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# The diverse nature of island isolation and its effect on land bridge insular faunas

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## Abstract

**Aim:** Isolation is a key factor in island biology. It is usually defined as the distance to the geographically nearest mainland, but many other definitions exist. We explored how testing different isolation indices affects the inference of impacts of isolation on faunal characteristics. We focused on land bridge islands and compared the relationships of many spatial and temporal (i.e., through time) isolation indices with community-, population- and individual-level characteristics (species richness, population density and body size, respectively).

**Location:** Aegean Sea islands, Greece.

**Time period:** Current.

**Taxon:** Many animal taxa.

**Methods:** We estimated 21 isolation indices for 205 islands and recorded species richness data for 15 taxa (invertebrates and vertebrates). We obtained body size data for seven lizard species and population density data for three. We explored how well indices predict each characteristic, in each taxon, by conducting a series of ordinary least squares regressions (controlling for island area when needed) and a meta-analysis.

**Results:** Isolation was significantly (and negatively) associated with species richness in 10 of 15 taxa. It was significantly (and positively) associated with body size in only one of seven species and was not associated with population density. The effect of isolation on species richness was much weaker than that of island area, regardless of the index tested. Spatial indices generally out-performed temporal indices, and indices directly related to the mainland out-performed those related mainly to neighbouring islands. No index was universally superior to others, including the distance to the geographically nearest mainland.

**Main conclusions:** The choice of index can alter our perception of the impacts of isolation on biological patterns. The nearly automatic, ubiquitous use of distance to the geographically nearest mainland misrepresents the complexity of the effects of isolation. We recommend the simultaneous testing of several indices that represent different aspects of isolation, in order to produce more constructive and thorough investigations and avoid imprecise inference.

## 1 | INTRODUCTION

Isolation and area are the two main abiotic factors purported to affect insular evolutionary ecology and biogeography (Hamilton & Armstrong, 1965; Itescu, 2019; MacArthur & Wilson, 1967; Santos, Field, & Ricklefs, 2016; Whittaker & Fernández-Palacios, 2006). According to the dynamic equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967), island area and isolation determine species richness by affecting rates of extinction (mainly a function of area) and immigration (mainly a function of isolation). This theory predicts that species richness generally increases with island area and declines with isolation. The original dynamic equilibrium model (MacArthur & Wilson, 1963, 1967) regards area and isolation as equally important for determining species richness. Later studies suggested that diversification (i.e., cladogenesis) is another, in some cases the most, important factor determining species richness, especially in remote archipelagos, where colonization rates are low (Heaney, 2000; Rosindell & Phillimore, 2011; Whittaker, Triantis, & Ladle, 2008, cf. Ali & Meiri, 2019).

A large proportion of island biogeography studies focus on oceanic islands, although land bridge islands compose the vast majority of islands worldwide (Meiri, 2017). The dynamics of species assembly on land bridge islands are fundamentally different from those on oceanic islands because the former harbour life when they become isolated, whereas the latter start devoid of life (Itescu, 2019; Santos et al., 2016). According to the "general dynamic theory of island biogeography" (Whittaker et al., 2008), which deals principally with oceanic islands, geographical (i.e., spatial) isolation plays a key role in determining species richness on islands (Santos et al., 2016; Whittaker et al., 2008). Colonization is crucial on oceanic islands (Cabral, Whittaker, Wiegand, & Kreft, 2019), and poor dispersers are unlikely to reach very distant islands (Borges & Hortal, 2009). Subsequent modifications of the dynamic equilibrium theory of MacArthur and Wilson (1967) have also postulated a concomitant impact of isolation on extinction rates, which are reduced on near islands via meta-population "rescue" effects (Brown & Kodric-Brown, 1977). Consequently, on land bridge islands, which are often much closer to the source landmass, spatial isolation (i.e., the minimal geographical distance of a focal island from other landmasses) is expected by some to affect species richness only weakly (Case, 1975; Palmeirim, Vieira, & Peres, 2017). On such islands, richness has been shown to be determined mainly by community relaxation processes (i.e., species extinction driven by reduced carrying capacity of the landmass after its isolation; Case, 1975; Diamond, 1972; Foufopoulos & Ives, 1999; Foufopoulos, Kilpatrick, & Ives, 2011; Wilcox, 1978). Extinction (= "relaxation") dynamics are time dependent (Brown, 1971; Whittaker, Fernández-Palacios, Matthews, Borregaard, & Triantis, 2017). Temporal isolation, the length of time

during which an insular biota has been shaped in isolation from other biotas, might therefore be more important than spatial isolation for land bridge islands. The longer an island has been isolated, the lower the richness will be, until an equilibrium is reached.

Island area is straightforward and relatively easy to estimate, but isolation is not. Indices of isolation that are based on the minimal distance of an island from another landmass or on the length of time for which it has been separated from other landmasses can be defined with respect to different landmasses. One can quantify isolation (either spatial or temporal) from the nearest mainland, the nearest mainland from which it acquired its fauna (see Materials and Methods), the nearest island, the nearest larger island, the landmass to which it was most recently connected, etc. (Figure 1). Other factors, such as surrounding landmass area, wind regimens, sea currents and habitat similarity between islands, may also contribute to the isolation of an island (Foufopoulos & Mayer, 2007; Weigelt & Kreft, 2013). In particular, the amount of surrounding land area was found to be very important for plant species richness (Diver, 2008; Weigelt & Kreft, 2013). This is another type of spatial isolation index; it indicates the amount of potential source area available within a defined radius around a focal island, while accounting for the shape of the focal island and the source landmasses. The larger the land area found within the radius, the less isolated an island is, and therefore the higher the species richness is expected to be (everything else being equal; Weigelt & Kreft, 2013). Although a multitude of potential isolation indices exists, studies that test and compare more than two indices (e.g., Itescu et al., 2018; Weigelt & Kreft, 2013) or examine composite isolation indices (e.g., Boyer & Jetz, 2010) are uncommon.

Despite the multifaceted nature of isolation, the distance to the geographically nearest mainland is by far the most frequently used index and is often the only one. This may be because the nearest mainland is usually assumed to be the richest gene pool and species source for a focal island (Weigelt & Kreft, 2013). This measure may also be popular because it is the easiest and most straightforward to calculate. But is it the most informative or powerful index? Diver (2008) and Weigelt and Kreft (2013) examined this for plant species richness, comparing a variety of spatial isolation indices, and found that it was not. Instead, other indices, such as the amount of surrounding land area and the distance from close larger islands, performed better. The response of species richness to environmental factors, however, often differs between animals and plants (Currie, 1991; Hawkins et al., 2003). The consistency of the effect of isolation on animal richness, or traits, was never explored thoroughly across different metrics. Millien-Parra and Jaeger (1999) showed that neighbouring islands were more important than the mainland as sources of mammal island colonizers. In other cases, none of the examined isolation indices, including the distance to the nearest mainland, was
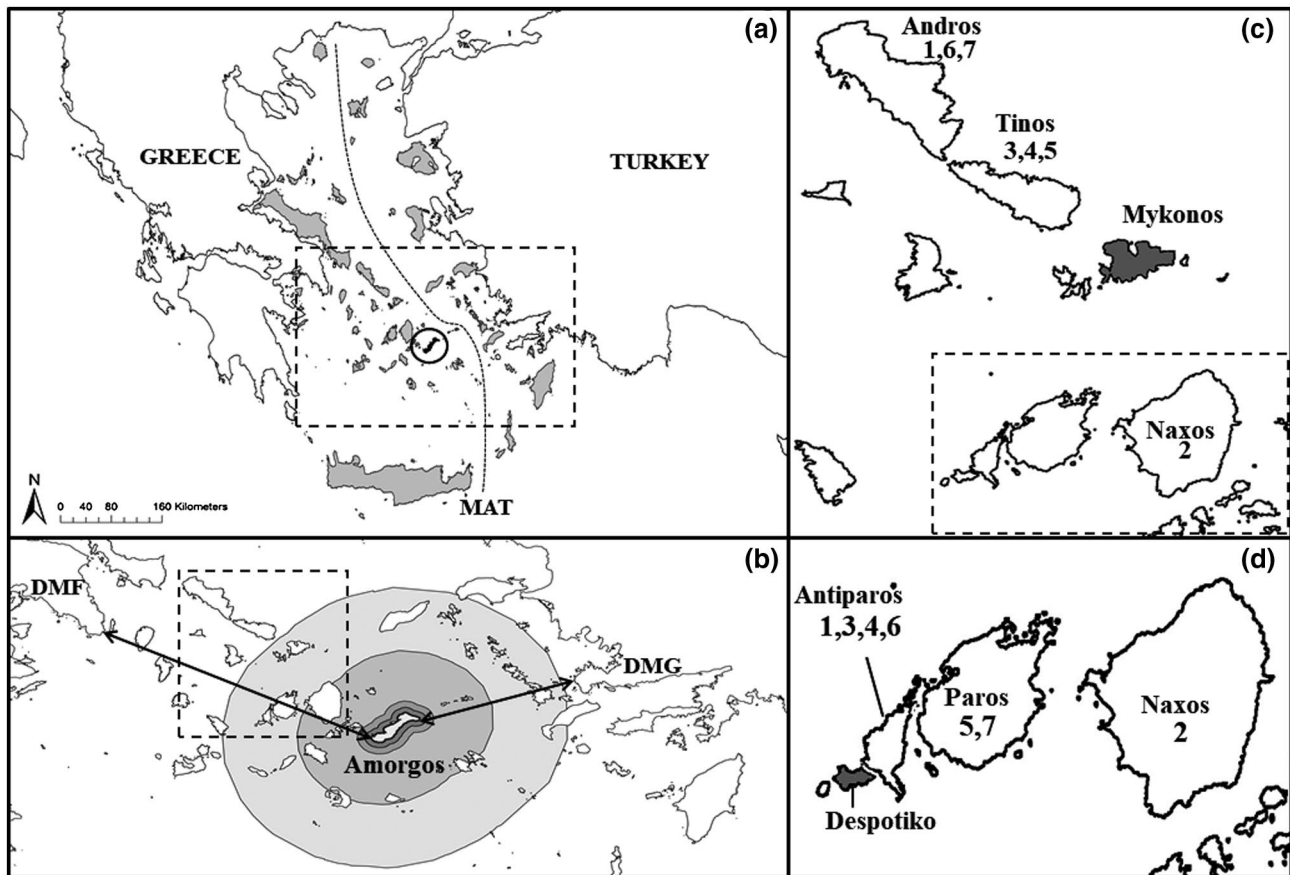
**FIGURE 1** Schematic visualization of the different source land masses from which isolation indices have been calculated in this study, exemplified by real cases. Abbreviations: DMG = distance to the geographically nearest mainland; DMF = distance to the nearest mainland with similar fauna; MAT = Mid Aegean Trench (see main text). Numbers in panels c and d correspond to the codes of "D" (distance) and "T" (time) indices given in Table 1. Each panel zooms in to the dashed shape within the previous panel. (a) A map of the Aegean Sea showing the islands studied (in grey, except for Amorgos, which is encircled and marked in black) and the location of the MAT. (b) Amorgos Island surrounded by six buffers (in the grey gradient) illustrating indices B1–B6. Arrows indicate DMF and DMG, which are different for this island. (c,d) Focal islands Mykonos (c) and Despotiko (d), marked in dark grey, present an example of different spatial and temporal settings with regard to the neighbouring islands from which each "T" and "D" isolation index was calculated

found to affect species richness (e.g., Fattorini, 2002; Heaney, 1984; Sfenthourakis, 1996). Two recent studies, in which data from both oceanic and land bridge archipelagos were analysed, suggested that the effect of distance to the geographically nearest mainland on species richness is often overshadowed by the effects of intra-archipelago processes, driven by the spatial structure of islands (Ali & Meiri, 2019; Matthews, Rigal, Triantis, & Whittaker, 2019).

The explanatory power of temporal isolation indices (or "island age" parameters) has never been compared with that of spatial isolation indices for any group of organisms. Temporal isolation is hard to estimate, especially for land bridge islands. This might be the reason why it is studied less often than spatial isolation in general and why it is studied more often in oceanic islands (e.g., Ali & Meiri, 2019; Borges & Brown, 1999; Cameron et al., 2013) than in land bridge islands (but see e.g., Heaney, 1984; Wilcox, 1978).

Species richness is the most studied feature in island biogeography, but many other characteristics of insular animals are also thought to be affected by isolation (Lomolino, Riddle, Whittaker, & Brown, 2016; Losos & Ricklefs, 2009). Body size is arguably the

most studied phenotypic trait of animals, on islands and in general, and it is often thought to increase in small species and decrease in large species with increasing isolation (Itescu et al., 2018; Lomolino, 2005; Meiri, Dayan, & Simberloff, 2005). The logic behind this prediction is that increased isolation induces ecological conditions that drive animal size to an intermediate optimum (Lomolino, 2005). Increased spatial isolation means lower gene flow, and increased temporal isolation means a longer time for genetic differences to accumulate. More spatially or temporally isolated islands are therefore expected to show more extreme in situ evolution (Adler & Levins, 1994; Boback, 2003; Kisel & Barraclough, 2010; Pergams & Ashley, 2001). Isolation can also affect population-level characteristics. For example, because it is predicted to drive decreased species richness it is thought that highly isolated island populations enjoy reduced interspecific competition, which leads ultimately to increased population densities (Adler & Levins, 1994; Adler, Wilson, & Derosa, 1986; MacArthur, Diamond, & Karr, 1972; cf. Novosolov et al., 2016).

We investigated how the choice of which isolation index to study affects our inference of the impact of isolation on biological

**TABLE 1** The isolation indices examined in this study

| Isolation type | Spatial index code | Temporal index code | Response |
|---|---|---|---|
| Isolation from the geographically nearest mainland | DMG | | Richness and traits |
| Isolation from the nearest mainland with similar fauna | DMF | TM | Richness and traits |
| Isolation from the nearest (larger) landmass (mainland or larger island) to which an island was last connected | D1 | T1 | Richness and traits |
| Isolation from the largest island in the cluster of the focal island | D2 | T2 | Richness and traits |
| Isolation from the nearest larger island | D3 | T3 | Richness and traits |
| Isolation from the nearest (reptile) species-richer landmass (mainland or larger island) | D4 | T4 | Lizard traits |
| Isolation from the nearest lizard predator-richer landmass (mainland or larger island) | D5 | T5 | Lizard traits |
| Isolation from the last reptile-richer landmass (mainland or larger island) to which an island was connected | – | T6 | Lizard traits |
| Isolation from the last lizard predator-richer landmass (mainland or larger island) to which an island was connected | – | T7 | Lizard traits |
| Landmass area within a buffer of 0.5 km radius around a focal island | B1 | – | Richness and traits |
| Landmass area within a buffer of 1 km radius around a focal island | B2 | – | Richness and traits |
| Landmass area within a buffer of 5 km radius around a focal island | B3 | – | Richness and traits |
| Landmass area within a buffer of 10 km radius around a focal island | B4 | – | Richness and traits |
| Landmass area within a buffer of 50 km radius around a focal island | B5 | – | Richness and traits |
| Landmass area within a buffer of 100 km radius around a focal island | B6 | – | Richness and traits |

*Note:* Units are distance (in kilometres) for "D" (spatial) indices, area (in square kilometres) for "B" (spatial) indices and time (in years) for "T" (temporal) indices.

patterns on islands, and whether some indices consistently have a higher explanatory power across taxa. We examined community, population and individual characteristics to understand the extent to which patterns are general. We tested the most common prediction in the literature for each property we studied: (a) that species richness (a community-level property) declines with isolation (MacArthur & Wilson, 1963); (b) that population density (a population-level property) increases with isolation (Adler & Levins, 1994); and (c) that body size (an individual-level property) of small species is larger and that of large species is smaller on more isolated islands (Lomolino, 2005). We studied the fauna of the Aegean Archipelago (Greece), a system that, in recent decades, has been widely used in biogeographical studies of land bridge islands (Sfenthourakis, Pafilis, Parmakelis, Poulakakis, & Triantis, 2018). For species richness, we tested 15 isolation indices (11 spatial and four temporal) across 15

taxa. We tested the effects of 21 isolation indices (13 spatial and eight temporal) on body size across many populations of seven lizard species and the effects of the same 21 indices on the population density of three lizard species. We previously found that isolation has little effect on lizard body size (Itescu et al., 2018; Meiri, 2007) and now test whether our previous choice of isolation indices was the reason why the theory was refuted.

We hypothesized that:

1. Island area and the best isolation index would have similarly strong effects on patterns of insular fauna characteristics, as predicted by MacArthur and Wilson (1963, 1967).
2. The Aegean land bridge islands are often very young and were formed with an existing non-equilibrium fauna. If richness declines through extinction over time, temporal isolation would

have a stronger effect than spatial isolation on the properties of the fauna. Furthermore, we predicted that surrounding landmass area is more important than distances to other landmasses.

3. Most islands are closer to, and have been connected more recently to, nearby islands than to the mainland. Therefore, as recent results imply (Matthews et al., 2019), isolation from adjacent islands would be more strongly related to faunal characteristics than isolation from the mainland.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

The Aegean archipelago comprises c. 7,500 islands and islets that vary by several orders of magnitude in area and isolation (Sfenthourakis & Triantis, 2017). The geological and palaeozoological history of these islands is diverse and complex and has been thoroughly reviewed (Lymberakis & Poulakakis, 2010; Poulakakis et al., 2014; Sfenthourakis et al., 2018; Sfenthourakis & Triantis, 2017; Simaiakis et al., 2017). Most of the Aegean islands are land bridge islands, which were connected either to Europe or to Asia Minor at various points in time, but a few have never been connected to any mainland. Some islands have been isolated since the Messinian salinity crisis (c. 5.3 Ma; Lymberakis & Poulakakis, 2010), whereas others became isolated more recently during the Pliocene and Pleistocene (Anastasakis & Dermitzakis, 1990). The majority of islands, however, became isolated only after the Last Glacial Maximum (LGM), mostly as a result of rising sea levels (Kapsimalis et al., 2009; Sakellariou & Galanidou, 2016; Simaiakis et al., 2017).

### 2.2 | Data collection

#### 2.2.1 | Area and isolation indices

We obtained faunal data for 205 islands. We defined and estimated 21 isolation indices (13 spatial and eight temporal) for each island (Table 1). These represent a diversity of possible "source" landmasses. The indices we quantified include several previously studied ones and a few that we developed anew because we suspected that they could be important. We estimated three types of isolation indices: (1) temporal isolation indices (time, "T") quantifying the time (in years) since separation between an island and a defined source landmass; (2) spatial isolation indices (distance, "D") representing the minimal distances (in kilometres) between each focal island and a defined focal source landmass; and (3) spatial "buffer" (= B) isolation indices quantifying the amount of land area (in square kilometres) within a defined radius around the focal island. These three types reflect substantial variability in how they measure "isolation", and we were able to calculate them with confidence for even the smallest islands. We focused on contemporary values of area and spatial isolation, because Weigelt, Steinbauer, Cabral, and Kreft (2016) showed that they were more important than past conditions (e.g., in late Quaternary) for total plant species richness on islands worldwide.

The potential source landmasses were mostly similar for "T" and "D" indices (Table 1). We calculated two alternative indices of distance from the mainland. The "geographically nearest mainland" is the part of the mainland from which the straight-line distance to the focal island is the shortest, regardless of their fauna. The "nearest mainland with similar fauna", however, represents the nearest mainland region to which species pool the fauna of the focal island belongs. The fauna of the Aegean Sea islands is affected fundamentally by the Mid-Aegean Trench (MAT), a deep chasm in the Aegean Sea that opened 9–12 Ma (see Figure 1; Lymberakis & Poulakakis, 2010; Poulakakis et al., 2014). Islands east of the MAT were usually connected to Asia Minor during periods of low sea levels, whereas most islands west of the MAT were connected to islands further west or even to mainland Europe. For some taxa (e.g., reptiles and amphibians; Lymberakis & Poulakakis, 2010), this palaeogeographical feature separates the islands east of the MAT from those to its west, biologically. In many taxa, islands on each side of the MAT have sets of species that are not found on islands on the other side, and only a few cases of species that have crossed this biogeographical barrier have been documented so far (Lymberakis & Poulakakis, 2010; Poulakakis et al., 2014). Geographically, however, some islands west of MAT (e.g., Amorgos, Fig. 1b) are closer to mainland Asia Minor which harbors the fauna characterizing islands east of MAT, than to Europe, to which their fauna is more similar. All islands east of the MAT are geographically closer to Asia Minor than to continental Europe. This discrepancy means that the potential mainland source for the fauna of some of the "western" islands is not necessarily the geographically nearest mainland. In terms of temporal isolation, however, this distinction is practically irrelevant. Continental Greece and Asia Minor have remained a continuous landmass ever since the end of the Messinian crisis (Lymberakis & Poulakakis, 2010) and therefore any temporal estimation of land mass disconnection (i.e., island isolation) from the mainland would be the same with regard to both regions.

An island cluster (with regard to the distance and temporal isolation from the largest island in a cluster: D2 and T2, respectively, in Table 1; Figure 1) was defined as all present-day islands that formed one continuous landmass during the LGM (i.e., c. 20,000 years ago; Figure 2). Indices relating a focal island to source landmasses with more potential competitor and predator species (D4, D5 and T4–T7 in Table 1; Figure 1) were studied for body size and population density of lizards only. They were based on data on potential competitors and predators provided by Itescu et al. (2018). We were unable to obtain enough reliable data to study them in other taxa.

We recorded the area of each island from official publications of the Hellenic Statistical Authority (2011) and, for small islets, using Google Maps tools (https://www.daftlogic.com/projects-google-maps-area-calculator-tool.htm). Distances between islands and source landmasses were calculated using Google Earth distance measurement tools. Disconnection times between each island and its source landmass were calculated by crossing fine-resolution bathymetric data (from the Hellenic Navy Hydrographic Service: www.hnhs.gr/geoindex/) with charts of sea level change since the
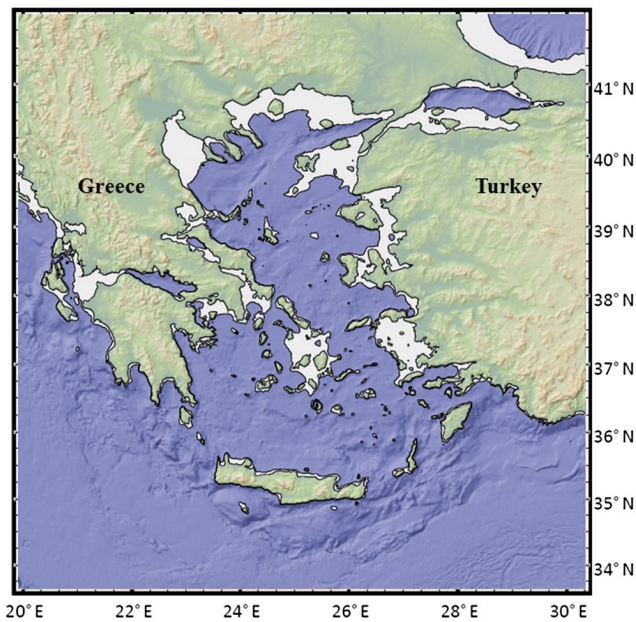
**FIGURE 2** The Aegean Sea region at the Last Glacial Maximum (*c.* 20,000 years ago). The white areas were dry land at that time and today are under water. This map was created via GeoMapApp (http://www.geomapapp.org/; see Ryan et al., 2009)

LGM (see Foufopoulos & Ives, 1999; Foufopoulos et al., 2011). This method has been implemented successfully in biological studies of land bridge archipelagos (e.g., Meik, Lawing, & Pires-daSilva, 2010; Wang et al., 2014).

Sea level rise since the LGM was not uniform across the Aegean region. Lambeck (1996) suggested that sea levels have risen more slowly towards the centre and south of the Aegean Sea. To refine the resolution of sea level time charts compared with previous estimates of this types in the Aegean region (e.g., Foufopoulos & Ives, 1999), we divided the Aegean Sea into 23 different sub-regions based on sea level rise data and maps (Dermitzakis, 1990; Kapsimalis et al., 2009; Lambeck, 1995, 1996; Perissoratis & Conispoliatis, 2003; Poulos, Ghionis, & Maroukian, 2009; Van Andel & Shackleton, 1982). We then calculated region-specific hypothesized time–depth charts (see Supporting Information Appendix S1, Table S1.1; Figure S1.1). These sub-regions represent areas that have presumably experienced different rates of sea level rise since the LGM, which means that a given present-day depth might have been flooded at different times in different regions (Simaiakis et al., 2017). We recorded the estimated depths in each sub-region at several time periods as given in these publications. Then, for each pair of consecutive recorded time periods, we divided the number of years between them by the total change in depth during this time frame. The result was the hypothesized time at which sea level changed by each 1 m for that time frame.

The sub-regional charts were supplemented by island-specific estimations from the literature (see list of sources in Supporting Information Appendix S1) for islands that were isolated because of events such as earthquakes (e.g., Saria, Telendos). For islands that

were isolated before the LGM, we either used explicit estimations published in the literature or used a rough estimation of the minimal period for which the island was disconnected from any larger landmass, based on maps and data in the biogeographical literature (see Appendix 1). To estimate the disconnection time of islands from potential source landmasses, we recorded the maximal depth between each focal island–source landmass pair. We then extracted the matching hypothesized time period from the corresponding subregional time–depth chart.

Simaiakis et al. (2017: see their appendix B, table S1) used a different model that also took into account the spatially non-uniform rise in Aegean Sea level since the LGM to estimate the timing of isolation of 31 Aegean islands. To examine whether the use of a different model (more straightforward, in our opinion) to estimate temporal isolation produced different results, we performed a sensitivity test in which we compared our island disconnection time estimations with those of Simaiakis et al. (2017) for these 31 islands. Absolute estimations were older by 1,160 years, on average, in the study by Simaiakis et al. (2017) than in our method. They were, however, very strongly correlated (Spearman's $\rho = 0.96$, $p < .001$, $n = 31$ islands). Simaiakis et al. (2017) explicitly mentioned that they trusted the chronological order of the island separation events they found, which is practically similar to what we found, more than the specific calculated timing in years. Thus, we feel confident that the choice of estimation model has not affected our inference, despite the slight difference in timing estimations.

To calculate the "B" indices (i.e., surrounding land area) we used the QGIS v.3.6.3-Noosa software and followed the procedure described by Weigelt and Kreft (2013). Given that studies showed that the effect of surrounding land area on species richness varies across spatial scales (Diver, 2008; Weigelt & Kreft, 2013), we applied the "buffer" tool, with six different radii for each focal island, on azimuthal equidistant projected maps: 0.5, 1, 5, 10, 50 and 100 km (B1–B6, in that order). The buffers were drawn around and relative to the circumference of the focal island. We then calculated the land area locked within each buffer and subtracted the area of the focal island from the total area. This gave us six "B" indices, varying in the geographical range they cover, for each focal island (for values of all 21 indices for each island, see Supporting Information Appendix S2, Table S2.1).

### 2.2.2 | Species richness and lizard body size

We recorded data (see Supporting Information Appendix S2, Table S2.1) on species richness of mammals (Masseti, 2012), breeding land birds (Simaiakis et al., 2012), reptiles (our own data; see below), land snails (Triantis, Vardinoyannis, & Mylonas, 2008; Welter-Schultes & Williams, 1999), centipedes (Simaiakis, Minelli, & Mylonas, 2005), non-halophilous isopods (Sfenthourakis, 1996; Sfenthourakis & Triantis, 2009), butterflies (Dennis, Shreeve, Olivier, & Coutsis, 2000), darkling beetles (Tenebrionidae; Anastasiou, Papadopoulou, & Trichas, 2018; Fattorini, 2002;

Trichas, Lagkis, Triantis, Poulakakis, & Chatzaki, 2008), orthopterans (Willemse, Kleukers, & Odé, 2018) and *Merodon* flies (Vujić et al., 2016). These taxa represent a diversity of life-forms and dispersal abilities. We analysed only islands that had data for at least one taxon and had at least one species of that taxon. To examine whether patterns are consistent across taxonomic levels, we also analysed species richness of the following, well-sampled and species-rich, subsets: rodents, snakes, lizards, bush-crickets and grasshoppers.

We recorded all known distribution records of Aegean reptiles from > 350 publications and six museum catalogues [Zoologische Staatssammlung München, Zoologisches Forschungsmuseum Alexander Koenig (Bonn), Museum für Naturkunde Berlin, Naturhistorisches Museum Vienna, Natural History Museum of Crete and Museum of Comparative Zoology at Harvard University; see Itescu, 2017]. To that, we added our own field observations (e.g., Itescu, Jamison, et al., 2017; Itescu, Schwarz, Moses, Pafilis, & Meiri, 2016; Itescu, Slavenko, Schwarz, Meiri, & Pafilis, 2016).

Mean body size [snout–vent length (SVL)] data for lizard species (*Ablepharus kitaibelii*, *Hemidactylus turcicus*, *Lacerta trilineata*, *Mediodactylus kotschyi*, *Mediodactylus oertzeni*, *Ophisops elegans* and *Podarcis erhardii*) were taken from Itescu et al. (2018; supplemented with a few minor updates). These represent our measurements in museums and in the field, and literature data. We included only species for which we had mean body size data from ≥ 10 islands, for which we could calculate all 21 isolation indices. Fourteen island populations that were classified as *M. kotschyi* by Itescu et al. (2018) were reclassified here as *M. oertzeni*, following a recent update to their taxonomy (Kotsakiozi et al., 2018), and were thus analysed separately.

We estimated population density in the field by applying species-specific methods. To estimate relative population densities of *M. kotschyi* across 40 islands, we calculated, for each population, the mean number of geckos one of us (Y.I.) found per hour of search in clear sky conditions during peak activity hours (Buckley & Roughgarden, 2005, 2006; Itescu, Schwarz, Meiri, & Pafilis, 2017). We estimated relative densities of *P. erhardii* from 55 islands through straight-line transects performed by three people simultaneously walking 100 m in parallel 10 m from each other during the peak activity time of the lizards and counting lizards seen or heard 1.5 m from each side. The three counts were then averaged. This was performed twice at a 48 hr interval and averaged. This method has been used successfully to estimate *Podarcis* densities (Brock, Bednekoff, Pafilis, & Foufopoulos, 2015; Donihue, Brock, Foufopoulos, & Herrel, 2016; Pérez-Mellado et al., 2008). For *H. turcicus* (*n* = 21 islands), we estimated relative densities by averaging the number of geckos found by one searching person during a full day (both during the day and at night; Itescu, Schwarz, et al., 2017).

## 2.3 | Statistical analyses

We evaluated the statistical significance of results in the present study at the α = .005 level. This decision followed recent calls for a more conservative approach in using statistical significance for testing hypotheses (Benjamin et al., 2018; Johnson, 2013). It was also required here because all our analyses included multiple comparisons and repeated tests. Nevertheless, given that α = .05 is still commonly used to determine statistical significance, we present all results with a *p*-value of .005 < *p* < .05 either in the main text or in the Supporting Information (Appendix S3).

To analyse the data adequately, we log$_{10}$-transformed the species richness of all taxa, the mean body size of *P. erhardii* (the residual distribution of other species was normal without transformation), the population density of *P. erhardii* and *H. turcicus*, and all predictor variables, because a Shapiro–Wilk normality test indicated that they differed significantly from normality (at α = .005). This procedure normalized the residuals of the regression tests we performed to a large extent. Landmass area ≤ 10 km radius around certain islands (B1–B4 indices) was zero. To be able to log$_{10}$-transform these indices, we converted these zeros to 0.0000001. This made them transformable but still smaller than the smallest value for any island in any of these indices.

We first regressed each response variable (log$_{10}$-transformed if necessary) against log$_{10}$-transformed island area and included island area as a covariate in all analyses where it proved significant (i.e., species richness for all taxa and population density of *P. erhardii*). Area was excluded from analyses of mean body size of all species and population density analyses of *H. turcicus* and *M. kotschyi*. We tested for collinearity between each isolation index and island area (using the HH package in R; Heiberger, 2009). No variance inflation factors were higher than the conservative cut-off value of four (O'Brien, 2007).

To test how each isolation index affects each property in each taxon, we performed a series of ordinary least squares regression tests, with species richness, mean body size and population density as the response variables. We used a single isolation index at a time as the predictor variable, and added island area as a covariate when necessary. We also tested for two-way interactions between each isolation index and island area, to investigate whether large islands respond to isolation in a different manner to small islands, like the reported pattern in plants (Weigelt & Kreft, 2013).

To test which isolation indices explain most of the variance in species richness of each taxon, we used the "calc.relimp" function in the "relaimpo" R package (Grömping, 2006), which calculated the partial $R^2$ for isolation in each model. We did not use information criteria, such as the Akaike information criterion (AIC), for model selection because it is not rare for the AIC to select models that statistically reflect no effect of the predictor variable on the response variable (MacNally, Duncan, Thomson, & Yen, 2018; see also Itescu et al., 2018). Another reason was that the AIC method scores full models (i.e., area and isolation, not only isolation) and therefore might score models in which island area explains more variance better, although isolation explains less variation in them than in alternative models with higher AIC scores. This would not allow us to compare the explanatory contribution of different isolation indices, which is what we were interested

in. Thus, we preferred to rank the statistically meaningful models (those with $p \leq .005$) by the partial $R^2$ explained by the tested isolation index. We think this is a more informative procedure with regard to the aim of this study. We applied a similar selection procedure for mean body size and population density models (comparing the model's total $R^2$ for univariate isolation models).

To examine which isolation indices were superior overall (we were able to test this only for species richness) and whether they were temporal or spatial indices, we used a DerSimonian–Laird random-effect meta-analysis of correlation coefficients of all studied taxa. Here, the square root of the partial $R^2$ scores of each isolation index were treated as the effect sizes, which we treated as random effects. This procedure calculates the mean relationship between isolation and species richness across "studies" (in our case, taxa) for each "treatment" (i.e., isolation index) (see Laliberté et al., 2010). Thus, it enabled us to determine which isolation index had the strongest effect across taxa. We performed the meta-analysis with the function "metacor.DSL" in the "metacor" R package (Laliberté, 2011).

## 3 | RESULTS

### 3.1 | Species richness

Isolation was a statistically significant predictor of species richness in 10 of 15 taxa. In the remaining five taxa (Tenebrionids, *Merodon* flies and the three orthopteran groups), no isolation index significantly affected species richness. The isolation index with the highest explanatory power varied across taxa (Table 2; Figure 3), but in all 10 taxa the spatial indices were superior to the temporal ones. The distance to the nearest mainland with similar fauna (DMF) explained more variance than any other index in four groups, land area within a buffer of 100 km radius (B6) in two groups (all reptiles and lizards alone), and the distance to the geographically nearest mainland (DMG), land area within a buffer of 0.5 km radius (B1) and the distance to the nearest larger landmass (D3) in one group each (land snails, isopods and mammals, respectively). For butterflies, DMF and DMG were identical and explained more variance than any other index. Distance to the nearest mainland with similar fauna (DMF) and to the geographically nearest mainland (DMG) were the most frequently significant indices (each in seven taxa, including butterflies), followed by the most frequently significant temporal index, which was the time of isolation from the mainland (TM; in six groups), and land area within buffers of 50 and 100 km radii (B5 and B6, respectively; each in five groups). These five indices, which are directly related to the mainland (DMF, DMG and TM) or largely (B5 and B6, in which the buffers include parts of the mainland for the majority of islands), were the top three for all taxa except mammals and isopods. Of all indices, land area within buffers of 5 and 10 km radii (B3 and B4, respectively) were the least important. They were not significant for any group (all models with $p$-values of $.005 < p < .05$ are presented in Supporting Information Appendix S3, Table S3.1). Only four out of 224 potential interaction terms between isolation indices and island area were statistically significant. Four additional interaction terms

were marginally non-significant (i.e., had $.005 < p < .05$; Supporting Information Appendix S3, Table S3.2).

Island area was strongly and positively correlated with species richness in all taxa. Area alone explained 31.5–85.3% of the variance in species richness across taxa (see Supporting Information Appendix S3, Table S3.2). When area and isolation were tested together, the partial $R^2$ for the most important isolation index in each group ranged between 10.4 and 27.8%, whereas island area explained 72.2–89.6% of this variance (Table 2), except for butterflies, for which the partial $R^2$ for isolation was 50.9% (for the distance from the mainland; see comment in Table 2). This was the only case, across 224 models, in which isolation explained more variance than area.

In the meta-analysis (Table 3; Supporting Information Appendix S3, Figure S3.1), island area alone explained 66.4% of the variance in species richness across all studied taxa. The isolation index with overall highest partial $R^2$ was the distance to the nearest mainland with similar fauna (DMF; 14.7%). The only significant temporal index was the time since isolation from the mainland (TM). Eight indices were not significant overall (land area within a buffer of 0.5 km radius, B1, was marginally non-significant). All significant indices showed the same expected trend: a negative association between isolation and species richness.

### 3.2 | Body size and population density

Only one of 147 models for mean body size was statistically significant: a positive relationship between mean body size of *A. kitaibelii* and the distance from the largest island in the cluster of the focal island (D2). For the other six species, the effect of the strongest isolation index on mean body size was borderline non-significant ($.005 < p < .061$). Nonetheless, it is noteworthy that, across these six species, five different indices were chosen, and these represent all three tested isolation types (D, B and T) and the two main source types (i.e., the mainland or adjacent landmasses; Table 4). All the best models showed that body size increases, albeit not significantly, with isolation (Table 4; Figure 3).

No isolation index significantly predicted population density in any species (Table 4). In *P. erhardii* (only), island area was negatively associated with population density. Even under the permissive threshold for statistical significance ($p < .05$), none of the 21 indices we tested was correlated with the population density of *H. turcicus*, one had a negative effect in *M. kotschyi*, and three had a positive effect in *P. erhardii* (Table 4). Under this threshold, *M. kotschyi* density increased with landmass area within a buffer of 5 km radius around a focal island (B3). The best (but still not very good) index for *P. erhardii* was distance from the nearest (larger) landmass to which an island was last connected (D1).

## 4 | DISCUSSION

We found that isolation is negatively correlated with richness in most taxa. In contrast, isolation seems to affect neither lizard body

**TABLE 2** Regression statistics of $\log_{10}$-transformed species richness as a function of different isolation indices of studied taxa

| Taxon | Model | Slope | Total $R^2$ | Partial $R^2$ area (%) | Partial $R^2$ isolation (%) | p | n |
|---|---|---|---|---|---|---|---|
| Mammals | **D3** | **−0.088** | **.768** | **89.6** | **10.4** | **.001** | 116 |
| | D1 | −0.080 | .771 | 92.2 | 7.8 | <.001 | |
| | B2 | 0.022 | .763 | 94.8 | 5.2 | .003 | |
| | T1 | −0.054 | .762 | 97.6 | 2.4 | .005 | |
| Rodents | **DMF** | **−0.097** | **.719** | **73.7** | **26.3** | **<.001** | 102 |
| | DMG | −0.094 | .712 | 75.4 | 24.6 | <.001 | |
| | B6 | 0.169 | .708 | 79.7 | 20.3 | <.001 | |
| | TM | −0.048 | .702 | 83.7 | 16.2 | <.001 | |
| Land birds | **DMF** | **−0.147** | **.857** | **76.2** | **23.8** | **<.001** | 65 |
| | DMG | −0.149 | .855 | 78.0 | 22.0 | .001 | |
| | TM | −0.067 | .860 | 83.0 | 17.0 | <.001 | |
| Reptiles | **B6** | **0.194** | **.718** | **85.3** | **14.7** | **<.001** | 205 |
| | DMF | −0.092 | .722 | 85.9 | 14.1 | <.001 | |
| | DMG | −0.082 | .717 | 88.4 | 11.4 | .004 | |
| | TM | −0.054 | .723 | 89.0 | 11.0 | <.001 | |
| | B5 | 0.129 | .720 | 91.6 | 8.4 | <.001 | |
| | B2 | 0.022 | .715 | 97.0 | 3.0 | <.001 | |
| Lizards | **B6** | **0.119** | **.658** | **85.7** | **14.3** | **.001** | 202 |
| | DMF | −0.053 | .664 | 86.7 | 13.3 | .005 | |
| | B5 | 0.088 | .663 | 90.9 | 9.1 | <.001 | |
| Snakes | **DMF** | **−0.153** | **.695** | **72.2** | **27.8** | **<.001** | 90 |
| | DMG | −0.151 | .691 | 73.5 | 26.5 | <.001 | |
| | B6 | 0.291 | .691 | 77.6 | 22.4 | <.001 | |
| | TM | −0.168 | .670 | 85.3 | 14.7 | .001 | |
| | B5 | 0.224 | .675 | 90.3 | 9.7 | <.001 | |
| Butterflies | **DM[a]** | **−0.216** | **.840** | **49.1** | **50.9** | **<.001** | 28 |
| | B6 | 0.344 | .790 | 51.8 | 48.2 | <.001 | |
| | TM | −0.100 | .731 | 54.0 | 46.0 | <.001 | |
| | D2 | −0.255 | .762 | 56.3 | 43.7 | <.001 | |
| | D1 | −0.217 | .756 | 58.8 | 41.2 | <.001 | |
| | B5 | 0.276 | .723 | 59.5 | 40.5 | <.001 | |
| | D3 | −0.251 | .740 | 63.6 | 36.4 | <.001 | |
| | T3 | −0.093 | .601 | 66.7 | 33.3 | <.001 | |
| | T2 | −0.086 | .539 | 71.3 | 28.7 | .002 | |
| | T1 | −0.086 | .539 | 71.4 | 28.6 | .002 | |
| Centipedes | **DMF** | **−0.167** | **.655** | **73.2** | **26.8** | **<.001** | 55 |
| | DMG | −0.182 | .664 | 73.9 | 26.1 | <.001 | |
| | TM | −0.098 | .613 | 81.2 | 18.8 | <.001 | |
| Land snails | **DMG** | **−0.122** | **.781** | **88.7** | **11.3** | **.002** | 85 |
| | B5 | −0.133 | .781 | 96.3 | 3.7 | .002 | |
| Isopods | **B1** | **0.018** | **.875** | **86.2** | **13.8** | **.001** | 68 |
| | B2 | 0.021 | .879 | 94.4 | 5.6 | <.001 | |
| *Merodon* flies | None | | | | | | 27 |
| Tenebrionid beetles | None | | | | | | 57 |

(Continues)

**TABLE 2** (Continued)

| Taxon | Model | Slope | Total $R^2$ | Partial $R^2$ area (%) | Partial $R^2$ isolation (%) | p | n |
|---|---|---|---|---|---|---|---|
| Orthopterans | None | | | | | | 65 |
| Bush-crickets | None | | | | | | 52 |
| Grasshoppers | None | | | | | | 60 |

*Note:* Log$_{10}$-transformed island area was a covariate in all models. Only statistically significant models ($p \leq .005$) are shown. Partial $R^2$ area and partial $R^2$ isolation are the relative contribution of each variable to the total $R^2$. The highest partial $R^2$ isolation in each taxon is in bold.
[a]In butterflies, the distance to the nearest mainland with similar fauna (DMF) and distance to the geographically nearest mainland (DMG) were identical and were referred to as DM.

size nor population density. We have demonstrated that isolation indices are not equally important across taxa, and sometimes even across taxonomic levels within a single taxon, for the same focal characteristic. We found no support for the hypothesis that area and isolation explain substantial and equal portions of the variance in insular fauna characteristics. Area explained substantially more of the variance in species richness than any isolation index in 223 out of 224 models. For body size and population density, neither area nor isolation explained a substantial portion of the variance.

These results also sharply refute our second hypothesis, that temporal isolation is more important than spatial isolation for land bridge island fauna. Temporal isolation indices seem to be the least influential of the studied metrices, whereas distance-based indices seem to be the most influential. Additionally, indices that are directly related to the mainland seem to be more important in predicting the species richness of most studied taxa, refuting our third hypothesis. Thus, overall, the results do not support any of our three hypotheses.

Isolation is expected to be negatively correlated with species richness (MacArthur & Wilson, 1963, 1967; Whittaker et al., 2008). This seems to be true for two-thirds of the taxa on the Aegean islands. Notably, all five taxa in which isolation had no impact are insect groups. The simplest explanation for the results of these five groups is that they are not constrained by isolation. Another possibility is that the current published data for species richness of these groups is too incomplete to be reliable, owing to problems such as unequal sampling efforts across islands and taxonomic uncertainties. These are likely in small animals. A non-mutually exclusive alternative is that the range of isolation in the set of islands we analysed for these taxa (which differed across taxa) was too small for isolation to play a major role in this system. We note that additional factors, such as the prevalence and direction of winds and sea currents, are especially important for insects. These factors, however, cannot explain our findings for butterflies and isopods. Weigelt and Kreft (2013) found that these factors affect plant species richness. In some taxa for which we found an association between isolation and species richness, studies conducted in other regions found no such relationship (e.g., SE Asian and Australian mammals: Burbidge, Williams, & Abbott, 1997; Heaney, 1984; British butterflies: Dennis & Shreeve, 1997; Brazilian snakes: Portillo et al., 2019). This could be a consequence of these studies not including the best indices. Alternatively, we suggest that the impact of isolation might depend on the spatial structure of a focal archipelago: patterns may be different between

archipelagos close to the mainland and those far from it (see e.g., Ås, 1984; Dennis & Shreeve, 1997; Foufopoulos & Mayer, 2007; Nilsson, Bengtsson, & Ås, 1988). This seems plausible, especially in cases where the same index shows inconsistent patterns across regions for the same taxon. For example, the distance from the geographically nearest mainland did not affect the richness of snakes in Brazilian Atlantic Forest coastal islands (Portillo et al., 2019) but had a significant negative effect on snake richness in the Aegean Sea islands and explained 18.3% of its variance (present study, Table 2).

Our results for animals are also inconsistent with those of Weigelt and Kreft (2013), who found that worldwide species richness of plants on large islands was less affected by isolation than on small ones. Biogeographical patterns are often dissimilar between plants and animals (Currie, 1991; Hawkins et al., 2003); therefore, this result is not surprising. Nevertheless, it could also be a matter of the scale of study; perhaps, interactions between island area and isolation are easier to detect at the global scale.

The influence of isolation (both spatial and temporal) on species richness was much weaker than that of island area, which affected all our studied taxa strongly and positively. This is in line with the results of a meta-analysis by Watling and Donnelly (2006), who showed that 92% of studies find a significant species–area relationship, but only 33% find a significant species–isolation relationship. Our results also agree with those of Matthews et al. (2019), who found that isolation (measured as the distance from the geographically nearest mainland) affected species richness much more weakly than did area, across multiple archipelagos. The relative weakness of isolation, however, stands in sharp contrast to the predictions of the dynamic theory of island biogeography (MacArthur & Wilson, 1963, 1967), where it was portrayed to have as strong effect as island area. Here, we demonstrated that the superior explanatory power of island area compared with that of isolation is consistent regardless of which isolation index is tested. Butterflies are the only group for which we found an index of isolation (but only one index, the distance from the mainland) that had an equally strong influence on species richness as island area (c. 50% of the explained variance each).

The relative weakness of isolation has several non-mutually exclusive potential explanations. One possibility is that present-day species–isolation relationships are severely obscured by anthropogenic activity (Helmus, Mahler, & Losos, 2014), which has been ongoing for several thousand years in our study system, as described
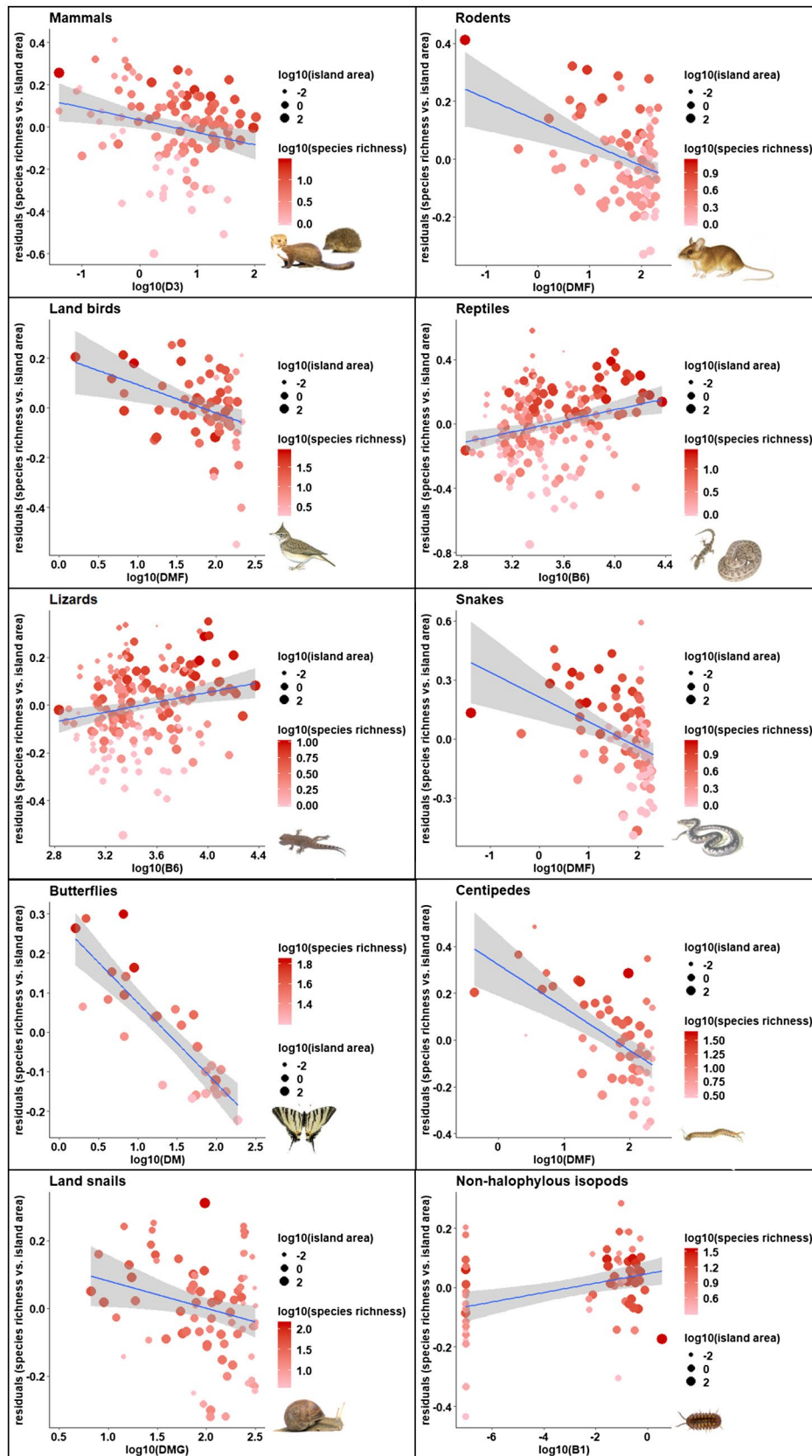
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**FIGURE 3** Scatter plots describing the relationship between the most important isolation index and species richness (controlled for island area) in the 10 taxa in which we found a statistically significant relationship. The area and species richness of islands (both $\log_{10}$-transformed) are visualized by the size and the colour of points, respectively

**TABLE 3** Results of a meta-analysis for the effect of area and isolation on species richness across all 15 taxa

| Index | Mean $r$ | Range ($r$) | $p$ |
|---|---|---|---|
| **Area** | **.815** | **.775 to .849** | **<.001** |
| **DMF** | **−.383** | **−.474 to −.284** | **<.001** |
| **DMG** | **−.370** | **−.464 to −.270** | **<.001** |
| **B6** | **.232** | **.146 to. 316** | **<.001** |
| **D3** | **−.219** | **−.375 to −.052** | **.005** |
| D1 | −.184 | −.338 to −.021 | .014 |
| **TM** | **−.174** | **−.331 to −.007** | **.002** |
| **B5** | **.148** | **.062 to .232** | **<.001** |
| B1 | .113 | .021 to.204 | .007 |
| **B2** | **.095** | **.040 to .150** | **<.001** |
| B4 | .048 | −.008 to .103 | .047 |
| B3 | .036 | −.020 to .092 | .101 |
| D2 | .034 | −.145 to .210 | .356 |
| T3 | −.020 | −.184 to .145 | .408 |
| T1 | −.010 | −.170 to .150 | .451 |
| T2 | .004 | −.153 to .162 | .478 |

*Note:* For isolation indices, the analysed values are of partial $R^2$ (from bivariate models with area), but for area they are derived from univariate models. Significant indices ($p \leq .005$) are in bold. Variables are presented in descending order of their mean explanatory power.

by the famous Greek classical poet, Homer (Lattimore, 1951). This activity has impacted local ecosystems through land-use change and species introductions. In some cases, it is not clear whether a newly discovered species is a "missed" native or a recent introduction (e.g., Itescu, Slavenko, et al., 2016), and this might have an impact on species richness counts. A second possibility is that the variation in island area is far larger than that of spatial isolation. In our system, island area spans six orders of magnitude, whereas distance-based isolation indices spans four at most. This may hamper finding strong relationships between species richness and isolation (Watling & Donnelly, 2006). Another possibility is that the rapid rates of area change in the region (as a result of changes in sea level) have not yet allowed islands to reach equilibrium (Simaiakis et al., 2017). Be that as it may, our results strongly imply that the length of the isolation period is a weak force, and thus explanations based on insufficient time for reaching equilibrium (assuming that equilibrium exists) are highly unlikely, even in this land bridge island-dominated system.

Surprisingly, we found that land bridge island faunas are generally affected more strongly by spatial isolation than by temporal isolation. This contrasts with conclusions of previous studies (Case, 1975; Foufopoulos & Ives, 1999) and with our own predictions. Distance-based indices performed consistently better than indices of surrounding land area (in contrast to patterns found in plants; Diver, 2008; Weigelt & Kreft, 2013), which in turn were superior to temporal indices. This pattern might be a consequence of very rapid changes in the Aegean insular fauna after isolation. Gibson et al. (2013) demonstrated that extinction may occur very quickly after an island disconnects from its "mother" landmass, and the system

enters a new state within a very short time period (a few hundreds of years or less; see also Burkey, 1995). This has direct implications for species richness, and a potential indirect influence on body size and population density, by reducing the numbers of interspecific competitors and predators (MacArthur et al., 1972; cf. Meiri et al., 2014). Studies demonstrated that phenotypic characteristics, such as body size, might indeed change drastically in short time-scales after isolation (Aubret, 2015; Lister, 1989). Other factors can also induce rapid microevolutionary changes on islands: extreme weather events, such as storms (e.g., Donihue et al., 2018), larger-scale climatic oscillations, such as droughts or rainy years (Grant et al., 2017), and anthropogenic activities, such as introduction of predators or competitors, land use changes, etc. (e.g., Jackson, Fuller, & Campbell, 2004; Littleford-Colquhoun, Clemente, Whiting, Ortiz-Barrientos, & Frère, 2017; Stuart et al., 2014). Under these scenarios, being isolated for 10,000 or 100,000 years makes no difference if richness has reached a plateau, or a phenotypic trait has reached an "optimal" state, after only a few hundreds of years. The vast majority of the islands we studied have been separate entities for at least a few thousand years. In contrast, spatial isolation affects species richness and evolutionary changes by controlling species and individual (i.e., gene) flow into islands, which is independent of any biological process occurring on the island.

No isolation index we tested, including the distance to the geographically nearest mainland (DMG), which is the most commonly examined index in the literature, was universally superior to other indices. Moreover, no index predicted species richness, mean body size or population density similarly well in all taxa. The relative importance of isolation indices and their magnitude of effect on species richness were inconsistent even across phylogenetically close taxa, taxonomic levels within certain taxa (e.g., rodents compared with all mammals, snakes compared with all reptiles), or taxa that presumably hold similar dispersal abilities. In the case of flying insects, for example, butterfly richness declined significantly as isolation increased, regardless of index, whereas *Merodon* fly richness did not respond significantly to any isolation index. Likewise, centipedes and isopods, both of which are ground-dwelling arthropod taxa, showed different patterns (Table 2).

The interpretation of the effects of isolation on mean body size is complicated. Isolation has little effect on body size in lizards, consistent with previous findings (Itescu et al., 2018; Meiri, 2007). We tested 21 different indices on seven species (i.e., 147 models), and only one of them emerged as significant at α = .005. This suggests that isolation and body size are genuinely not related and that this pattern is not a result of disregarding important isolation indices. However, researchers working with $p < .05$ as their threshold for statistical significance might interpret the results differently, because for each lizard species there was at least one significant result (at $p = .061$ for *M. oertzeni*, $.005 < p < .05$ for all other species). The less conservative thresholds suggest that size is larger on more isolated islands. Yet, even in this case, the prediction that body size reacts to isolation as a function of whether it is small or large (Lomolino, 2005) is not supported. The size of the smallest species in our dataset

**TABLE 4**  Model statistics for lizard mean body size (snout–vent length) and population density as a function of isolation

| Attribute | Species | Model | Slope | Total $R^2$ | Partial $R^2$ (%) | p | n |
|---|---|---|---|---|---|---|---|
| Mean snout–vent length | Ablepharus kitaibelii | **D2** | **2.426** | **.591** | – | **<.001** | 18 |
| | | DMF | 1.787 | .386 | – | .006 | |
| | | DMG | 1.620 | .330 | – | .013 | |
| | Hemidactylus turcicus | B5 | -7.331 | .220 | – | .021 | 24 |
| | Lacerta trilineata | DM | 9.734 | .303 | – | .033 | 15 |
| | Mediodactylus kotschyi | DMF | 3.889 | .104 | – | .010 | 62 |
| | | DMG | 3.114 | .097 | – | .014 | |
| | | B6 | -3.426 | .073 | – | .034 | |
| | Mediodactylus oertzeni | None | – | – | – | – | 14 |
| | Ophisops elegans | B4 | -2.248 | .455 | – | .011 | 13 |
| | | D3 | 2.711 | .351 | – | .033 | |
| | | D1 | 2.365 | .344 | – | .035 | |
| | | T1 | 1.604 | .329 | – | .040 | |
| | Podarcis erhardii | T6 | 0.008 | .069 | – | .031 | 67 |
| | | D4 | <0.001 | .066 | – | .035 | |
| | | D5 | <0.001 | .063 | – | .041 | |
| Population density | Hemidactylus turcicus | None | – | – | – | – | 21 |
| | Mediodactylus kotschyi | B3 | 0.597 | .110 | – | .037 | 40 |
| | Podarcis erhardii | **Area** | **-0.128** | **.220** | – | **<.001** | 55 |
| | | **Area** | **-0.197** | **.279** | 84.4 | **<.001** | |
| | | D1 | 0.133 | | 15.6 | .044 | |
| | | **Area** | **-0.184** | .297 | 86.6 | **<.001** | |
| | | T3 | 0.160 | | 13.4 | .020 | |
| | | **Area** | **-0.161** | .281 | 89.0 | **<.001** | |
| | | B3 | -0.150 | | 11.0 | .039 | |

*Note:* Only models with *p* < .05 are presented. Statistically significant models (*p* ≤ .005) are in bold. All predictor variables, mean body size of *P. erhardii*, and population density of *P. erhardii* and *H. turcicus* were log$_{10}$-transformed. *n* is the number of islands.

In *L. trilineata*, the distance to the nearest mainland with similar fauna (DMF) and distance to the geographically nearest mainland (DMG) were identical and were referred to as DM. Island area was statistically significant and included as a covariate only for population density of *P. erhardii*.
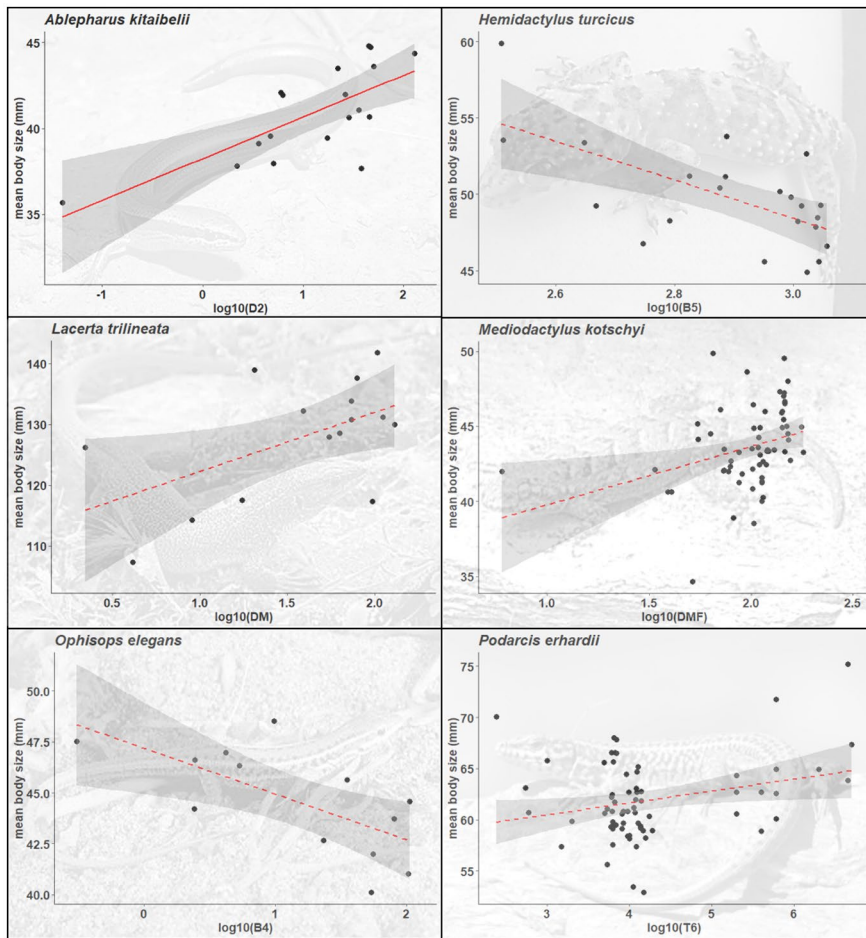
**FIGURE 4** Scatter plots describing the relationship between the isolation index with lowest *p*-value (for the six species in which *p* < .05; a different index in each case, as shown on the *x* axis labels) and mean body size. Trend lines illustrate statistical significance levels: continuous lines are for *p* < .005; dashed lines are for .005 < *p* < .05. Isolation is stronger when "D" and "T" indices are larger but "B" indices are smaller (thus all six trends here are essentially in the same direction)

(*A. kitaibelii*) increased with isolation, as expected, but so did the size of the largest species (*L. trilineata*), which was predicted to decrease. At the same time, it is clear that had we tested (using an α of .05) only one index for all species, our conclusions would be different for alternative indices we tested. For example, testing only the distance to the geographically closest mainland (DMG), we would have concluded that three of the seven species are affected by isolation. Using isolation indices such as land area within relatively large buffers (e.g., B5 or B6) would show that only one species is affected by isolation, and testing the time of isolation from the mainland (TM) would have driven us to conclude that isolation is not related to mean body size in lizards at all.

The indices that are directly related to the mainland (distance to the nearest mainland with similar fauna, distance to the geographically nearest mainland and time of isolation from the mainland) explained species richness better than indices of isolation from other islands. This stands in contrast to the finding of Matthews et al. (2019) and might mean that species richness in the Aegean Sea islands reflects a relaxation process with minimal contribution of between-island dispersal generating new colonizers (Foufopoulos & Ives, 1999). Out of the buffer (type B) indices, the largest radii (up to 50–100 km around islands) had the strongest impact on species richness of most taxa. Considering that, for most of the study islands, the mainland is well within buffers with such radii, we think that this is further evidence

emphasizing the importance of the mainland to species richness. Moreover, this result is largely in line with findings (for plants) that in a small-scale system, such as an archipelago in Lake Ontario (Diver, 2008), the amount of land area in the very close surroundings (within 0.25 km around islands) is most important, whereas at a global scale, area within 100–10,000 km around islands is most influential (Weigelt & Kreft, 2013). The Aegean archipelago is of an intermediate scale compared with the two other aforementioned systems, and thus the higher explanatory power of the indices quantifying land area within buffers of 50–100 km around islands fits this trend.

We conclude that the choice of which definition of isolation to use for studying insular biota can affect our inference of the magnitude of impact of isolation on biological patterns. Several relatively clear patterns emerge from our results for species richness. First, the effect of isolation on species richness is far weaker than that of island area, regardless of which index is tested. Second, spatial isolation indices tend to explain more variance than temporal indices. Third, isolation from the mainland explains more variance of species richness than isolation from adjacent islands. Finally, although the distance to the geographically nearest mainland (DMG) is the most straightforward index of isolation to measure, it is not necessarily the most informative. Although this index is not a bad choice per se, for many taxa it was inferior to other indices, including to its refined version, the distance to the nearest mainland with similar fauna (DMF). For body size,

it was not significant in most cases, and some indices performed better (but still poorly). Therefore, we recommend that the distance to the geographically nearest mainland should not be chosen automatically as the only index of isolation in a study, regardless of the attributes, taxa and system studied. We agree with Diver (2008) and Weigelt and Kreft (2013) that the impact of isolation on characteristics of insular biota could be modelled and understood better by studying additional indices. We think that the best way to approach this issue is to study several types of isolation indices simultaneously (e.g., the three we studied here and others that are based on, for example, climatic parameters or oceanographic parameters), to be able to encompass the complexity of this factor and its influence on insular biota. Despite the relative prominence of spatial isolation and mainland-related indices in this study, compared with other indices, we acknowledge the possibility that in other study systems the patterns might well be different. Simultaneous multi-index testing is essential to understand whether the weaker effects of temporal isolation are the norm across island systems and taxa.

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## CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

## AUTHOR CONTRIBUTIONS

Y.I. conceived the idea, performed the analyses and led the writing; all authors collected the data and contributed to the writing process.

## DATA AVAILABILITY STATEMENT

All the data supporting the results in the paper will be archived in Dryad [Itescu, Yuval; Foufopoulos, Johannes; Pafilis, Panayiotis; Meiri, Shai (2019), The diverse nature of island isolation and its effect on land bridge insular faunas, Dryad, Dataset, https://doi.org/10.5061/dryad.15dv41ns9] and are available in the Supporting Information (Appendix S2).

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## BIOSKETCH

**Yuval Itescu** is interested in biogeographical patterns, the processes shaping biodiversity at all spatial scales, and the way in which natural and anthropogenic factors affect the evolution and ecology of animal traits. He is especially fascinated by the implications of urban and insular environments on the ecology and evolution of their fauna.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

## APPENDIX 1. DATA SOURCES

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