
	0.82	1	1	1					-	+		+				-		+
250	0.86	1	1	1		-				+		+		-	+			+
	0.85	1	1	1	1		+			+		+			+		-	+
	0.85	1	1	1	1				-	+		+			+		-	+
	0.84	1	1	1	1					+	-	+			+		-	+
	0.84	1	1	1	1				-	+		+			+	-		+
	0.83	1	1	1	1				-	+		+		-	+			+
	0.85	1	1	1	1					+		+	+		+		-	+
	0.84	1	1	1	1					+		+	+		+	-		+
	0.83	1	1	1	1					+		+	+	-	+			+
500	0.85	1	1	1		-				+		+		-	+			+
750	0.86	1	1	1	1	-				+		+		-	+			+
	0.79	1	1	1	1						-	+		-	+			+
	0.83	1	1	1	1						-	+		-	+		-	+
1000	0.83	1	1	1	1		+	-		+				-	+			+
	0.8	1	1	1	1		+	-		+					+		-	+
1500	0.85	1	1	1	1		+	-		+				-	+			+
2000	0.86	1	1	1	1		+	-		+				-	+			+
2500	0.86	1	1	1	1		+	-		+				-	+			+
3000	0.86	1	1	1	1		+	-		+				-	+			+
	0.83	1	1	1	1		+			+				-	+		-	+
	0.84	1	1	1	1	+		-			-		-		+		-	

Only variables explaining occupancy probability are shown and the direction of variables' effect is marked as positive (+) or negative (-). Models with the same set of variables represent models with different combinations of the three variables explaining detection probability.

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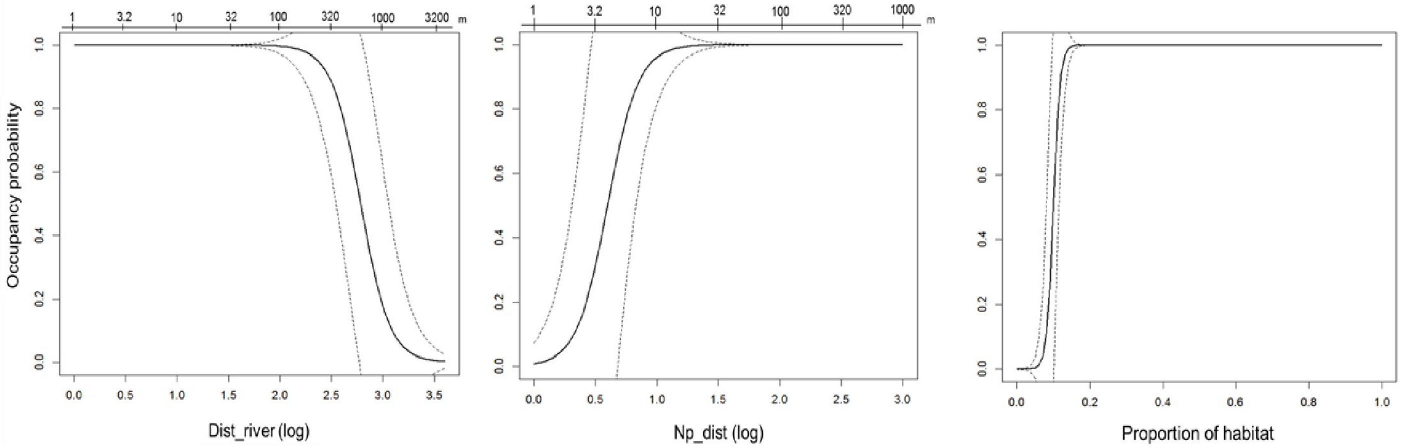

Fig 3. Predicted occupancy probability as function of distance to river (Dist_river), distance to nearest patch (Np_dist), and proportion of habitat in the best model at scale 750m. For Dist_river and Np_dist the x axis at the top represents distance values in meters.

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in this region, despite being present in the best model at 750m. In the periphery, variables that appeared in much fewer models were np_dist, prox and veg_str. Isolation effects, either as np_dist or prox, were concentrated at large scales and appeared in all models above >1000m having a positive effect on occupancy. Veg_str was common in models at small scales (50-250m) and its effect on occupancy was negative.

Multi-scale versus single-scale models

In the core region, when including composition-focused variables at its individual scale of effect in MS models, those with only habitat as predictor of occupancy probability performed better than models with any other combination of variables. However, in this region the best MS models did not outperform the best SS models at all scales for any of the model indicators (Table 2).

At the periphery, the performance of the MS models was equal to that of all SS models (Table 3). MS models in the periphery were partially similar to those in SS models, with

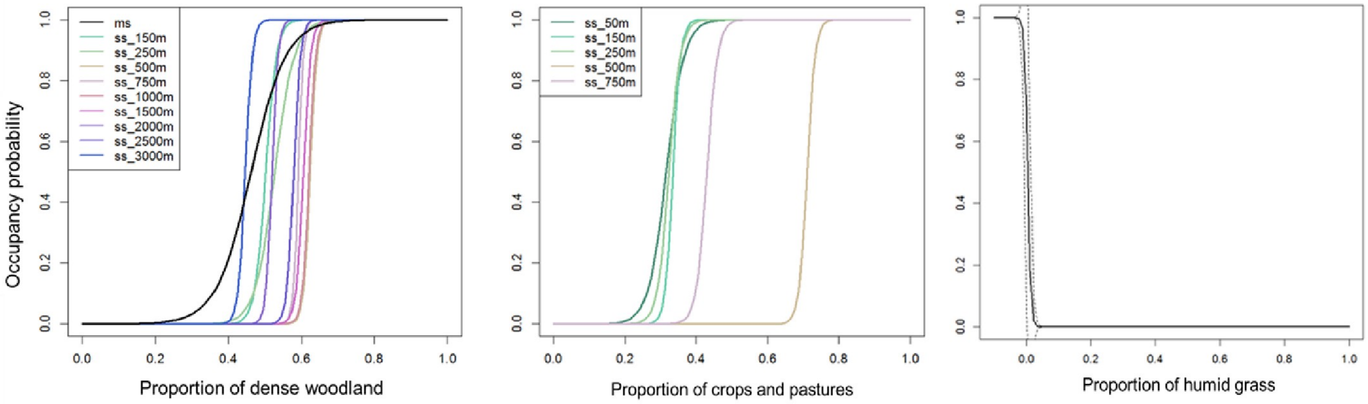

Fig 4. Predicted occupancy probabilities in the periphery as function of the proportion of dense woodland and crops and pastures across single scales. Probability curves plotted for each single scale (ss) correspond to the best model among the models in which the variable appears. Humid_grass curve correspond to the best MS model in which this variable was present.

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densewood and perimeter still being very important and present in all MS models. Additionally, veg_str, np_dist and humid_grass were found to gain importance and were present in most of the MS models in the periphery. Humid_grass had a strong effect on occupancy probability, which dropped to zero at a very low coverage of this land cover class (Fig 4).

Discussion

This study supports the hypothesis that the landscape structure and patch characteristics resulting from habitat loss affect differently the occupancy probability of *Lacerta viridis* in core versus peripheral populations. When comparing study areas with nearly similar landscape structure, we found that landscape composition had an overall stronger effect in the periphery compared to the core when land-cover classes were analyzed individually. In spite of the fact that the scale of effect of urban areas and crops and pastures was smaller in the core compared to the periphery, the effect of these variables was higher in the periphery at all scales (Fig 2). Similarly, the amount of habitat around patches had a stronger individual effect across all scales above 500m in the periphery compared to the core, while at smaller scales the strength of the effect was similar between regions. Therefore, our evaluation of the individual effects of landscape composition variables confirms the hypothesis of peripheral populations being more sensitive to habitat loss, not due to stronger effects appearing at smaller scales compared to the core, but because effects are stronger across all single scales.

Lower effects of individual landscape composition variables in the core compared to the periphery reflect what we found later in multivariate models: occupancy probability in the core was influenced by landscape configuration across single scales, whereas in the periphery occupancy was much more determined by landscape composition (Tables 2 and 3). The characteristics of the landscape surrounding a patch (patch context) affect occupancy probabilities mainly through their influence on the dispersal of individuals among patches [56, 57], an essential component for population persistence in structured landscapes [58]. Therefore, based on our study, it can be inferred that the most relevant parameter that might affect dispersal in the core is the spatial relation between patches and the river, while in the periphery our findings indicate a key parameter to be the proportion of different land covers in the matrix across scales. Thus, in the core, dispersal would be facilitated through connectivity defined by spatial configuration, while in the periphery it is overall landscape permeability that affects occupancy.

This sensitivity to matrix permeability in the periphery might be principally associated to the positive effect of crops and pastures on occupancy probability up to the 750 m scale (Table 3, Fig 4), suggesting that up to medium dispersal distances lizards in the periphery can cope with these land covers. Interestingly, although the variable crops and pastures was not ranked as important parameter in the core, when present in any model, its effect was positive as well (Table 2). The positive effect of crops and pastures on occupancy might be related with their effect on ecological processes that can occur during dispersal, like feeding, thermoregulation and predators avoidance [59, 60]. Despite higher exposure to predators, crops and pastures might offer food resources, as well as thermoregulation possibilities in the peripheral region, given a need for microhabitats with lower vegetation structure in this region. Open land covers might also be suitable for juvenile dispersal, as they are less conspicuous for predators than adults; and seasonal changes of crops might allow lizards to use different vegetation structures throughout the year. Moreover, age of individuals and vegetation structure of crops can have a positive interactive effect on the movement of some species. For example, in the case of the Franklin's ground squirrel (*Poliocitellus franklinii*), crops have been shown to have low resistance to movement, especially for juveniles in late summer and autumn, when vegetation is higher and can hide them from predators [61, 62]. This might be especially important for the persistence of populations of lacertid species, in which juvenile dispersal is one of the most important dispersal events in life [63, 64], occurring precisely in late summer and autumn.

Tolerance to agricultural land cover might also be related with the maintenance of specific structures in the landscape that can increase the connectivity among populations, like vegetation in riparian zones, which are often inhabited by Lacertid species. For instance, the distribution of *Lacerta schreiberi* in Portugal was found not to be negatively affected by agriculture as long as vegetation along watercourses is maintained [65]. Our results suggest a similar finding in the core, with crops and pastures not having a negative effect and distance to river being one of the most important factors explaining population persistence (Table 2, Fig 3). Indeed, the vegetation at the banks of the Maritza River, as well as those of tributary rivers like the Tshaja river, is continuous along most of the river, thus potentially serving as an important corridor among patches. Hedges between fields are another landscape feature that might reduce the resistance of crops and pastures to the movement of lizards. Hedges were already found to play an important role for lizards at the community level, with cultivation patterns that include hedgerows sustaining higher species richness in a natural reserve in Cyprus [66]. Hence, in this region, the restoration of hedges around fields may improve connectivity and, with it, potentially occupancy probabilities. Regarding dense woodland in the periphery, which was present in all models in the periphery, its consistent positive effect (Table 3, Fig 4) might be due to the high correlation with prevalence of open woodland at all scales, which is one of the habitat types that *L. viridis* occupies in the periphery, rather than with permeability to dispersal.

In both regions, isolation had a positive effect on occupancy probability of habitat patches when combined with other variables. It was present across most single scales in the core but only above 1000 m in the periphery (Tables 2 and 3). Although the Island Biogeography Theory (IBT) [67] and meta-populations dynamics models [68] predict a negative effect of isolation, other conceptual models propose that the sensitivity to habitat configuration -isolation and patch area- vary depending on the overall amount of habitat in the landscape. The 'fragmentation threshold' hypothesis [69], for instance, states that habitat configuration is important when habitat amount is below ~30%; and the habitat amount hypothesis (HAH,[70]) postulates that due to a sample area effect, habitat configuration can perfectly be replaced by habitat amount surrounding the sampled site, with isolation having either any or positive effect (eg. [71]). However, in our study, habitat amount did not have a paramount effect on occupancy probability across single scales in any region, and therefore, the HAH does not apply to our case.

A conceptual model that could explain our results, is the one proposed by Villard and Metzger [72]. They propose that habitat configuration is important for the persistence of populations at intermediate levels of habitat amount. At low levels of habitat loss the species' density is high irrespective of isolation; as habitat loss proceeds, populations become dependent on configuration and dispersal among patches; finally at high levels of habitat loss -and subsequent increase in isolation- the species pool in the landscape has considerably decreased and populations' rescue is not possible anymore, even if connectivity is improved. The breadth and position of the range of intermediate values of habitat amount at which habitat configuration is important depends on the species sensitivity to both, habitat loss and habitat configuration. In our study, habitat amount was not important across models and isolation did not have a negative effect. Hence, following the model of Villard and Metzger ([72], fig 6-vi.), populations of *L. viridis* in the core and the periphery seem to have low sensitivity to both, habitat loss and isolation, which predicts a broad intermediate level that starts after considerable habitat loss.

In other words, lizards' populations seem to be able to cope with habitat loss independently of habitat configuration up to high levels of habitat reduction. With further habitat loss populations depend on configuration, but due to low sensitivity to it, they persist until considerable levels of isolation resulting from further reduction of habitat amount.

In terms of patch characteristics, the most important variable was perimeter, which was present in all models in both regions and had a positive effect on occupancy probability (Tables 2 and 3). Also, patch area was found in half of the models in each region, having in all but two cases a negative effect on occupancy probability. Positive perimeter effects coupled with negative effects of area are closely related to positive edge effects, [73], due to perimeter-to-area ratio increasing with decreasing area. In the core, additionally, shape index, which in our study increases with patch irregularity, had a negative effect on occupancy probability. Negative effects of shape index are related to decreasing core patch area [74, 75]. Thus, our results suggest that in the core occupancy probability might be influenced by positive edge effects together with sensitivity to core area, a pattern that has been found in species that use both, interior and patch edges [76]. Comparably, in the periphery, where shape index did not affected occupancy across scales, lizards might have preference for edges.

Differential preference in the use of patch edges between peripheral and core populations of *L. viridis* might result from differences in microhabitat selection between regions. In the periphery, overall radiation is lower compared to the core, and lizards compensate by selecting open microhabitats with low vegetation structure in order to maximize the exposure to radiation. In the core, where radiation and temperatures are higher, lizards select for microhabitats with higher vegetation structure that provide shadow and allow lizards to cool after basking hours. Thus, lizards in the periphery might use edge more often along the day and throughout the year, while in the core the preference of lizards for edges may correspond to basking hours in the early morning and late afternoon, and more often in early spring compared to late spring and summer. The relation between the effect of patch characteristics on occupancy probability and microhabitat selection and thermoregulatory behavior of lizards was also indicated by vegetation structure, which had a positive effect on occupancy probability in the core but a negative effect in the periphery. These results suggest that ecological processes at the individual level, like microhabitat selection and thermoregulation, might affect population persistence in the patch and generate occupancy patterns at the landscape scale.

Although vegetation structure was important for the occupancy probability in both regions in models at small scales (<500 m) (Tables 2 and 3), it was only in the periphery where another variable defining habitat quality, which is slope, was important across all single scales and retained in multi-scale models, suggesting a stronger dependency of peripheral populations of *L. viridis* on habitat quality when interacting with other parameters at multiple scales. Northern peripheral populations of *L. viridis* have a smaller niche size compared to core ones, which makes them more stenoecious or habitat specialist than core populations [24], a pattern also found in insects [26, 77], fishes [78] and other lizards [77]. Furthermore, habitat specialization is closely related with higher dependency on habitat quality [13], and occupancy probabilities have been found to be strongly influenced by habitat quality in specialist species of insects [79, 80], small mammals [81, 82] and lizards [83] inhabiting modified landscapes, in comparison with generalist species. In this regard, our study supports the existence of this pattern, but this time at the intraspecific level, with populations differing in their degree of habitat specialization depending on their geographic position in the distribution range of the species.

Several studies have linked the position in the distribution range with vulnerability to extinction, and point out that peripheral populations might be at higher risk of local extinction [84, 85]. Moreover, specific traits of peripheral populations, like lower abundance [86], lower genetic variability [87, 88] and smaller niche [78, 89], have been proposed to explain its higher vulnerability. Position in the range and vulnerability of extinction have also been linked with sensitivity to human modified landscapes (e.g. [90]), and extensive multispecies approaches have demonstrated higher sensitivity to habitat loss of peripheral populations in the Palearctic region [91]. However, only very few studies have made the complete link between position in the range, species traits and vulnerability of extinction in modified landscapes. For instance, [92] found that peripheral populations of the lizard *Lacerta agilis* had a lower genetic variability and also a higher sensitivity to patch size, compared to core populations. In this context, our work also throws some light upon the possible ecological mechanisms behind the relationship between position in the range, sensitivity to habitat loss and populations' traits, by identifying the parameters of landscape structure and patch characteristics to which northern peripheral and more specialized populations of a broad ranging species are more sensitive compared to core populations.

With respect to the analysis performed and the model selection procedures, it is important to note that the high values obtained for model evaluation indices in all of our models, can be strongly related to the fact that we tried as much as possible to cover the range and type of variables that might influence occupancy. Also, it might be strongly related to the model selection procedure that we applied, in which models were first selected based on ΔAIC < 2 and then, from this group of best models, we selected those with the highest values for the indices evaluated. High indices values indicate that the models can discriminate very well between patches where the lizard is present and those where it isn't, which in a binary classification scheme can be expected for models that explain also high levels of variance ($>$ 63% in the single scale models in the core, and $>$79% in all models in the periphery), and thus, our results highlight even more the fact that the inclusion of specific variables (the most common ones found in the models) might be important for model accuracy. In the periphery very high indices values of selected models (= 1) might also be due to the fact that the majority of the patches in the sample were not occupied, and then, the classification ability is higher. However, given models presented in the results represent an extremely reduced group among all the model initially run, we still consider that the predictive and classification abilities of selected models, by themselves and not due to sample distribution, is very high.

An additional important remark regarding models' output, is that in multivariate models the direction of the effect of each variable can change depending on other variables present in the model [93]. For some of the variables that we considered, like isolation in the core and crops and pasture in both regions, the individual effect was negative (S8 Appendix), but in combination with other variables the effect was positive. Positive effects of these variables were systematic in all multivariate selected models where these variables were present, and therefore, we rely on our results, and highlight the importance of testing coefficients direction when variables are alone or in combination with other variables.

Regarding the land cover classification approach that we apply, it is important to consider that although the ideal methodological approach to compare among landscapes is to produce classified maps with data obtained from the same source, our approach was perfectly sufficient to perform the ecological analysis that we carried out. As stated by Fynn and Campbell [94], possible shortcomings of landscape ecology studies using imagery from different sources might come out in cases when images with coarse resolution are compared with finer resolution imagery. However, in our study the resolution of both, the IPR map used for the periphery and the rapid eye satellite imagery used for the core, was the same (5m), and additional information used for the classification in both regions had the same source (Urban atlas, TCD and imperviousness layers of CORINE) and resolution; orthophotos used for some parts of the map in the periphery were rectified by IPR and had also a very high accuracy. Dissimilar sources of information might as well represent a disadvantage due to the different methods used for the classification process in the IPR map of the periphery compared to those we applied to the Rapid Eye satellite imagery in the core region. However, given the high specificity of the original classification of the IPR map (> 60 classes), which we afterwards reclassified in broader classes, we consider that the output of both maps had similar accuracy (>90%), and therefore, perfectly allowed to compare between landscapes and precisely calculate percentages of land cover classes. Comparability was also achieved through careful examination of maps by the first coauthor who knows both study sites extremely well after having spent several months in both regions, and therefore had trustable on-the-ground information, and by means of thorough and systematic application of specific criteria to classify each land cover in both regions (Table 1).

Implications for conservation measures

In the periphery, the most important was the landscape composition and the permeability represent mostly by the presence of crops and pastures. Our results show that this effects are present already at very low scales, and that in scales between 50 to 500m occupancy probability increases already over 0.8 with percentages of crops and pastures between 30 to 40%. On the other side this permeability decreases very fast with already a low percentage of humid grasses. Therefore, we strongly recommend to increase matrix permeability by applying a more heterogeneous cultivation pattern that includes hedges and line structures with vegetation corresponding to the habitat of the species, as well as the inclusion of such structures through areas with humid grassland.

With respect to patch characteristics, it is very important to increase the availability of edge in the patches. This can be achieved by increasing patch size with linear structures to maintain a high perimeter to area ratio. In parallel, these linear structures can also serve to connect through the agricultural landscape. Finally, maintaining high levels of habitat quality is also very important in this region, and can be achieved by keeping low levels of vegetation structure, and specially by protecting valley's slopes from overgrown vegetation. Similarly, overgrown vegetation should be avoided in open woodlands, which are usually located in slopes and at the borders of dense woodland areas.

In the core, regarding configuration of the landscape, the most important management measures are, first to protect the patches that are close to the river, or at the riverside, and second to structurally connect with the river those patches that are further. Based on our analysis, patches with a distance to the river lower than 320m have an occupancy probabilities over 0.8, and patches with distances longer than ~650 m have probabilities lower than 0.5. Then, we recommend to protect -and restore where necessary- the river bank vegetation along the Maritza River and its tributary rivers, as this areas might act as important corridors for the species, and to connect further habitat remnants with this large riverside corridor, through additional structures with habitat vegetation. As in the periphery, hedges and habitat lines surrounding crops could improve connectivity through the landscape.

Regarding composition, it is very important to protect the habitat surrounding patches, principally at a scale of 250m, which is the scale of effect of this land cover and at which the variable was included in multi-scale models, being the only variable present in these models. Habitat was also present in the best model at the scale of 750m, and our results show that with only a small increment in the percentage of habitat at this scale (~ 10%) the probability of occupancy substantially increases (Fig 3).

With respect to patch characteristics, we found that the shape of the patches is very important for both, maintaining a large perimeter and also sufficient core area. Therefore, we strongly recommend to not alter the shape of remnant patches that already have a regular shape, and to restore habitat at the direct borders of patches with irregular shapes, in order to increase perimeter and core area by 'softing' angular and irregular shapes. Regarding habitat quality, we suggest to protect the vegetation structure in remnant patches, avoiding practices that can diminish it. This means, maintaining different vegetation levels that include grasses, shrubs, rocks, fallen trunks, trees, etc. Grazing, for instance, can have a very rapid negative effect in the quality of the patches by substantially reducing vegetation structure (pers. observation), given cows and goats feed on the low and medium strata, and goats also lower branches of woody plants. As a consequence lizards lose refuge and structures to bask. Also, as vegetation structure decreases radiation incidence increases, consequently augmenting temperatures and diminishing humidity, with the habitat becoming drier and less suitable for the species.

In both regions we recommend to monitor the populations. Further insights in the abundance and condition status of individuals would be very useful to more deeply asses the status of populations.

Conclusions

Our study shows that northern peripheral, more specialized populations of *L. viridis* are also more sensible to the effects that habitat loss has on the landscape structure and on the characteristics of remnant habitat patches. In comparison with populations in the core, the occupancy probability of populations in the periphery was found to be more affected by landscape composition, which suggests substantial dependency on matrix permeability; also, habitat quality had a stronger influence on populations in the periphery and our results regarding patch geometric characteristics in this region suggest a preference of the species for patches with more edge in relation to patch core area. Comparably, in the core, we found that persistence of populations is mainly affected by the possible connectivity that the river bank vegetation offers through the landscape. Also, the species in this region seems to be an omnipresent species regarding its use of the patch, requiring both long edges and also enough core area in the interior of the patch. Finally, in both regions the species had low sensitivity to habitat amount and to habitat configuration, an outcome that strongly differs from the expectations of the IBT, the meta-populations dynamic models and also from the HAH, but one that fits conceptual–and empirically tested–models that describe a more gradual relationship between habitat amount and isolation.

Supporting information

S1 Appendix. Distribution of variables representative of habitat configuration in each region.
(DOCX)

S2 Appendix. Location of visited patches in each region.
(DOCX)

S3 Appendix. Maps of classified land cover classes in each region.
(DOCX)

S4 Appendix. Models for detection probability in each region. Variables were included to model only detection probability (p) while maintaining occupancy probability (psi) constant.
(DOCX)

S5 Appendix. Spearman rank correlations of no scale dependent variables in each region.
(DOCX)

S6 Appendix. Different sets of models ran in each single scale and multiscale models in each region. Each set includes all variables plus the variable or combination of variables indicated.
(DOCX)

S7 Appendix. Best selected models at small scales from 50m to 250m in the core region.
(DOCX)

S8 Appendix. Individual effects of non-scale and scale dependent variables.
(DOCX)

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Author Contributions

Conceptualization: Ana María Prieto-Ramirez, Guy Pe'er, Dennis Rödder, Klaus Henle.

Data curation: Ana María Prieto-Ramirez.

Formal analysis: Ana María Prieto-Ramirez.

Funding acquisition: Ana María Prieto-Ramirez.

Investigation: Ana María Prieto-Ramirez.

Methodology: Ana María Prieto-Ramirez, Leonie Röhler, Anna F. Cord.

Resources: Klaus Henle.

Software: Leonie Röhler, Anna F. Cord.

Supervision: Guy Pe'er, Dennis Rödder, Klaus Henle.

Visualization: Leonie Röhler, Anna F. Cord.

Writing – original draft: Ana María Prieto-Ramirez.

Writing – review & editing: Guy Pe'er, Dennis Rödder, Klaus Henle.

References

1. Fahrig L. Effects of Habitat Fragmentation on Biodiversity. Annual Review of Ecology, Evolution, and Systematics. 2003; 34(1):487–515.
2. Blanchet S, Rey O, Etienne R, Lek S, Loot G. Species-specific responses to landscape fragmentation: implications for management strategies. Evol Appl. 2010; 3(3):291–304. https://doi.org/10.1111/j.1752-4571.2009.00110.x PMID: 25567925
3. Jauker B, Krauss J, Jauker F, Steffan-Dewenter I. Linking life history traits to pollinator loss in fragmented calcareous grasslands. Landscape Ecology. 2013; 28(1):107–20.
4. Swihart RK, Gehring TM, Kolozsvary MB, Nupp TE. Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Diversity and Distributions. 2003; 9(1):1–18.
5. Davies KF, Margules CR, Lawrence JF. A synergistic effect puts rare, specialized species at greater risk of extinction. Ecology. 2004; 85(1):265–71.
6. Henle K, Davies KF, Kleyer M, Margules C, Settele J. Predictors of Species Sensitivity to Fragmentation. Biodiversity & Conservation. 2004; 13(1):207–51.

7. Keinath DA, Doak DF, Hodges KE, Prugh LR, Fagan W, Sekercioglu CH, et al. A global analysis of traits predicting species sensitivity to habitat fragmentation. Global Ecology and Biogeography. 2017; 26 (1):115–27.
8. Krauss J, Steffan-Dewenter I, Tscharntke T. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? Journal of Biogeography. 2003; 30 (6):889–900.
9. Öckinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, Kuussaari M, et al. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters. 2010; 13(8):969–79. https://doi.org/10.1111/j.1461-0248.2010.01487.x PMID: 20482577
10. Devictor V, Julliard R, Jiguet F. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos. 2008; 117(4):507–14.
11. Hoehn M, Sarre SD, Henle K. The tales of two geckos: does dispersal prevent extinction in recently fragmented populations? Molecular Ecology. 2007; 16(16):3299–312. https://doi.org/10.1111/j.1365-294X.2007.03352.x PMID: 17688534
12. Soga M, Koike S. Patch isolation only matters for specialist butterflies but patch area affects both specialist and generalist species. Journal of Forest Research. 2013; 18(3):270–8.
13. Ye X, Skidmore AK, Wang T. Within-patch habitat quality determines the resilience of specialist species in fragmented landscapes. Landscape Ecology. 2013; 28(1):135–47.
14. Carrara E, Arroyo-Rodríguez V, Vega-Rivera JH, Schondube JE, de Freitas SM, Fahrig L. Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biological Conservation. 2015; 184:117–26.
15. Püttker T, Bueno AA, dos Santos de Barros C, Sommer S, Pardini R. Habitat specialization interacts with habitat amount to determine dispersal success of rodents in fragmented landscapes. J Mammal. 2013; 94(3):714–26.
16. Vergara PM, Armesto JJ. Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. Landscape Ecology. 2009; 24(1):25–38.
17. Jackson HB, Fahrig L. What size is a biologically relevant landscape? Landscape Ecology. 2012; 27 (7):929–41.
18. Cozzi G, Müller CB, Krauss J. How do local habitat management and landscape structure at different spatial scales affect fritillary butterfly distribution on fragmented wetlands? Landscape Ecology. 2008; 23(3):269–83.
19. Morris DW. Coexistence of Specialist and Generalist Rodents Via Habitat Selection. Ecology. 1996; 77 (8):22352–2364.
20. Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L. What determines the spatial extent of landscape effects on species? Landscape Ecology. 2016; 31(6):1177–94.
21. Kühnelt W. Grundriß der Ökologie mit besonderer Berücksichtigung der Tierwelt. Jena: Fischer Verlag; 1965.
22. Böhme W, Rödder D. Amphibien und Reptilien: Verbreitungs- und Verhaltensänderungen aufgrund der Erderwärmung. In: Lozán JL, Grassl H., Karbe L. & Jendritzky G editor. Warnsignal Klima: Gefahren für Pflanzen, Tiere und Menschen. 2 ed. Hamburg2014. p. 77–81.
23. Olsson M. Ecology of a Swedish population of the sand lizard (Lacerta agilis)- preliminary report. Mertensiella. 1988; 1:86–91.
24. Prieto-Ramirez AM, Pe'er G, Rödder D, Henle K. Realized niche and microhabitat selection of the eastern green lizard (Lacerta viridis) at the core and periphery of its distribution range. Ecology and evolution. 2018; 8(22):11322–36. https://doi.org/10.1002/ece3.4612 PMID: 30519446
25. Blanco-Fontao B, Fernández-Gil A, Obeso JR, Quevedo M. Diet and habitat selection in Cantabrian Capercaillie (Tetrao urogallus cantabricus): ecological differentiation of a rear-edge population. Journal of Ornithology. 2010; 151(2):269–77.
26. Svensson BW. Changes in Occupancy, Niche Breadth and Abundance of Three Gyrinus Species as Their Respective Range Limits Are Approached. Oikos. 1992; 63(1):147–56.
27. Mollov IA. Habitat distribution of the amphibians and reptiles in the city of Plovdiv, Bulgaria. Biharean Biologist. 2011; 5(1):25–31.
28. Lacerta viridis. The IUCN Red List of Threatened Species 2009: e.T61530A12507156. http://dx.doi.org/10.2305 [Internet]. 2009.
29. ESRI. ArcGIS Desktop: Release 10.3.1.: Redlands, CA: Environmental Systems Research Institute.; 2015.
30. Mackenzie DI, Royle JA. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology. 2005; 42(6):1105–14.

31. Janssen I, Zuiderwijk A. Detection probability derived from the national reptile monitoring program in the Netherlands. Monitoring Network of Reptile, Amphibian & Fish Conservation the Netherlands, RAVON. http://eumon.ckff.si/files/porto/3_janssen.pdf; 2006.

32. Sewell D, Guillera-Arroita G, Griffiths RA, Beebee TJC. When Is a Species Declining? Optimizing Survey Effort to Detect Population Changes in Reptiles. PLoS One. 2012; 7(8):e43387. https://doi.org/10.1371/journal.pone.0043387 PMID: 22937044

33. Korsós Z. Comparative niche analysis of two sympatric lizard species (*Lacerta viridis and Lacerta agilis*). Vertebrata Hungarica. 1983; 22:5–14.

34. ESRI. ArcGIS Desktop: Release 10.6. Redlands, CA: Environmental Systems Research Institute. 2018.

35. Solutions EVI. ENVI 5.0. Boulder, Colorado.

36. IPR. Plán využití ploch—funkční plochy (územní plán). http://www.geoportalpraha.cz/cs/opendata/21733E1F-21B7-4ABC-B1C2-DC19C0237380. 2010.

37. Grimm A, Prieto Ramírez AM, Moulherat S, Reynaud J, Henle K. Life-history trait database of European reptile species. Nature Conservation. 2014; 9:45–67.

38. Mangiacotti M, Scali S, Sacchi R, Bassu L, Nulchis V, Corti C. Assessing the Spatial Scale Effect of Anthropogenic Factors on Species Distribution. PLoS One. 2013; 8(6):e67573. https://doi.org/10.1371/journal.pone.0067573 PMID: 23825669

39. Saint-Girons H, Bradshaw SD. Séd enlaril é, déplacements et répartit ion des individus dans une population de Lacerla viridis (Lau renti, 1768) (Lacertil ia, Lacertidae). Bijdragen tot de Dierkunde. 1989; 59 (2):63–70.

40. Böker T. Zur Ökologie der Smaragdeidechse Lacerta viridis (LAURENTI, 1768) am Mittelrhein II. Populationsstruktur, Phänologie Salamandra. 1990; 26(2–3):97–115.

41. Moser J. Beutrag zur Kenntnis der Verbreitung der Smaragdeidechse in Oberösterreich. Beitr Naturk Oberösterreichs. 1998; 6:391–2.

42. Waitzmann M, Sandmaier P. Zur Verbreitung, Morphologie und Habitatwahl der Reptilien im Donautal zwischen Passau und Linz (Niederbayern, Oberösterreich). Herpetozoa. 1990; 3((1/2)):25–53.

43. MacArthur RH, MacArthur JW. On Bird Species Diversity. Ecology. 1961; 42(3):594–8.

44. Conrad O, Bechtel B, Bock M, Dietrich H, Fischer E, Gerlitz L, et al. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4, Geosci. Model Dev., 8, 1991–2007. https://doi.org/105194/gmd-8-1991-2015 2015.

45. McGarigal K, Cushman SA, Ene E. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html: Computer software program produced by the authors at the University of Massachusetts, Amherst.; 2012.

46. MacKenzie DI, Nichols JD, Lachman GB, Droege S, Andrew Royle J, Langtimm CA. Estimating site occupancy rates when detection probabilities are less than one. Ecology. 2002; 83(8):2248–55.

47. Fiske I, Chandler R. Unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. Journal of Statistical Software. 2011; 43(10):1–23.

48. Team RC. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2018.

49. Burnham KP, Anderson DR. Model selection and multimodel inference: A practical information-theoretic approach 2nd edition ed. New York: Springer-Verlag; 2002.

50. Augustin NH, Mugglestone MA, Buckland ST. An Autologistic Model for the Spatial Distribution of Wildlife. Journal of Applied Ecology. 1996; 33(2):339–47.

51. MacKenzie DI, Bailey LL. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics. 2004; 9(3):300–18.

52. Mazerolle MJ. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.2–1. https://cran.r-project.org/package=AICcmodavg. 2019.

53. Bartón K. MuMIn: Multi-Model Inference. https://cran.r-project.org/web/packages/MuMIn/index.html; 2015.

54. Fielding AH, Bell JF. A review of methods for the assessment of prediction errors inconservation presence/absence models. Environmental Conservation. 1997; 24(1):38–49.

55. Freeman EA, Moisen G. PresenceAbsence: An R Package for Presence-Absence Model Analysis. Journal of Statistical Software. 2008; 23(11):1–31.

56. Fahrig L. How much habitat is enough? Biological Conservation. 2001; 100(1):65–74.

57. Cushman SA, Brad M, Adriaensen F, Beier P, Shirley M, Zeller K. Biological corridors and connectivity. In: Macdonald D, Willis K, editors. Key Topics in Conservation Biology 2: John Wiley and Sons, Oxford; 2013.

58. Brachet S, Olivieri II, Godelle B, Klein E, Frascaria-Lacoste N, Gouyon PH. Dispersal and metapopulation viability in a heterogeneous landscape. Journal of theoretical biology. 1999; 198(4):479–95. https://doi.org/10.1006/jtbi.1999.0926 PMID: 10373349

59. Baguette M, Stevens V, Clobert J. The pros and cons of applying the movement ecology paradigm for studying animal dispersal. Movement Ecology. 2014; 2:13.

60. Vasudev D, Fletcher Jr RJ, Goswami VR, Krishnadas M. From dispersal constraints to landscape connectivity: lessons from species distribution modeling. Ecography. 2015; 38(10):967–78.

61. Martin JM, Heske EJ. Juvenile Dispersal of Franklin's Ground Squirrel (Spermophilus franklinii) from a Prairie "Island". The American Midland Naturalist. 2005; 153(2):444–9.

62. Duggan JM, Schooley RL, Heske EJ. Modeling occupancy dynamics of a rare species, Franklin's ground squirrel, with limited data: are simple connectivity metrics adequate? Landscape Ecology. 2011; 26(10):1477–90.

63. Ronce O, Clobert J, Massot M. Natal dispersal and senescence. Proceedings of the National Academy of Sciences. 1998; 95(2):600–5.

64. Cote J, Clobert J. Social personalities influence natal dispersal in a lizard. Proceedings of the Royal Society B: Biological Sciences. 2007; 274(1608):383–90. https://doi.org/10.1098/rspb.2006.3734 PMID: 17164202

65. Brito JC, Paulo OS, Crespo EG. Distrubution and habitats of schreiber's green lizard (Lacerta schreiberi) in Portugal. Herpetological Journal. 1998; 8:187–94.

66. Michaelides G, Kati V. Diversity patterns and conservation management of the lizard community in a Mediterranean reserve (Cyprus). J Biol Res- Thessalon. 2009; 12:211–20.

67. MacArthur RH, Wilson EO. The Theory of Island Biogeography: Princeton, New Jersey: Princeton University Press; 1967.

68. Hanski I. Metapopulation dynamics. Nature. 1998; 396(6706):41–9.

69. Andrén H. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. Oikos. 1994; 71(3):355–66.

70. Fahrig L. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography. 2013; 40(9):1649–63.

71. Melo GL, Sponchiado J, Cáceres NC, Fahrig L. Testing the habitat amount hypothesis for South American small mammals. Biological Conservation. 2017; 209:304–14.

72. Villard M-A, Metzger JP. REVIEW: Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology. 2014; 51(2):309–18.

73. Fletcher JRJ, Ries L, Battin J, Chalfoun AD. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined?This review is one of a series dealing with some aspects of the impact of habitat fragmentation on animals and plants. This series is one of several virtual symposia focussing on ecological topics that will be published in the Journal from time to time. Canadian Journal of Zoology. 2007; 85(10):1017–30.

74. Helzer CJ, Jelinski DE. The realtive importance of patch area and perimeter-area ratio to grassland breeding birds. Ecological Applications. 1999; 9(4):1448–58.

75. Ries L, Robert J. Fletcher J, Battin J, Sisk TD. Ecological Responses to Habitat Edges: Mechanisms, Models, and Variability Explained. Annual Review of Ecology, Evolution, and Systematics. 2004; 35 (1):491–522.

76. Bender DJ, Contreras TA, Fahrig L. Habitat loss and population decline: A meta-analysis of the patch size effect. Ecology. 1998; 79(2):517–33.

77. Thomas JA, Rose RJ, Clarke RT, Thomas CD, Webb NR. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. Functional Ecology. 1999; 13:55–64.

78. Lappalainen J, Soininen J. Latitudinal gradients in niche breadth and position—regional patterns in freshwater fish. Naturwissenschaften. 2006; 93(5):246–50. https://doi.org/10.1007/s00114-006-0093-2 PMID: 16538374

79. Biedermann R. Patch occupancy of two hemipterans sharing a common host plant. Journal of Biogeography. 2004; 31(7):1179–84.

80. Münsch T, Helbing F, Fartmann T. Habitat quality determines patch occupancy of two specialist Lepidoptera species in well-connected grasslands. Journal of Insect Conservation. 2019; 23(2):247–58.

81. Gardiner R, Bain G, Hamer R, Jones ME, Johnson CN. Habitat amount and quality, not patch size, determine persistence of a woodland-dependent mammal in an agricultural landscape. Landscape Ecology. 2018; 33(11):1837–49.

82. Gomez Md, Goijman AP, Coda J, Serafini V, Priotto J. Small mammal responses to farming practices in central Argentinian agroecosystems: The use of hierarchical occupancy models. Austral Ecology. 2018; 43(7):828–38.

83. Thompson ME, Halstead BJ, Donnelly MA. Thermal quality influences habitat use of two anole species. Journal of Thermal Biology. 2018; 75:54–61. https://doi.org/10.1016/j.jtherbio.2018.05.007 PMID: 30017052

84. Donald PF, Greenwood JJD. Spatial patterns of range contraction in British breeding birds. Ibis. 2001; 143(3):593–601.

85. Yackulic CB, Sanderson EW, Uriarte M. Anthropogenic and environmental drivers of modern range loss in large mammals. Proceedings of the National Academy of Sciences. 2011; 108(10):4024–9.

86. Brown JH. On the relationship between abundance and distribution of species. Am Nat. 1984; 124 (2):255–79.

87. Hampe A, Petit RJ. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters. 2005; 8(5):461–7. https://doi.org/10.1111/j.1461-0248.2005.00739.x PMID: 21352449

88. Peterman WE, Feist SM, Semlitsch RD, Eggert LS. Conservation and management of peripheral populations: Spatial and temporal influences on the genetic structure of wood frog (Rana sylvatica) populations. Biological Conservation. 2013; 158:351–8.

89. Yurkowski DJ, Ferguson S, Choy ES, Loseto LL, Brown TM, Muir DCG, et al. Latitudinal variation in ecological opportunity and intraspecific competition indicates differences in niche variability and diet specialization of Arctic marine predators. Ecology and evolution. 2016; 6(6):1666–78. https://doi.org/10.1002/ece3.1980 PMID: 26909143

90. Lucas PM, González-Suárez M, Revilla E. Toward multifactorial null models of range contraction in terrestrial vertebrates. Ecography. 2016; 39(11):1100–8.

91. Boakes EH, Isaac NJB, Fuller RA, Mace GM, McGowan PJK. Examining the relationship between local extinction risk and position in range. Conservation Biology. 2018; 32(1):229–39. https://doi.org/10.1111/cobi.12979 PMID: 28678438

92. Henle K, Andres C, Bernhard D, Grimm A, Stoev P, Tzankov N, et al. Are species genetically more sensitive to habitat fragmentation on the periphery of their range compared to the core? A case study on the sand lizard (Lacerta agilis). Landscape Ecology. 2016; 32(1):131–45.

93. Banner KM, Higgs MD. Considerations for assessing model averaging of regression coefficients. Ecological Applications. 2017; 27(1):78–93. https://doi.org/10.1002/eap.1419 PMID: 27874997

94. Fynn IEM, Campbell J. Forest fragmentation analysis from multiple imaging formats. Journal of Landscape Ecology. 2019; 12(1):1–15.