RESEARCH PAPER

Cryptic niche conservatism among evolutionary lineages of an invasive lizard

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ABSTRACT

Aim There is increasing evidence that the quality and breadth of ecological niches vary among individuals, populations, evolutionary lineages and therefore also across the range of a species. Sufficient knowledge about niche divergence among clades might thus be crucial for predicting the invasion potential of species. We tested for the first time whether evolutionary lineages of an invasive species vary in their climate niches and invasive potential. Furthermore, we tested whether lineage-specific models show a better performance than combined models.

Location Europe.

Methods We used species distribution models (SDMs) based on climatic information at native and invasive ranges to test for intra-specific niche divergence among mitochondrial DNA (mtDNA) clades of the invasive wall lizard *Podarcis muralis*. Using DNA barcoding, we assigned 77 invasive populations in Central Europe to eight geographically distinct evolutionary lineages. Niche similarity among lineages was assessed and the predictive power of a combination of clade-specific SDMs was compared with a combined SDM using the pooled records of all lineages.

Results We recorded eight different invasive mtDNA clades in Central Europe. The analysed clades had rather similar realized niches in their native and invasive ranges, whereas inter-clade niche differentiation was comparatively strong. However, we found only a weak correlation between geographic origin (i.e. mtDNA clade) and invasive occurrences. Clades with narrow realized niches still became successful invaders far outside their native range, most probably due to broader fundamental niches. The combined model using data for all invasive lineages achieved a much better prediction of the invasive potential.

Conclusions Our results indicate that the observed niche differentiation among evolutionary lineages is mainly driven by niche realization and not by differences in the fundamental niches. Such cryptic niche conservatism might hamper the success of clade-specific niche modelling. Cryptic niche conservatism may in general explain the invasion success of species in areas with apparently unsuitable climate.

Keywords
Europe, invasion success, mtDNA, niche conservatism, niche evolution, *Podarcis muralis*, species distribution model.

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INTRODUCTION

Globalization has dramatically accelerated the introduction of alien species (Perrings *et al.*, 2005). The threat to biota posed by invasive species has been identified as one of the most severe problems in nature conservation (Strayer *et al.*, 2006). In addition to negative consequences for species richness and ecosystem function, invasive species can have severe economic impacts

(Pimentel *et al.*, 2000). There is a large body of literature focusing on the identification of common patterns that facilitate invasion processes. Generally, it is thought that climate matching of the novel area to the climate of the native range is a prerequisite for successful establishment (e.g. Bomford *et al.*, 2009). Other key factors considered as highly correlated with successful establishment are propagule pressure (e.g. Simberloff, 2009), pre-adaptation (e.g. Treier *et al.*, 2009) and escape from natural enemies in the introduced range (e.g. Colautti *et al.*, 2004).

Species distribution models (SDMs) are useful tools for identifying climatically suitable regions for possible establishment and hence for predicting the potential invasive range of species (e.g. Peterson & Vieglais, 2001; Jeschke & Strayer, 2008; Gallien *et al.*, 2010; Rödder & Lötters, 2010). When interpreting the potential distribution of invasive species in new regions derived from SDMs it is important to distinguish between a species' fundamental and realized niche. The realized niche is a fraction of the fundamental niche considering physical dispersal limitations and biotic interactions (Hutchinson, 1957; Soberón, 2007; Godsoe, 2010). Up to now, most studies have assumed that niches are constant across the geographical range of a species and some even suggest niche conservatism above species level (e.g. Losos, 2008; Revell *et al.*, 2008; Holf *et al.*, 2010). However, there is increasing evidence that niches may be variable among individuals, populations and consequently across the geographic ranges of species (e.g. Peterson & Holt, 2003). Niche evolution may be particularly likely among intra-specific evolutionary lineages (Holt, 2009).

Detailed knowledge on fundamental niche divergence among clades might thus be crucial for correctly predicting the invasive potential of different intra-specific lineages. Such a lineage-specific modelling approach might provide a more differentiated risk assessment. However, for this kind of modelling an integration of phylogenetic information, distribution data for each lineage and environmental data is inevitably needed. Up to now, these integrative approaches have been restricted to the species level and above (e.g. Warren *et al.*, 2008). Studies on the invasion potential of different evolutionary lineages within invasive species are still missing.

Among reptiles, lizards spread via the pet trade or cargo and nursery pathways are suggested to exhibit a high establishment success (e.g. Kraus, 2009; Rödder & Lötters, 2009). Nevertheless, only a few non-native reptile species have successfully colonized Europe (Kraus, 2009), most of which are found in the Mediterranean (e.g. Carranza & Arnold, 2006; Ficetola *et al.*, 2009). The wall lizard, *Podarcis muralis*, represents an exception, as it has colonized regions in north-western Europe far outside its sub-Mediterranean native range. Anthropogenic introductions of wall lizards into north-western Europe date back to the 1870s and were mainly seen as a form of environmental enhancement (Dürigen, 1897). Nowadays, about 140 non-native *P. muralis* populations are documented from north-western Europe and some additional populations are known from the New World (Schulte, 2008; Burke & Deichsel, 2009; Fig. 1a,b). The ecological impact of introduced wall lizards on native communities in north-western Europe has

been little studied. However, there are cases in which a competitive displacement of the native sand lizard (*Lacerta agilis*) and common lizard (*Zootoca vivipara*) has been reported (Schulte *et al.*, 2008). In addition, it has been assumed that, at the edge of their range, native wall lizards may be genetically swamped by introduced alien lineages (Schulte *et al.*, 2008). Therefore, invasive wall lizard populations may threaten the native local fauna. The origin of most alien populations is unknown (Schulte, 2008), but those with existing history stem from different regions in the Mediterranean. Hence, it is of particular interest whether differences of establishment and invasion probability do exist among *P. muralis* of different geographic origin, i.e. of different phylogenetic lineages. Since there is reason to assume that such lineages have evolved adaptations to local environmental conditions (e.g. Holt, 2009), we hypothesize that the potential distribution and the invasive occurrence of phylogenetically distinct wall lizard clades are linked to the climates at their native occurrences.

For the first time, we present here a combined mitochondrial DNA (mtDNA) barcoding and SDM approach in order to test the hypothesis that intra-specific niche variation may influence the invasive occurrence of a species. Furthermore, we test if such lineage-specific models show a better performance than combined models. The goals of the present study are: (1) to identify the origin of invasive wall lizard populations in Central Europe using mtDNA barcoding; (2) to test if different evolutionary lineages as identified by mtDNA sequences differ in their realized climate niches and in their potential for invasion; and (3) to test if the combination of SDMs developed for each lineage has a better predictive power than a combined SDM using the pooled records of all lineages.

METHODS

Study species

Podarcis muralis is a small heliothermic, synanthropic and saxicolous lacertid species, which is widely distributed throughout southern and western Europe. Within its native range the species shows a clear phylogeographic structure (Giovannotti *et al.*, 2010; S.S. *et al.*, unpublished data). The Western France Clade is confined to the Atlantic part of France and parts of the Pyrenees (see Fig. 1a). The northernmost genetic clade, the Eastern France Clade, is distributed across the south-eastern and eastern parts of France, western Switzerland and western Germany up to Maastricht in The Netherlands. Eastwards the Southern Alps Clade occurs in north-western Italy, the southern Alps and the Inn Valley. The Venetian Clade can be found in southern-most Slovenia, north-western Croatia, and the eastern part of the Po Plain. In Tuscany, Latium and parts of the Campania, a green-backed and morphologically clearly separated clade (the Tuscany Clade) is known (Giovannotti *et al.*, 2010). The Romagna Clade is situated within the north-eastern-most Apennine region, whereas the Marche Clade is distributed within central Italy and western Istria. The Central Balkan Clade
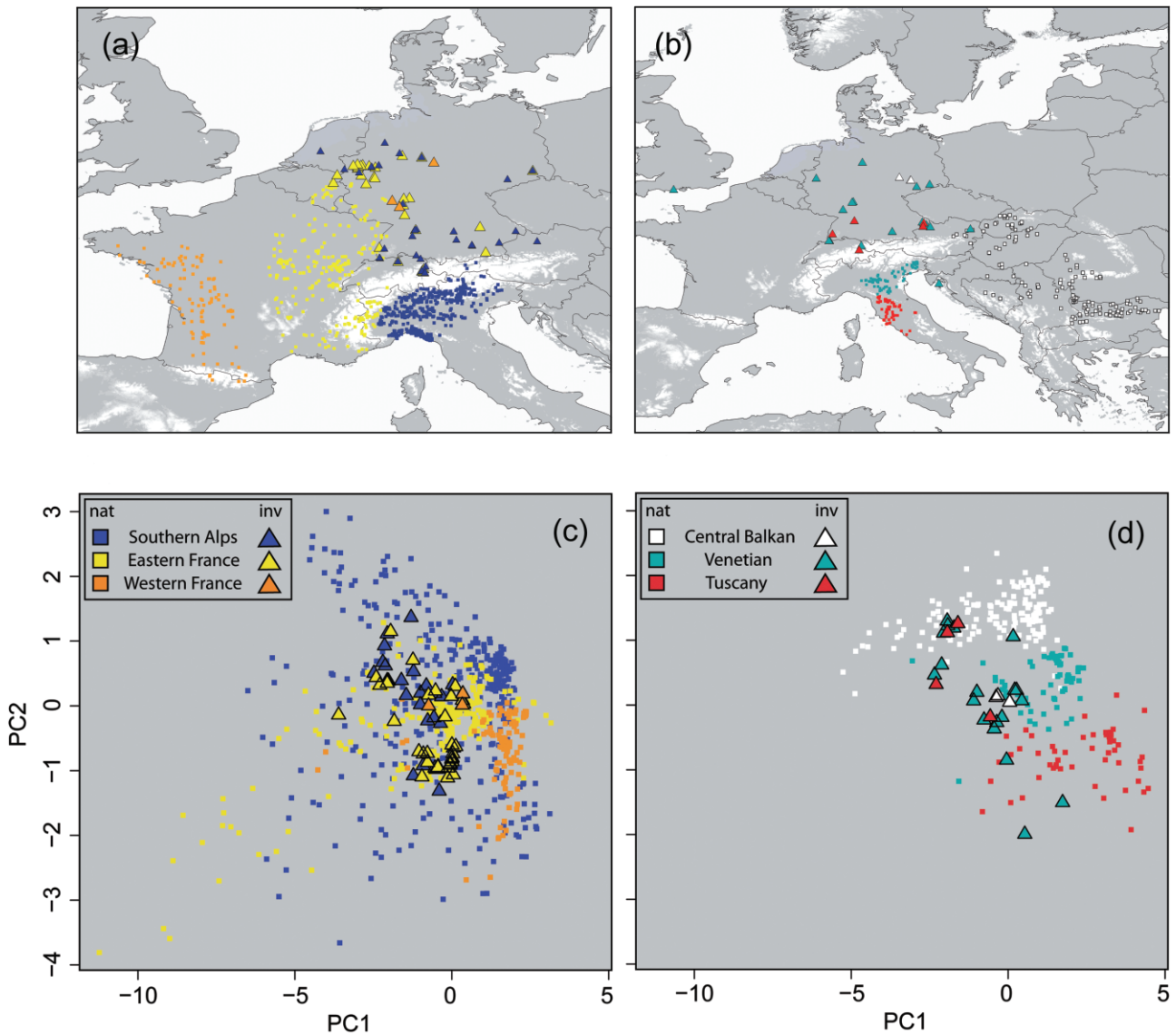
Figure 1 (a) Distribution of the Western France, Eastern France and Southern Alps clades of *Podarcis muralis* in the native (= nat; rectangles) and introduced (= inv; triangles) ranges in Europe. Constraints of a clade's native range were defined by genetically analysed records (see text). Orange symbols represent native and introduced populations of the Western France Clade (nat = 107, inv = 3), yellow symbols of the Eastern France Clade (266, 33) and blue symbols of the Southern Alps Clade (402, 32). (b) Distribution of the Venetian (light blue symbols, 82, 21), Tuscany (red symbols, 55, 5) and Central Balkan (white symbols, 149, 3) clades in their native and introduced ranges in Europe. (c) Principal components analysis (PCA) based on six environmental characteristics at native and invasive occurrences of the clades presented in (a) (same colours). (d) PCA of the clades presented in (b) (same colours). The first two PCs explain *c.* 81% of the variance (PC1 = 63.58%, PC2 = 18.27%). The correlation circle, eigenvalues and eigenvectors are provided in Appendix S6.

occurs on the Balkan Peninsula, in Hungary and Slovakia as well as in an isolated area of north-eastern Austria (S.S. *et al.*, unpublished data; Fig. 1b).

Invasive populations and sampling

To obtain information on the distribution of non-native populations, we posted e-mail messages on the major Central European herpetology mailing list (http://amphibienschutz.de, 1070 subscribers) during autumn and winter 2007/2008. We particu-

larly focused on Germany, where the majority of successful introductions have been reported. In addition, we compiled localities of *P. muralis* introductions from the literature and unpublished reports (Schulte *et al.*, 2008 and Appendix S2 in Supporting Information). We only considered non-native populations in which reproduction was confirmed and a minimum of 10 adults have been observed.

In total, 184 lizards (1 to 10 individuals per population) were captured by hand or by noosing within 77 alien populations of *P. muralis* in Germany (*n* = 61), Austria (6), Liechtenstein (1)

and Switzerland (9). Lizards autotomized the tip of their tail after pressure was exerted and were immediately released afterwards. The tail tip was stored in 99.8% ethanol p.a. We also included information from four additional populations from Germany as well as one from The Netherlands, Liechtenstein, Great Britain and Croatia for which reliable information on their origin was available (Appendix S7).

Genetic analysis

We extracted genomic DNA from muscle tissue using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. In a preliminary study, 24 populations had already been sequenced for an 887 base pair (bp) fragment of the mitochondrial cytochrome *b* gene (cyt *b*) (Schulte *et al.*, 2008). Additionally we sequenced 25 populations for this fragment. For the remaining 28 populations, we sequenced a 656-bp fragment using the primers LGlulk (5′-AACCGCCTGTTGTCTTCAACTA-3′) and HPod (3′-GGTGGAATGGGATTTTGTCTG-5′) (Deichsel & Schweiger, 2004; Podnar *et al.*, 2007). Sequencing was performed with the DYEnamic ET Terminator Cycle Sequencing Premixkit (GE Healthcare, Munich, Germany) for sequencing reactions run on a MegaBACE 1000 automated sequencer (GE Healthcare). DNA sequences were corrected and aligned by eye. We did not include ambiguous data from the beginnings and ends of the fragments in the analyses. Sequences were deposited in GenBank under the accession numbers HQ652874–HQ652973. For lineage identification, sequences of invasive populations were aligned to sequences from individuals sampled across the entire native range of *P. muralis* (FJ867389–FJ867394; Giovannotti *et al.*, 2010; S.S. *et al.*, unpublished data) and *Podarcis liolepis* (AF469436, AF469442, DQ081144; Harris & Sá-Sousa, 2002) and fitted into a phylogenetic tree using *Podarcis siculus* and *Podarcis melisellensis* as outgroups (HQ154646, AY185097; Podnar *et al.*, 2004; Appendix S8). We used Bayesian inference to infer the phylogeny as implemented in MrBayes 3.1.1 (Ronquist & Huelsenbeck, 2003), applying the parameters of the substitution model suggested by MrModeltest 2.2 (Nylander, 2004). We ran the Monte Carlo Markov chain for 1 million generations, sampling every 100 generations. We discarded 2500 trees as burn-in after checking for stationarity and convergence of the chains. Support of the nodes was assessed with the posterior probabilities of reconstructed clades as estimated in MrBayes (Ronquist & Huelsenbeck, 2003). This barcoding approach allowed us to unambiguously assign invasive haplotypes to intra-specific evolutionary *P. muralis* lineages and their respective distribution areas.

Species native occurrence data

To achieve a reliable delineation of the native range of each genetic clade through SDMs, we used 95 unique records (latitude/longitude) of haplotype groups obtained through an extensive sampling for a phylogeographic analysis (Giovannotti *et al.*, 2010; S.S. *et al.*, unpublished data). The genetic analysis revealed 22 genetic clades of *P. muralis* with unique haplotype groups and well-confined ranges, eight of which were found in our invasive samples. We excluded the Romagna and Marche clades due to limited availability of native and invasive species records and focused on the six remaining clades in our modelling approach. For an estimation of the native range of each clade, we constructed a minimum convex polygon (MCP) considering only samples that were used in the phylogeographic analysis ($n = 95$). We incorporated 884 additional records in our SDM that fell into one of these MCPs (Fig. 1a,b), 206 species records of which were compiled through literature screening and personal communications (see Appendix S1). The remaining 678 records were obtained from the German Federal Agency for Nature Conservation (Bundesamt für Naturschutz, BfN) database on Natura 2000 sites; these were only considered for modelling when their spatial accuracy was lower than 1 km^2. Overall, we compiled 266 records of the Eastern France Clade, 107 records for the Western France Clade, 402 records for the Southern Alps Clade, 82 records of the Venetian Clade, 55 records for the Tuscany Clade, and 149 records for the Central Balkan Clade. When necessary, the BioGeoMancer (http://bg.berkeley.edu/latest; accessed December 2009 to January 2010) and the Alexandria Digital Library Gazetteer Server Client (http://www.middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp; accessed December 2009 to January 2010) were used for geo-referencing.

SDM predictor selection

For climate data, we used monthly climate layers available through the WorldClim database version 1.4, which is based on weather conditions recorded from 1950–2000 with a spatial resolution of approximately 900 m × 900 m throughout Central Europe (Hijmans *et al.*, 2005). Available climate data include monthly mean minimum and maximum temperatures and monthly mean precipitation. Of these, we calculated so-called 'Bioclim' variables with DIVAGIS 5.4 (http://www.divagis.org; downloaded April 2009; Hijmans *et al.*, 2005). We selected variables that are suitable as predictors of the wall lizard's potential distribution based on the species' ecology and life-history traits, which should significantly improve the reliability of SDMs (Rödder *et al.*, 2010). The final variable set comprised: (1) mean temperature of the warmest quarter representing a good predictor for reproduction success as incubation temperature strongly influences hatching time as well as hatchling condition (Van Damme *et al.*, 1992); (2) mean temperature of the coldest quarter which is important for the lizard to display partial winter activity; (3) minimum temperature of the coldest month, a predictor for successful partial hibernation; (4) precipitation of the warmest quarter, a predictor for the species' occurrence in its Mediterranean distributional range due to its strong preference for humidity in certain areas (Capula *et al.*, 1993). In addition, we included: (5) annual aridity and (6) annual potential evapotranspiration (PET) derived from the WorldClim data by Trabucco & Zomer (2009). Neither of these variables is correlated with other variables and they are especially important for

microhabitat-specific distribution (avoidance of xeric habitats) of the species in its southern range (e.g. Capula *et al.*, 1993; Martín-Vallejo *et al.*, 1995).

Species distribution models

For SDM computation Maxent 3.3.0 (Phillips *et al.*, 2004, 2006; http://www.cs.princeton.edu/~schapire/Maxent; downloaded 15 April 2009) was used, which is a machine learning algorithm for SDM generation derived from environmental (e.g. Bioclim) predictors. It yields largely better results than other presence-only/presence–pseudoabsence SDM methods (Elith *et al.*, 2006; Heikkinen *et al.*, 2006). Maxent performs well even when the number of species point records available for modelling is small (e.g. Hernandez *et al.*, 2006; Wisz *et al.*, 2008). This approach processes randomly chosen background points as a contrast to the actual records of the species under study during model building. Definition of an area for appropriate background selection is crucial for successful modelling and should reflect the areas potentially accessible to the target species (Phillips, 2008). Background points used herein were randomly chosen within the native and invasive areas enclosed by a MCP for each clade (see above and Fig. 1a,b). Maxent allows for model testing by calculation of the area under the ROC (receiver operating characteristic) curve (AUC), based on training and test data, which represent the ability of the model to distinguish presence data from background data (Phillips *et al.*, 2006). Furthermore, we tested for the explanatory power of each predictor using a jackknife approach, i.e. in Maxent SDMs each predictor was sequentially omitted or, in a second approach, used as single variable and corresponding AUC values were assessed. We compared the predictive power of a combination of SDMs developed for each lineage with a SDM developed with all records of all clades pooled by computing overlaps in terms of Schoener's *D* (see below) and a simple linear regression. In the former approach, we combined the potential distributions of each linage by computing the maximum prediction per grid cell.

Depending on the settings and data types used for model computation, the resulting maps may characterize a species' realized or potential distribution (Elith & Leathwick, 2009). This may have severe implications for the interpretation of results. Inclusion of biotic or accessibility predictors may allow an approximation of a species' realized niche, wherein using only presence data and restricting the predictors to environmental variables as we did may rather represent the species' fundamental niche (Peterson, 2006; Soberón, 2007).

Spatial statistical analyses

In order to visualize the overall levels of divergence in climate niche space, we conducted a principal components analysis (PCA) in XLSTAT 2010 comprising all clades and based on climate conditions extracted at native and invasive occurrences (Fig. 1). To test for niche overlap, similarity and equivalence (for definitions see below), we compared potential distributions between all six native clades and crosswise between native and

invasive ranges of three clades with strong invasive occurrence (Southern Alps, Eastern France and Venetian clades). Within our modelling approach, invasive occurrences of each lineage occurring in populations with more than one origin were treated separately. In the past, niche conservatism was tested using different hypotheses. For example, Graham *et al.* (2004) tested for niche equivalency by asking whether niches of two species are effectively indistinguishable, whereas Peterson *et al.* (1999) tested for niche similarity by assessing whether the niche of one species holds more information about the niche of its sister taxa than expected at random. To test for these hypotheses, we used spatial statistics as proposed by Warren *et al.* (2008) and modified by Rödder & Lötters (2009). As the niche overlap index, we used Schoener's *D* (Schoener, 1968), which quantifies common parts of two probability distributions as suggested by SDMs trained with native records (*X*) and invasive records (*Y*). *D*-values range from 0 (no overlap) to 1 (identical SDMs). The significance of results was evaluated with null models testing for niche similarity and equivalence (see below).

For niche equivalency, we applied a randomization test as proposed by Warren *et al.* (2008) that relies on the metric *D*. To compare climate niches of two clades or native and invasive records belonging to one clade (i.e. Eastern France Clade native = 266 versus Eastern France Clade invasive = 33; Southern Alps Clade native = 402 versus Southern Alps Clade invasive = 32; Venetian Clade native = 82 versus Venetian Clade invasive = 21), we created 100 pseudoreplicates by randomly partitioning the pooled sets of occurrence records of both test groups into sets of the same size. Subsequently, SDMs were created from each pseudoreplicate and compared using *D*. The observed values were compared with the percentiles of these null distributions in a one-tailed test assessing the significance of niche identity. The test assesses niche conservatism in a strict sense, i.e. the effective equivalency of the climatic niche in the native and invasive range of a certain clade. It is expected to only be met if native and invasive populations of one clade exactly tolerate the same climatic conditions and have the same set of environmental conditions available to them (Warren *et al.*, 2008).

In order to assess niche similarity, we again used the randomization test of Warren *et al.* (2008). This test compares the similarity of SDMs based on native records in terms of *D*-values to the distribution of similarities obtained by comparing them to a SDM obtained by randomly choosing n_{inv} cells from among the cells in the study area of the invasive records. The same procedure was performed in both directions (invasive ↔ native records) 100 times each for two groups to construct an expected distribution of *D*-values between a SDM generated using actual occurrences and one generated from random background data points. Appropriate selection of background points is important, since they can influence the significance of the test. Therefore, we restricted background points to the area defined within a MCP comprising all native (likewise invasive) records of each genetic clade (see Fig. 1a,b). These null distributions served as a two-tailed test to assess the following null hypothesis: measured niche overlap between native and invasive ranges is explained by regional similarities or differences in available habitat. This

hypothesis is rejected if the actual similarity falls outside the 95% confidence limits of the null distribution. Significantly higher values suggest that SDMs are more similar than expected by chance and lower values indicate greater differences. The distance between the observed overlap value and the closest overlap value in the null distribution can be used as a quantitative measure of distinctness (Rödder & Lötters, 2009). Computations of D, niche similarity and equivalency were performed with a Perl script (software ENMTOOLS; http://www.enmtools.com/; downloaded June 2009) developed by Warren *et al.* (2008).

RESULTS

Geographic origin of invasive *P. muralis* populations

Based upon cyt *b* haplotypes, we found eight geographically distinct mtDNA clades (following S.S. *et al.*, unpublished data) in 77 invasive populations in Central Europe (Fig. 1a,b; Appendix S7). Posterior probabilities of the clades were high (100) and only some inter-nodes had a lower support (Appendix S8). Combined with reliable information on the origin of eight further populations the two most common haplotypes belonged to the Eastern France Clade (38.8%; 33/85 populations) and the Southern Alps Clade (37.6%; 32/85 populations). Invasive populations of the Eastern France Clade were mainly detected in western Germany, particularly in the Ruhr Basin (Fig. 1a). Three of these alien populations belong to the Languedoc Subclade within the Eastern France Clade (3.5%; 3/85 populations). Populations belonging to the Southern Alps Clade were widespread outside their native range up to northern and eastern parts of Germany. The next most frequent clade was the Venetian Clade (24.7%; 21/85 populations). The Tuscany Clade was found less frequently (mainly in southern Germany, 5.9%; 5/85 populations). The Western France Clade (3.5%; 3/85 populations) was found in Rhineland-Palatine and southern Lower Saxony, while the Central Balkan Clade (3.5%; 3/85 populations) occurred in eastern Germany (Fig. 1a,b). We found the Marche and Romagna Clades (from Italy) at few localities. In 19 introduced populations we found haplotypes from more than one source area. Most frequently we determined combinations of the Southern Alps Clade and the Venetian Clade (see Appendix S7). In one population belonging to the Western France Clade we even discovered a haplotype belonging to a different species, *Podarcis liolepis* of the *Podarcis hispanicus* species complex (Renoult *et al.*, 2010).

Niche overlap among native clades

On the first two axes of the PCA, all native clades showed a separation in their multidimensional niche space (Fig. 1c,d, correlation circle; for eigenvalues and eigenvectors see Appendix S6). Pairwise niche overlap derived from SDMs based on the combination of the six variables ranged from 0.08–0.52 using Schoener's D (Table 1). The highest niche overlap among native clades was found between the Eastern France and Southern Alps

clades ($D = 0.52$), whereas niche overlap of the Central Balkan and Tuscany clades was much lower ($D = 0.08$). The hypothesis of niche equivalency was rejected in all cases (Table 1). D-values of background tests of overlap between clade$_X$ versus clade$_{Y \, background}$ were significantly more similar than expected by chance in one case (Cbalk vs. Tusc$_{background}$) and significantly more different than expected by chance in two cases (Tusc vs. Ven$_{background}$, Tusc vs. Wfra$_{background}$). D-values of background tests in the contrary direction (clade$_{X \, background}$ vs. clade$_Y$) were significantly more similar than expected by chance in six cases (see Table 1).

Niche overlap among clades in their native and invasive range

Overall, the environmental niches in native and invasive ranges were most similar for the Eastern France Clade ($D = 0.52$, Table 2). Both niches were centred at the intersection of both axes, but the native niche was more influenced by the variable 'aridity' (Fig. 1c). Niches of the Southern Alps Clade were slightly less similar ($D = 0.4$). The potential distribution of the native Southern Alps Clade covered a large geographic range, which included all invasive occurrences (Fig. 1c). The relatively variable contribution of the SDM indicated an influence of nearly all variables, but slightly less contribution of 'annual PET' and 'mean temperature of the warmest quarter'. In contrast, the niches between native and invasive ranges of the Venetian Clade ($D = 0.27$) exhibited limited niche overlap. This clade shifted in its invasive climate characteristics along axes 1 and 2 (Fig. 1d), indicating that 'precipitation of the warmest quarter' and 'minimum temperature of the coldest month' were the underlying gradients in niche differentiation. Results of the niche similarity test based on native records compared with the invasive background of this clade revealed that D-values were significantly more similar than expected by chance (Table 2). Overall, the total overlap between native and invasive occurrences of all clades was higher (mean $D = 0.4$) than the total overlap between all native clade combinations (mean $D = 0.24$).

Comparisons of single variables among native clades

For single variables among native clades, D-values ranged from 0.10–0.94 (Table 1). Native clades were separated mainly by temperature gradients (e.g. minimum temperature of the coldest month and mean temperature of the coldest quarter), but less so by precipitation gradients. Thus, the highest niche overlap ($D \geq 0.70$) was detected in 'aridity' (average $D = 0.74$) and 'annual PET' (average $D = 0.71$). The lowest overlap ($D \leq 0.50$) was detected in the 'minimum temperature of the coldest month' (average $D = 0.44$) and 'mean temperature of the coldest quarter' (average $D = 0.45$). The values of other variables were intermediate (Table 1). The results of an identity test among native clades revealed that most climatic conditions were significantly different. Only few clade combinations revealed similar D-values (e.g. in Table 1: Ven vs. Wfra or Ven vs. Efra for variable 'aridity').

Table 1 Total overlap and overlap of single niche dimensions between native clades of *Podarcis muralis.*

	D Total overlap	D Aridity	D Annual pet	D bio6	D bio10	D bio11	D bio18
Cbalk vs. Salps	$0.36^{*,ns,X}$	$0.50^{*,ns,ns}$	$0.82^{*,X,X}$	$0.58^{*,X,X}$	$0.82^{*,X,ns}$	$0.58^{*,X,X}$	$0.85^{*,ns,ns}$
Cbalk vs. Tusc	$0.08^{*,X,X}$	$0.79^{*,ns,ns}$	$0.80^{*,ns,X}$	$0.10^{*,X,X}$	$0.74^{*,X,ns}$	$0.24^{*,X,X}$	$0.34^{*,ns,ns}$
Cbalk vs. Ven	$0.19^{*,ns,ns}$	$0.65^{*,ns,ns}$	$0.65^{*,ns,x}$	$0.20^{*,ns,ns}$	$0.41^{*,ns,ns}$	$0.23^{*,ns,X}$	$0.90^{ns,ns,X}$
Cbalk vs. Wfra	$0.10^{*,ns,ns}$	$0.59^{*,ns,ns}$	$0.94^{ns,X,X}$	$0.15^{*,ns,X}$	$0.57^{*,x,x}$	$0.16^{*,ns,X}$	$0.71^{*,ns,ns}$
Cbalk vs. Efra	$0.34^{*,ns,X}$	$0.64^{*,ns,ns}$	$0.70^{*,ns,ns}$	$0.51^{*,ns,X}$	$0.73^{*,ns,X}$	$0.55^{*,x,X}$	$0.86^{ns,x,ns}$
Salps vs. Tusc	$0.25^{*,ns,X}$	$0.64^{*,ns,ns}$	$0.81^{*,X,X}$	$0.42^{*,X,X}$	$0.82^{ns,X,X}$	$0.56^{*,X,X}$	$0.37^{*,ns,ns}$
Salps vs. Ven	$0.33^{*,ns,ns}$	$0.79^{*,ns,ns}$	$0.53^{*,ns,x}$	$0.55^{*,ns,X}$	$0.51^{*,ns,ns}$	$0.58^{*,ns,X}$	$0.89^{ns,X,ns}$
Salps vs. Wfra	$0.20^{*,ns,X}$	$0.78^{*,ns,X}$	$0.80^{*,ns,X}$	$0.37^{*,ns,X}$	$0.51^{*,ns,X}$	$0.34^{*,ns,X}$	$0.67^{*,ns,ns}$
Salps vs. Efra	$0.52^{*,ns,ns}$	$0.84^{*,ns,ns}$	$0.78^{*,ns,ns}$	$0.81^{*,ns,X}$	$0.66^{*,ns,ns}$	$0.83^{*,ns,X}$	$0.83^{*,ns,X}$
Tusc vs. Ven	$0.20^{*,x,ns}$	$0.80^{*,ns,ns}$	$0.57^{*,ns,x}$	$0.48^{*,ns,X}$	$0.66^{*,ns,x}$	$0.56^{*,X,X}$	$0.39^{*,ns,ns}$
Tusc vs. Wfra	$0.28^{*,ns,ns}$	$0.74^{*,ns,ns}$	$0.80^{*,ns,ns}$	$0.76^{*,ns,ns}$	$0.46^{*,x,x}$	$0.52^{*,ns,x}$	$0.53^{*,ns,ns}$
Tusc vs. Efra	$0.21^{*,ns,X}$	$0.79^{*,ns,X}$	$0.68^{*,ns,X}$	$0.33^{*,ns,X}$	$0.50^{*,ns,X}$	$0.45^{*,ns,X}$	$0.28^{*,ns,ns}$
Ven vs. Wfra	$0.08^{*,ns,ns}$	$0.84^{ns,ns,ns}$	$0.64^{*,ns,ns}$	$0.41^{*,ns,ns}$	$0.16^{*,x,ns}$	$0.35^{*,ns,ns}$	$0.74^{*,ns,ns}$
Ven vs. Efra	$0.24^{*,ns,ns}$	$0.87^{ns,ns,X}$	$0.37^{*,ns,ns}$	$0.65^{ns,ns,ns}$	$0.21^{*,ns,ns}$	$0.56^{*,ns,ns}$	$0.81^{*,ns,ns}$
Wfra vs. Efra	$0.26^{*,ns,ns}$	$0.78^{*,ns,ns}$	$0.69^{*,ns,ns}$	$0.27^{*,ns,ns}$	$0.63^{*,X,x}$	$0.26^{*,ns,ns}$	$0.58^{*,ns,ns}$

Schoener's D was used as the niche overlap index. D-values range from 0 (no overlap) to 1 (identical species distribution models). The significance of the results is expressed by symbols. Multiple significance levels indicate niche identity tests as well as niche similarity tests in both directions. Note that niche similarity tests compare actually measured niche overlaps with null distributions based on randomizations of background data within the range of one species (i.e. clade herein). Therefore, these tests are by definition directional. Niche identity tests use a randomization between actual occurrence records and are therefore not directional.

Abbreviations: Salps, Southern Alps; Efra, Eastern France; Ven, Venetian; Cbalk, Central Balkan; Tusc, Tuscany; Wfra, Western France; bio6, minimum temperature of the coldest month, bio10, mean temperature of the warmest quarter; bio11, mean temperature of the coldest quarter; bio18, precipitation of the warmest quarter.

ns, not significant; $^*P < 0.05$; X = above the confidence interval (significantly more often detected than expected by chance); x = below confidence interval (significantly less often detected than expected by chance).

Table 2 Total overlap and overlap of single niche dimensions between native (= nat) and invasive (= inv) occurrences of clades.

	D Total overlap	D Aridity	D Annual pet	D bio6	D bio10	D bio11	D bio18
Salps$_{nat}$ vs. Salps$_{inv}$	$0.40^{*,ns,ns}$	$0.8^{*,ns,ns}$	$0.65^{*,ns,ns}$	$0.79^{*,ns,X}$	$0.55^{*,ns,ns}$	$0.57^{*,ns,X}$	$0.71^{*,x,x}$
Efra$_{nat}$ vs. Efra$_{inv}$	$0.52^{*,ns,ns}$	$0.84^{*,ns,x}$	$0.76^{*,ns,ns}$	$0.76^{ns,X,x}$	$0.87^{ns,X,ns}$	$0.74^{ns,X,ns}$	$0.86^{*,ns,ns}$
Ven$_{nat}$ vs. Ven$_{inv}$	$0.27^{*,X,ns}$	$0.83^{*,ns,ns}$	$0.40^{*,X,ns}$	$0.50^{*,ns,ns}$	$0.30^{*,X,ns}$	$0.47^{*,ns,ns}$	$0.76^{*,ns,ns}$

Abbreviations: Salps, Southern Alps; Efra, Eastern France; Ven, Venetian; bio6, minimum temperature of the coldest month; bio10, mean temperature of the warmest quarter; bio11, mean temperature of the coldest quarter; bio18, precipitation of the warmest quarter.

ns, not significant, $^*P < 0.05$; X = above the confidence interval (significantly more often detected than expected by chance); x = below confidence interval (significantly less often detected than expected by chance).

The results of niche similarity tests based on native records compared with native background between clades showed different values for the variable 'mean temperature of the coldest quarter' followed by 'mean temperature of the warmest quarter' and 'annual PET'. Niche similarity tests revealed that the Southern Alps Clade occurred at localities with higher values of the variables 'minimum temperature of the coldest month' and 'mean temperature of the coldest quarter' (Appendix S4).

Comparisons of single variables among clades in their native and invasive ranges

Between native and invasive clades, D-values ranged from 0.30 to 0.87 (see Table 2). The highest niche overlap ($D \geq 0.80$) was detected in 'aridity' (average $D = 0.82$) and 'precipitation of the warmest quarter' (average $D = 0.78$). Very different realized niches within native and invasive ranges of clades were detected in the 'mean temperature of the warmest quarter' (average $D = 0.57$) and 'mean temperature of the coldest quarter' (average $D = 0.59$). Results of the identity tests based on native records compared with invasive records of the Southern Alps, Eastern France and Venetian clades revealed that climatic conditions were significantly different. Only for the Eastern France Clade were D-values of three variables 'minimum temperature of the coldest month', 'mean temperature of the warmest quarter' and 'mean temperature of the coldest quarter' similar between native and invasive records (Table 2).

Results of the niche similarity tests based on conditions for the native records compared with the invasive background demonstrated that the Southern Alps Clade was not found at sites with low precipitation. In contrast to this, the clade was detected significantly less often in habitats with high precipitation in its native range (Table 2 and Appendix S4). The Eastern France Clade selected higher minimum temperatures of the coldest month, higher mean temperature of the warmest quarter and higher mean temperature of the coldest quarter within its invasive range than expected by chance. In its invasive range the Venetian Clade selected habitats with higher annual PET values and higher mean temperatures of the warmest quarter than expected by chance (Table 2 and Appendix S4).

Instead of computing niche comparisons between native and invasive ranges for the Tuscany, Western France and Central Balkan clades, we visualized them using boxplots, due to the restricted availability of occurrence data (Appendix S5). Most strikingly, the realized native and invasive niches of the Tuscany Clade mainly differed in temperature variables, whereas native and invasive niches of the Central Balkan Clade were rather similar in temperature regime.

Potential distribution and invasion potential of different wall lizard lineages

The AUC values for the SDMs ranged from 0.958–0.990, indicating in all cases 'excellent' model performance according to the classification system of Swets (1988) (see Table 3). Overall, the potential distributions showed a strong clade-level variation. The SDM developed with native records belonging to the Eastern France Clade performed best in describing the invasive range of its analogous clade. Its potential distribution is comparatively large, ranging from the Iberian Cordillera Cantabria, the Pyrenees, central and eastern France northward up to Lower Saxony, Germany (Appendix S3). The potential geographic range includes various invasive populations in Belgium, The Netherlands and western Germany (i.e. in North Rhine Westphalia). The 'minimum temperature of the coldest month' had the highest gain for this clade, followed by 'mean temperature of the coldest quarter' (Table 3). Highly suitable areas for the Southern Alps Clade are restricted to southern Switzerland, northern Italy and eastern central Italy as well as parts of Slovenia, Croatia and adjacent Albania. Nevertheless the SDM for this clade predicted numerous invasive populations in southern Germany, Liechtenstein and Austria (Appendix S3). The most important variables for the distribution of this clade were 'mean temperature of the warmest quarter' and 'aridity'. The Central Balkan Clade has a broad potential distribution, covering large parts of the Balkans and Eastern Europe, from Bulgaria to the Czech Republic. Parts of eastern Germany were also classified as suitable and are inhabited by three invasive populations of this clade. Its geographic range model was mainly determined by 'annual PET' and 'precipitation of the warmest quarter' (Table 3).

In contrast to these well matching SDMs, the models failed to predict the current invaded distribution for the Venetian, Tuscany and Western France clades (Appendix S3). Climatically

Table 3 Importance of different variables in species distribution models (SDMs) per clade (Appendix S3) and in SDMs based on pooled data for all six clades (Fig. 2a) tested using a jackknife approach, i.e. in MAXENT SDMs each predictor was sequentially omitted or, in a second approach, used as single variable and corresponding area under the receiver operating characteristic curve (AUC) values were assessed.

Variables/clades	Lineages combined	AUC without variable	AUC with only variable	Efra	AUC without variable	AUC with only variable	Salps	AUC without variable	AUC with only variable	Ven	AUC without variable	AUC with only variable	Tusc	AUC without variable	AUC with only variable	Wfra	AUC without variable	AUC with only variable	Cbalk	AUC without variable	AUC with only one variable
Annual aridity	15.7	0.899	0.657	15.6	0.952	0.729	33.9	0.967	0.742	4.7	0.987	0.787	5.5	0.972	0.639	1	0.974	0.761	9	0.949	0.786
Annual PET	19.6	0.902	0.769	14.5	0.951	0.801	1.9	0.97	0.786	10.3	0.988	0.931	1.3	0.974	0.782	14.4	0.961	0.825	35.5	0.948	0.831
bio 6	9.6	0.903	0.73	30.1	0.956	0.845	10.7	0.972	0.779	3	0.989	0.915	47	0.96	0.856	31.4	0.97	0.898	20.5	0.955	0.837
bio 10	12.7	0.894	0.690	10.2	0.956	0.749	37.7	0.956	0.783	38.3	0.982	0.921	18	0.96	0.822	7.5	0.958	0.85	4.3	0.951	0.732
bio11	16.3	0.901	0.744	16.2	0.956	0.834	4.2	0.971	0.784	21.7	0.989	0.927	1.3	0.966	0.842	25.7	0.97	0.92	9.5	0.954	0.841
bio 18	26.1	0.893	0.74	13.4	0.951	0.729	11.6	0.969	0.776	22	0.99	0.835	26.9	0.96	0.905	20	0.97	0.832	21.2	0.95	0.795
AUC values	0.917			0.971			0.981			0.991			0.980			0.978			0.971		

The two most important variables in each case are highlighted in grey.
Abbreviations: PET, potential evapotranspiration; Salps, Southern Alps; Efra, Eastern France; Ven, Venetian; Cbalk, Chalk, Central Balkan; Tusc, Tuscany; Wfra, Western France; bio6, minimum temperature of the coldest month; bio10, mean temperature of the warmest quarter; bio11, mean temperature of the coldest quarter; bio18, precipitation of the warmest quarter.
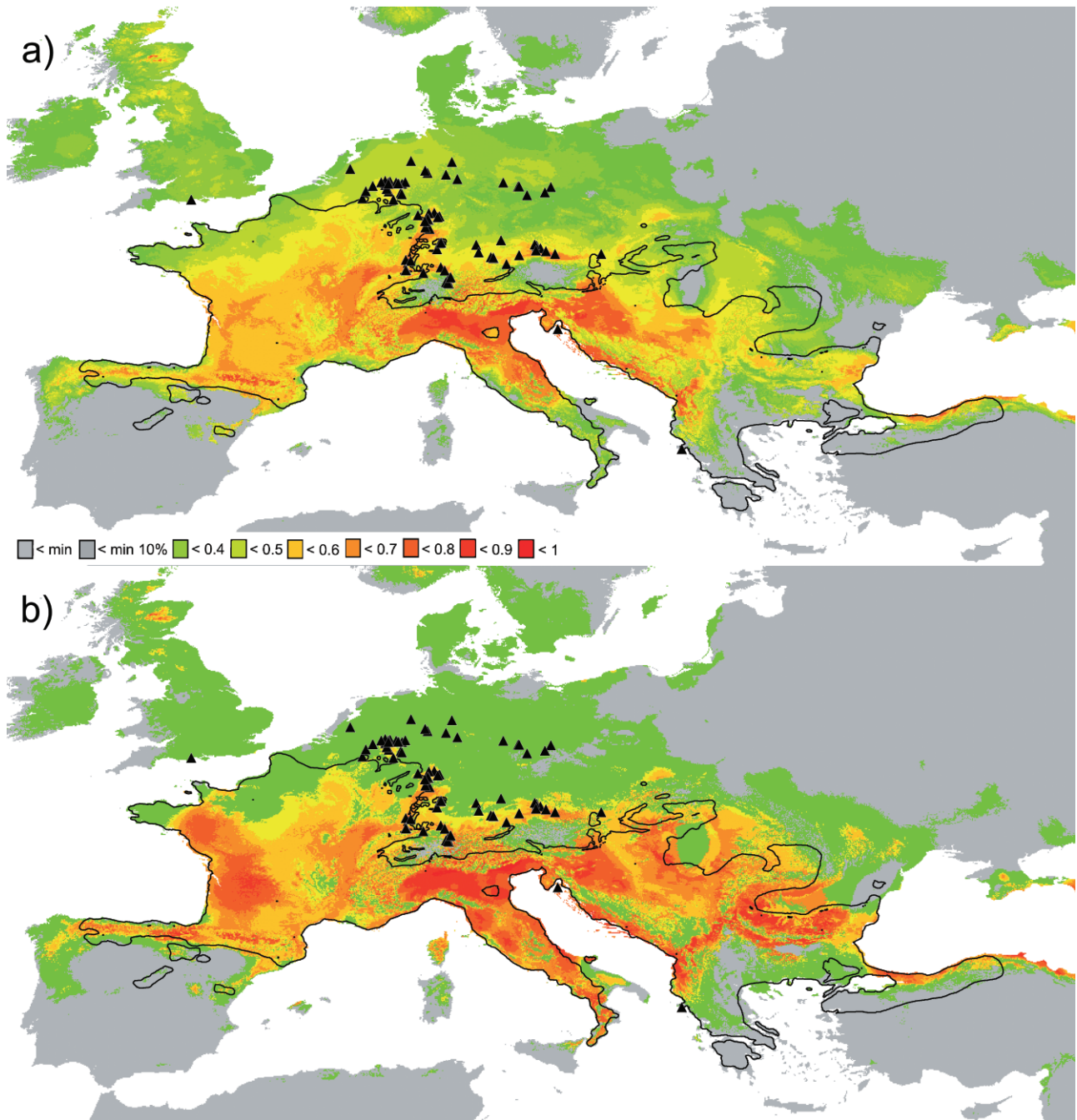
Figure 2 Potential distribution of *Podarcis muralis* predicted by climatic conditions of native occurrences of (a) all six clades pooled and (b) as a combination of the potential distributions of each linage by computing the maximum prediction per grid cell. For native records of the six clades see Figure 1(a, b). Invasive populations are indicated as black triangles. Warmer colours correspond to higher occurrence probabilities. The whole distribution range is framed by a solid black line.

suitable areas for the Venetian Clade were restricted to northern Italy, the eastern Po Valley up to the border of Slovenia. The most important variables describing the distribution of this clade were 'mean temperature of the warmest quarter' and 'precipitation of the warmest quarter'. Areas with the highest climatic suitability for the Tuscany Clade encompass Italy, beside the Abruzzi and large parts of the Mediterranean and Black Sea coasts. Climatically suitable areas for the Western France Clade

are restricted to the Basque Country, western Pyrenees and western France up to the Massif Central (Appendix S3). Important variables explaining the distribution of these clades are given in Table 3.

The sum of single SDMs for all six clades (Fig. 2b) compared with the SDM for the species using all records pooled (Fig. 2a) revealed largely overlapping potential distributions ($D = 0.83$; simple linear regression $R^2 = 0.760$, $P < 0.0001$), wherein the

model built by pooling data from all lineages performed better than the one combining the models from each lineage. Both models mainly predicted the invasive populations in western and southern parts of Central Europe, whereas they failed to predict those populations in the northern and north-eastern parts (Fig. 2a,b).

DISCUSSION

The origin of invasive wall lizard populations

We assigned 77% of all currently known invasive wall lizard populations in Central Europe, apart from the UK, to eight source lineages based upon their mitochondrial haplotypes and an extensive phylogeography covering the entire range of the species (Giovannotti *et al.*, 2010; S.S. *et al.*, unpublished data). Introduced populations of the same lineage sometimes occurred in close proximity, indicating human-facilitated jump dispersal. On the other hand, we also found 19 introduced populations with haplotypes belonging to different lineages, indicating multiple introductions of wall lizards from different source populations (Appendix S7). In such mixed populations hybridization may promote invasion success due to heterosis (Kolbe *et al.*, 2004). Interestingly, we even discovered the haplotype of the alien *Podarcis liolepis* at one location in southern Lower Saxony (Appendix S7) together with haplotypes of the Western France *P. muralis* Clade. Both species naturally co-occur across parts of the eastern Pyrenees. It is therefore likely that haplotypes of both species were translocated from this region simultaneously.

Niche differentiation among native clades

We found strong intra-specific variation in the realized niches among native clades, mainly based on temperature gradients. Realized niche differentiation was associated with geographic distance among clades. The two most similar clades (Eastern France and Southern Alps) occur in adjacent regions and together form the species' northern range border in western Central Europe. Within its native range, the Southern Alps Clade occurs at sites with higher minimum temperatures of the coldest month and higher mean temperatures of the coldest quarter compared with the native background. This may be due to the strong altitudinal gradient within its native range and its need for successful hibernation and partial winter activity (Schulte, 2008). In contrast, the geographically widely separated Central Balkan and Tuscany clades differed strongly in their realized climatic niches. Niche overlap and background tests of single variables indicated that both clades occur in areas that clearly differ in their minimum temperature of the coldest month and the mean temperature of the coldest quarter. The range of the Central Balkan Clade is also largely influenced by the annual PET. It is known that this lineage occurs in wetlands and humid oak forests of the Bulgarian Dobruja and avoids xeric habitats (Schulte, 2008). The distribution of the Tuscany Clade is mainly influenced by lower mean temperatures of the warmest quarter. This may be explained by the mediterranean climate, where the

lizards need to sustain hot and dry periods in the summer by inhabiting shady and humid habitats with dense vegetation (Capula *et al.*, 1993).

Niche overlap between native and invasive populations

Differentiation in realized niches between native and invasive populations within clades was on average lower than among native populations of different clades. In particular, the realized climatic niches of the native and invasive ranges of each the Southern Alps and the Eastern France clades were rather similar. Nevertheless, niche similarity tests based on single variables also revealed some differences. For example, records of the Southern Alps Clade were not related to high precipitation in the native range but in the invasive range. This may reflect a shift in habitat affiliation rather than differences in the availability of habitats in the novel range. Niche similarity tests for the Eastern France Clade within its invasive range revealed that minimum temperature of the coldest month, mean temperature of the warmest quarter and mean temperature of the coldest quarter were explaining most of the variability. This corresponds to both the need for high temperatures during early summer for reproduction and the need for successful hibernation and partial winter activity (Barbault & Mou, 1988). Similarly, invasive populations of the Venetian Clade were mainly recorded from sites with higher mean temperatures of the warmest quarter than expected by chance. Mean temperatures of the early summer are of major importance for the reproductive success of this oviparous lizard at its northern range border as they strongly affect incubation time (in the wild 6–11 weeks) and hatchling phenotype (Braña & Ji, 2000). In the northernmost native population of this clade (Maastricht), cold and rainy summers can cause almost complete hatching breakdowns (Stumpel, 2004). The Venetian Clade had the lowest niche overlap between its native and invasive range. In its invasive range, this clade occurs in areas with higher annual PET and higher mean temperatures of the warmest quarter. High values of both variables are typically found within its native range and are known to contribute to reproductive success and microhabitat selection (Mazzotti, 1999). Overall, the invasive distribution of the Venetian Clade and the low niche overlap between native and invasive ranges suggest that the fundamental niche of this clade might be larger than the niche realized in its actual native range.

Furthermore, it has to be considered that systematic human-mediated introductions of lizards into highly suitable habitats took place. Hence, the lizards were brought into areas that represent local extremes within the regional climate (e.g. water-filled quarries). Moreover, the introduction of lizards is influenced by the usual human travel routes. It is apparent that the Central Balkan Clade was only found in eastern Germany. Citizens of the former German Democratic Republic were not able to travel abroad, except to some other countries of the Eastern Bloc. Hungary was one of the most popular travel destinations and, indeed, the haplotypes found in invasive populations of the Central Balkan Clade were very similar to those

found in Hungarian native populations. On the other hand, it is striking that clades from the southernmost part of the range of *P. muralis* were not recorded in Central Europe, although at least Greece is a popular travel destination.

The cryptic niche conservatism hypothesis

The SDMs revealed clear inter-clade differences in the realized niches, but for some evolutionary lineages the models failed to predict the invasive range. The best predictive power was found for those clades that most frequently colonized Central Europe (Eastern France and Southern Alps clades). However, the native ranges of these two clades are also spatially closest to Central Europe, which might increase the climatic overlap with the invasive range. Hence, it is likely that these clades might have been pre-adapted to the environmental conditions in Central Europe. Both clades possess a broad thermal tolerance (Appendix S4), leading to a large potential invasive distribution (Appendix S3). Although the Southern Alps Clade is naturally restricted to a rather small native range, mainly south of the Alps, it occurs in a complex climate due to the great altitudinal gradient in this area. Populations of this clade have been reported up to 1770 m above sea level (Hofer *et al.*, 2001) and experiments in cooling chambers have demonstrated a moderate freeze tolerance (Claussen *et al.*, 1990).

SDMs for the Venetian, Tuscany and Western France clades failed to predict the invasive ranges. Despite a narrow realized niche of its native range, the Venetian Clade colonized areas in Central Europe (Appendix S3). Two hypotheses may explain this phenomenon: (1) a shift in the fundamental niche during the invasion process (niche shift hypothesis), or (2) the available climate space within its native range only reflects a part of the fundamental niche (cryptic niche conservatism hypothesis). The fact that the distribution of the Venetian Clade is strongly restricted by neighbouring conspecific clades and other *Podarcis* species supports the second hypothesis. The same is true for the Western France Clade and the Tuscany Clade.

Our results suggest that climate adaptations of the studied lineages are not strong enough to prevent them from becoming invasive, even if this would not be expected based upon their realized niche. However, the invaded areas were covered in SDMs for other lineages and for the complete data set. This suggests that modelling only one lineage might lead to wrong conclusions. It might well be true that reported niche shifts during species invasions (Broenniman *et al.* 2007; Treier *et al.*, 2009) simply reflect cryptic niche conservatism on a higher systematic level (i.e. genus level).

CONCLUSIONS

Niche conservatism has been reported in many species and even genera (Peterson *et al.*, 1999; Peterson & Holt, 2003; Pearman *et al.*, 2008). Our models revealed a strong niche differentiation among clades and mismatches between the realized niches in the native and invasive ranges, as recently reported also for other invasive species (Broenniman *et al.*, 2007; Rödder & Lötters,

2009; Treier *et al.*, 2009). Based upon SDMs it is impossible to disentangle whether such patterns represent shifts in the realized niche only or in both the realized and the fundamental niche (Broenniman *et al.*, 2007; Rödder *et al.*, 2010). SDMs simply match species distributions with climate variables and do not integrate scenopoetic or bionomic variables (e.g. competition, predation, dispersal; variables of the Eltonian niche; Soberón, 2007). Such models might thus fail to predict the invasive range, particularly if the native range size is rather small and a great part of the fundamental niche is hidden. This means that a small (realized) niche may hide a broad (fundamental) niche (cryptic niche conservatism).

Our results have important implications for the interpretation of geographic predictions for invasive species based upon SDMs. Although evolutionary lineages within a species may have distinct realized niches, these do not necessarily imply a niche differentiation. They might thus become invasive outside their native realized niches. On the other hand, using the pooled records of invasive clades performs better in predicting the invasion risk (Fig. 2a). Hence, building models for evolutionary lineages will not necessarily improve SDM predictions. Further studies should address the general validity of these patterns on different evolutionary time-scales (divergence times) and distribution patterns of species (Peterson & Holt, 2003). Understanding intra-specific niche evolution might be crucial for a more reliable risk assessment of invasive species as well as the impacts of climate change on taxa.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional references from which species records were obtained.

Appendix S2 References from which invasive records were obtained.

Appendix S3 Potential distribution of clades predicted by climatic conditions within their native range and predicted by climatic conditions within their invasive range.

Appendix S4 Comparison of Bioclim variable scores at native and invasive occurrences and within native and invasive background of clades.

Appendix S5 Comparison of Bioclim variable scores at native and invasive occurrences of the Tuscany, Western France and Central Balkan clades.

Appendix S6 Correlation circle, eigenvalues and eigenvectors of the principal components analysis (PCA).

Appendix S7 Invasive populations sampled with information on locality, coordinates, sample size, clade affiliation and references.

Appendix S8 Phylogenetic tree for the assignment of invasive haplotypes to intra-specific evolutionary *Podarcis muralis* lineages.

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BIOSKETCHES

This study is part of the PhD thesis of **Ulrich Schulte**, who is interested in biological invasions and conservation biology. He combines molecular genetic techniques with niche modelling to develop a differentiated risk assessment for invasive species.

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1**Appendix S7:** Table 8: Invasive populations sampled as well as populations for which

2reliable information on their origin was available with information on locality, coordinates,

3sample size, clade affiliation and references. Abbreviations: Salps = Southern Alps, Efra =

4Eastern France, Ven = Venetian, Cbalk = Central Balkan, Tusc = Tuscany, Wfra = Western

5France Clade.

Locality	Latitude	Longitude	n	Clade	reference
Germany					
1. NS, Bramsche	52,4424085	7,8758239	2	Salps	
2. NS, Nörten-Hardenberg	51,6303786	9,9357604	5	Wfra/*P. liolepis*	
3. NS, Hannover-Berggarten	52,3943537	9,6986961	3	Ven	
4. NRW; Bielefeld	52,0043285	8,4994697	1	Salps	
5. NRW; Schloss Holte-Stukenbrock	51,9063664	8,6101913	2	Efra	
6. NRW, Dortmund, Hengsteysee	51,4189074	7,4739646	2	Efra	
7. NRW; Kamp-Lintfort	51,4942097	6,5481948	1	Efra	
8. NRW, Duisburg Hüttenheim	51,3694227	6,7313575	1	Efra	
9. NRW, Duisburg-Ruhrort	51,4555044	6,7332458	0	Efra	pers. comm.
10. NRW, Duisburg-Hochfeld	51,4180509	6,7533302	2	Efra	
11. NRW, Duisburg-Innenhafen	51,4428807	6,7627716	3	Efra	
12. NRW, Dinslaken	51,5527397	6,7239761	1	Efra	
13. NRW, Bonn-Poppelsdorf	50,7222208	7,0890998	0	Efra	Dalbeck pers. comm.
14. NRW, Holzwickede	51,5010492	7,62331	1	Salps	
15. NRW, Witten-Bommern	51,420192	7,3380088	1	Salps	
16. NRW, Witten-Heven	51,4341062	7,3057365	3	Salps	
17. NRW, Bochum Bot. Garten	51,4819708	7,2159147	2	Efra	
18. NRW, Bottrop	51,5211343	6,9467926	3	Efra	
19. NRW, Oberhausen	51,4938891	6,8736648	1	Efra	
20. NRW, Kaldenkirchen	51,3267501	6,1804962	2	Salps	
21. NRW, Mülheim a. d. R.	51,4188538	6,8675708	2	Ven	
22. NRW, Düsseldorf Bot. Garten	51,1924697	6,7979621	1	Salps	
23. NRW, Monheim	51,0842237	6,8853378	3	Efra	
24. NRW, Remshagen	51,0216918	7,4249553	2	Efra	
25. NRW, Weiershagen	50,9652111	7,4629783	3	Efra	
26. NRW, Stahle	51,8357775	9,4290161	2	Efra/Salps	
27. SA, Halle a. d. S.	51,4768926	11,974411	2	Cbalk	
28. SN, Dresden	51,0422573	13,833847	2	Ven	
29. SN, Ammelshain	51,2981008	12,6420021	1	Cbalk	
30. SN, Altenhain	51,3013207	12,6823425	2	Cbalk	
31. SN, Kamenz	51,2760919	14,0942573	8	Salps/Efra	
32. SN, Frankenberg	50,9116924	13,033905	2	Salps/Ven	
33. HE, Frankfurt	50,1070382	8,672676	1	Efra	
34. HE, Hanau	50,1331238	8,911457	4	Efra	
35. HE, Darmstadt, Bessungen	49,8286816	8,6594581	4	Efra/Efra (Languedoc)	
36. HE, Darmstadt Hbf	49,872402	8,6304473	1	Salps	
37. HE, Gernsheim	49,7558743	8,4889984	2	Wfra	
38. RP, Mainz	50,0198179	8,1832695	3	Wfra	
39. BW, Mannheim	49,4851894	8,512001	1	Ven	
40. BW, Heidelberg	49,4170039	8,7075233	0	Efra	Baier 2008
41. BW, Tübingen (Spitzberg)	48,5173434	9,0377998	1	Salps	
42. BW, Stuttgart Birkenkopf	48,7652981	9,1316986	3	Salps	
43. BW, Stuttgart, Kriegsberge	48,7959523	9,1756439	2	Efra	

44. BW, Stuttgart, Schifflände	48,8031395	9,2104911	9	Tusc/SAlps	
45. BW, Stuttgart, Travertinpark	48,7994012	9,1975736	3	Efra (Languedoc), Salps	
46. BW, Stuttgart, Bad Cannstatt	48,7866364	9,2452955	7	Efra (Languedoc), Efra, Salps	
47. BW, Freiburg	47,9909089	7,8621178	10	Salps/Tusc	
48. BW, Ihringen	48,0418528	7,6427507	0	Efra	Laufer et al. 2007
49. BW, Mainau	47,7045345	9,2003095	1	Salps	
50. BW, Inzlingen	47,587468	7,6795291	2	Ven/Salps	
51. BW, Lörrach Stetten	47,6045643	7,6518917	5	Salps/Romagna	
52. BY, Augsburg	48,3652311	10,8859491	1	Salps	
53. BY, Neuötting	48,2436533	12,6821708	2	Salps	
54. BY, Obernzell	48,5568413	13,62957	2	Ven	
55. BY, Passau-Grubweg	48,5766071	13,4767913	2	Ven	
56. BY, Tittling	48,7278882	13,3808326	5	Efra/Ven	
57. BY, Hutthurm	48,671466	13,4706115	1	Tusc	
58. BY, München Aubing	48,1633374	11,4276695	1	Marche	
59. BY, München Südbahnhof	48,1217572	11,5536689	1	Salps	
60. BY, München Donnersb. Brücke	48,1430092	11,5345277	3	Salps/Ven	
61. BY, Rosenheim	47,8520467	12,11483	2	Efra	
62. BY, Kelheim	48,9140389	11,8751907	1	Efra	
63. BY, Aschaffenburg, Pompejanum	49,9778318	9,1393375	1	Ven	
64. BY, Aschaffenburg Hbf	49,9391651	9,063611	3	Ven	
65. BY, Donauwörth	48,7156574	10,7726955	1	Salps	
Austria					
66. O, Urfahr	48,3051778	14,2818832	1	Salps	
67. O, Schlögen	48,4242454	13,8728141	2	Ven	
68. O, Schärding	48,4604294	13,4316015	6	Tusc/Ven	
69. N, Klosterneuburg	48,2993755	16,3336122	2	Ven	
70. V, Feldkirch	47,2375491	9,5931673	1	Salps	
71. V, Rankweil	47,2725903	9,6377992	1	Ven	
Liechtenstein					
72. Vaduz	47,1444304	9,5084953	1	Efra	Mayer & Schurig unpublished
73. Triesen	47,1113782	9,5191383	0	Salps	Kühnis 2008
Switzerland					
74. Basel-Riehen	47,5783351	7,6335883	3	Romagna	Mayer & Deichsel unpublished
75. Basel-Wiesenmatte	47,5866647	7,6416993	4	Ven/Romagna	Mayer & Deichsel unpublished
76. Basel, Bot. Garten	47,5333711	7,6145982	2	EFra/Ven	Mayer & Deichsel unpublished
77. Buchs	47,4544425	8,4313201	2	Salps/Efra	Mayer & Gebhart unpublished
78. Autal	47,5841175	7,6660215	2	Ven	Mayer, Gebhart & Schurig unpublished
79. Trübbach	47,0657956	9,4681763	1	Efra	Mayer & Deichsel unpublished
80. Bad Ragatz	47,0109572	9,5039033	2	Efra/Tusc	Mayer & Gebhart unpublished
81. Sargans	47,0477856	9,4335651	2	Salps/Efra	Mayer & Gebhart unpublished
82. Romanshorn	47,5632645	9,3801784	1	Salps	Mayer & Gebhart unpublished
Netherlands					
83. Echt	51,0972697	5,872364	0	Efra	van Delft and Frissen-Moors, pers. comm.
England					
84. Bournemouth	50,721297	1,8926525	0	Ven	Deichsel et al. 2007
Croatia					
85. Cres	44,9602279	14,4051146	0	Ven	Mayer, pers. comm..

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