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Original Article

What can the parameters of the species-area relationship (SAR) tell us? Insights from Mediterranean islands

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ABSTRACT

Aim. The species-area relationship (SAR) is often modelled by the linearized power function $\log S = \log c + z \log A$, where S is species richness, A is area, $\log c$ is the intercept and z is the slope. Although investigating how c and z values vary across taxa and archipelagos can provide insights into the biology of the SAR, this approach has many caveats. In this study, we aim to clarify how and why SARs should be properly compared for the same taxon among different areas, or among different taxa in the same area.

Location. Mediterranean. We considered 18 to 46 Tyrrhenian islands (0.000024 to 223 km^2) and 32 to 65 Aegean islands (0.0058 to 8261 km^2).

Methods. We used OLS regressions to estimate c and z values for various taxonomic groups: land snails, isopods, centipedes, tenebrionids and reptiles. We used ANCOVAs to test (1) if different taxa have different z and c values within the same island group (possibly due to their dispersal ability and ecological characteristics), and (2) if the same taxon has different z and c values in different island groups (possibly due to differences in historical processes and isolation).

Results. z varied between 0.141 and 0.309, while c varied between 2.717 and 12.286 species per unit area (1 km^2). For tenebrionids, centipedes and land snails, we found higher c values in the Tyrrhenian islands than in the Aegean islands. Overall, c values were highest for land snails.

Main conclusions. Our results demonstrate the importance of comparing SARs either of different groups within the same area, or of the same group in different areas. Furthermore, we identify the intercept, rather than the slope, as being dependent on the biogeographical dynamics (relict versus equilibrium faunas) and species ecology (dispersal capabilities and population abundance).

Key words: allometric function, intercept, island biogeography, power function, regression lines, species-area relationship (SAR), slope

INTRODUCTION

The species-area relationship (SAR), i.e. the increase in species number with area, is one of the best documented patterns in ecology (Lomolino, 2000, 2001; Whittaker & Fernández-Palacios, 2007; Triantis *et al.*, 2012). Although several mathematical functions have been proposed to model SARs (Tjørve, 2003, 2009; Dengler, 2009; Williams *et al.*, 2009), comparative studies identify the power function as the model that, in general, best fits empirical data (at least for island systems, see Triantis *et al.*, 2012; Matthews *et al.*, 2015), and which is best supported by ecological theories (e.g., Rosenzweig, 1995; Martin & Goldenfeld, 2006). The power function $S = c A^z$ (where *S* represents species richness and *A* the area) can be linearized by a double logarithmic transformation as $\log S = \log c + z \log A$. In this form, log *c* and *z* represent, respectively, the intercept and the slope of the line fitting the relationship. Since the space of the linearized power function is not arithmetic but logarithmic, *z* can be interpreted as a scaling factor describing how fast the response of species richness to area changes along the SAR curve (see Lomolino, 2001).

Several hypotheses have been proposed to interpret the biological meaning of *z* and to explain its variation among organisms and island systems. In particular, it has been suggested that *z* should increase with area, isolation (Rosenzweig, 1995), species trophic ranks (Holt *et al*., 1999; Holt, 2010; Roslin *et al.*, 2014), nestedness (Matthews *et al.*, 2016) and spatial aggregation of the individuals (Tjørve & Turner, 2009), and should decrease with species dispersal ability (Wright, 1981; Williamson, 1988), abundance of common species (Tjørve *et al*., 2008), human impact on the islands (Ficetola & Padoa-Schioppa, 2009) and latitude (Willig & Lyons, 2000; possibly as a response to increasing energy availability; Storch *et al.*, 2005). It has been also noted that *z* tends to be higher in oceanic islands than in continental ones (Patiño *et al.*, 2014).

Conversely, the parameter *c*, which represents the expected mean number of species per unit area, has received much less attention, being often (and simplistically) interpreted as a direct result of species richness (with higher values of *c* expected for more diverse taxa). Yet, it is not difficult to imagine situations where the same mean number of species per unit area is found in groups with different regional species richness. For example, a very diverse group at a regional scale with a high degree of nestedness across islands could have the same *c* value of a less rich taxon with a more uniform local richness. This calls for a deeper evaluation of the potential causes behind variations in *c* values. Although this need has already been emphasized by Connor & McCoy (1979) and, even more, by Gould (1979), after more than thirty years, comparative analyses of *c* values are still scanty, with the most relevant studies being very recent.

Triantis *et al.* (2012) suggested that differences in *c* values may be related to the diverse ecological space required by species of different taxa (see also Öckinger *et al.*, 2010). Patiño *et al.* (2014) showed that the intercept increases from poor to more diverse taxa (ferns to bryophytes and seed plants) in all the archipelagos evaluated, while Matthews *et al.*

(2015) observed that the intercepts were significantly lower for oceanic than continental islands. These analyses have the important merit of exploring general patterns of variation in both *z* and *c*. However, because of their general approach, they were a bit elusive in providing specific interpretations about the possible mechanisms involved in the observed patterns.

When fitting the line $\log S = \log c + z \log A$, *c* and *z* are unrelated, in the sense that they are estimated independently and jointly describe the data. Nevertheless, in the log-log space, when *z* increases, the fitting line tends to be more vertical, and hence it has more chances to intercept the *y*-axis at lower values. Consequently, island systems with higher *z* tend, on average, to have lower *c*. Due to this expected negative relationship, Gould (1979: 336) emphasized that *c* values should be compared only in families of regression lines having the same slopes (i.e. between parallel lines).

Finding homogeneous *z* values and heterogeneous *c* values among SAR regressions would suggest that the observed differences are due to the "initial trajectory" of the curve, i.e. to area-independent factors. Conversely, differences in *z* values would indicate that the functional relationships described by the various regression lines are not the same, suggesting that SARs have emerged in different systems for different reasons, either ecological or historical.

However, as observed by Gould (1979), it only makes sense to compare SAR regression lines built for the *same taxon* in *different areas* (to investigate how island characteristics affect species richness), or for *different taxa* in the *same area* (to investigate how different groups respond to the same eco-geographical settings). This recommendation, however, has been often ignored, and several global scale studies analyzed patterns of variation in *c* values aggregating different taxa and island systems (Connor & McCoy, 1979), or used only coarse categorizations, such as a subdivision of islands into general types (e.g., inland, continental shelf, oceanic), and of organisms into broad groups (plants, invertebrates, vertebrates) (Triantis *et al.*, 2012; Patiño *et al.*, 2014; Matthews *et al.*, 2015; but see Aranda *et al*., 2013).

The Mediterranean islands are ideal candidates to investigate variations in *c* and *z* values by strictly adhering to Gould's recommendation, since they are numerous, biodiverse, and well surveyed for many taxonomic groups. Taking advantage of these properties, we built SARs for various taxonomic groups (land snails, isopods, centipedes, tenebrionid beetles and reptiles) in two island systems (the Tyrrhenian and the Aegean islands). Then we compared *z* and *c* values of SARs built for different organisms in the same island group, or for the same organisms in different island groups.

In particular, this approach permitted us to test if: (1) different taxa have different *z* values within the same island group as a reflection of their dispersal ability (*z* is expected to be higher in more sedentary animals); (2) different taxa have different *c* values within the same island group as a reflection of their ecology (*c* values are expected to be larger for animals requiring smaller spaces); (3) the same taxon has different *z* values in different island groups as a reflection of a different degree of isolation (a more isolated system is expected to have a higher *z*); (4) the same taxon has different *c* values in different island groups as a reflection of their degree of isolation (a more isolated system is expected to have a smaller *c*).

MATERIALS AND METHODS

We selected two island groups, namely the Tyrrhenian and the Aegean islands (Figure 1), sharing the same environmental, ecological and basic socio-economic conditions (e.g., climate, vegetation setting, and history of anthropogenic disturbance), but differing in their average distance to the mainland and in their palaeogeographical history. Most of the Aegean islands (which are, on average, 80-90 km far from the mainland) are land-bridge islands, whereas most of the Tyrrhenian islands (which are, on average, 30 km far from the mainland) have never been connected to each other and/or to the mainland in the past. We collected presence data for five taxa (see Appendix 1) for which both island groups have been thoroughly investigated. Because not all islands were equally studied for all taxa, the number of islands we considered in the analyses varied for the different taxonomic groups. Values of native species richness reported in Appendix S1 in Supporting Information should be considered virtually complete (see, for example, Foufopoulos & Ives, 1999; Hausdorf & Hennig, 2005; Fattorini, 2007, 2009, 2011a, Sfenthourakis, 1996; Simaiakis *et al.*, 2012). The relatively high number of islands considered for each taxon (from 18 to 65) allows us to exclude the possibility that estimates of *c* and z values are affected by the uncertainty in regression parameters estimated for small island groups (Sólymos & Lele, 2012). Island area data were extracted from Arnold (2008). For uninhabited islands not included in Arnold (2008), we referred to values reported in the papers used as source of species richness data.

Presence of islands with "no species" for a certain group in a certain archipelago in our datasets, does not imply that no species of that group occurs there, but only that the island has not been sampled for that group. In other words, zero values indicate lack of data, not zero species. We are not aware of islands for which "zero species" really indicates lack of species. For this reason, we did not include islands with no species in the analyses.

SARs were modelled using OLS regressions on the double logarithmic transformation (with decimal logarithms, log) of the power function. We checked regression results for violations of homoscedasticity by plotting residuals versus predicted values, and for normality by using normal quantile plots. We used analyses of covariance (ANCOVAs) to test for differences in *c* and *z* values. In the ANCOVAs, each pair of species-area data was a set of correlated *x* (area) - *y* (richness) values relative to the compared taxa; means were compared for species richness, while area was the covariate. Calculations were done using the software PAST 3.0 (Hammer *et al.*, 2001).

Because c values change according to the unit used to measure island surface, we always express areas in km^2, which makes values comparable across islands and taxa. This means that c values express the number of species per 1 km^2. Although any unit of measurement might be used in SARs, using km^2 is a rather standard practice, and is a reasonable choice in consideration of the area of the islands used in this study (0.00002 to 8261 km^2, mean ± SE: 131.2083 ± 53.330, n = 174), and the dimension of habitat requirements of the studied taxa (much bigger than 1 m^2, as an example). Changing units of measurement does not change regression slopes, but only rescales the x-axis. Therefore, c values can be easily recalculated for any unit area by using parameters of the fitted SAR. For example, if the fitted parameters of the SAR were obtained using km^2, c is the number of species expected for 1 km^2; to obtain the number of species per hectare, it is sufficient to solve the equation for $A = 0.01$. To explore how different unit areas affect ranking of c values, we performed a sensitivity analysis by calculating c at 0.001, 0.01, 0.1, 1, 10, 100, and 1000 km^2. We obtained substantially stable results, with few cases of different ranking (Table 1). Thus, we concentrate our dicussion only on c values calculated for 1 km^2. Also, as explained by White & Gould (1965) and Gould (1979), c values originally expressed using different systems of measurements (e.g. km^2 versus square miles) can be converted by using an appropriate conversion factor depending on the units chosen. All other studies that analysed c values cited in this paper used km^2 as unit of measurement.

RESULTS

Overall, regressions for the power function model of SARs explained 54 to 90% of variance (Figure 2). The best fitting curve was that of the Aegean isopods, while the worst fitting one was that of the Aegean tenebrionids. The residuals do not suggest any pattern, except in the case of Aegean land snails, where they seem to indicate that z increases with scale.

Same taxa, different island systems

The same taxonomic groups had homogeneous z values in the two island systems, with the exception of reptiles, that showed a z value significantly higher in the Aegean islands (Table 2). By contrast, we found significant differences in c values between the two island groups for land snails, centipedes and tenebrionids, but not for isopods and reptiles (Table 2).

Different taxa, same island system

In the Tyrrhenian islands, all taxonomic groups showed similar *z* values, with the exception of reptiles versus centipedes and reptiles versus tenebrionids (Table 3). Conversely, we found significant differences in *c* values between: (1) tenebrionids and reptiles, (2) centipedes and reptiles, (3) land snails and reptiles, (4) isopods and reptiles, and (5) land snails and centipedes. Marginally significant differences were also found between land snails and tenebrionids, centipedes and tenebrionids, and centipedes and isopods (Table 3). In the Aegean islands, we found significant differences in the *z* values between reptiles and land snails, and between reptiles and isopods. All other taxonomic groups had similar *z* values (Table 3). *c* values resulted significantly different in all comparisons except those between centipedes and tenebrionids and between isopods and land snails (Table 3).

DISCUSSION

Interactions among factors (taxa, area, and ecological conditions in different areas) that may vary from one area to another may complicate the interpretation of SARs. Bunnefeld & Phillimore (2012) proposed to use mixed effect models to investigate the effects of archipelago, taxon and island type on the variation in species richness. This is a promising approach for controlling sources of variation and hence to identify general trends across different archipelagos and taxa in island biogeographical studies. Our aim, however, was not to disentangle interactions of multiple factors that influence SARs, but to provide interpretation of the biological meaning of the two parameters that define the power function model of the SAR which, after decades of research, still remains elusive.

In all the SARs we analyzed, *z* values fell within the typical range (0.20 - 0.40) as observed in true isolated archipelagos/islands (Connor & McCoy, 1979; Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007; Triantis *et al.*, 2012; Matthews *et al.*, 2015). Consistent with previous studies (Connor & McCoy, 1979; Triantis *et al.*, 2012; Matthews *et al.*, 2015), most of our SARs did not show significant variations in *z* values. We detected significant differences in *z* values only in a few cases for SARs regarding different groups within the same area and no significant differences when comparing SARs of the same taxon between different areas, except for the vertebrate group (reptiles). In general, isolation is known as a major factor affecting *z* values (cf. Rosenzweig, 1995). Although the two study systems considered in this paper have a different degree of isolation, this discrepancy is not so large to produce differences in the *z* values as strong as those observed among oceanic archipelagos. The difference between the slopes of reptiles (the only vertebrate taxon included in this analysis) and those of land snails, isopods and centipedes, may suggest that factors regulating SARs in these groups are different and/or operate in different ways. The reptiles represent the largest predators among the groups we took into account, and their lowest slope in the Tyrrhenian islands contrasts with the hypothesis that slope should increase with trophic rank (Holt *et al*., 1999; Holt, 2010). Conversely, the slope of reptiles' SAR in the Aegean islands was similar to, or even significantly higher than, that recorded for other taxa. This may suggest that reptiles have colonized the two island systems with different mechanisms. The Aegean islands are inhabited by a relict fauna that has mostly arrived through no longer existing land-bridges, and which is now under relaxation (Foufopoulos & Ives, 1999; Lymberakis & Poulakakis, 2010). By contrast, in the Tyrrhenian islands the current reptile fauna seems to follow equilibrium models although land-bridge colonization has had some importance (Fattorini, 2009, 2010a), and is profoundly altered by recent introductions (Ficetola & Padoa-Schioppa, 2009).

In all the cases where slopes were significantly different among taxa, the *c* values were also significantly different, which makes it difficult to identify the biogeographical processes responsible for variation in *z* values.

Our study supports Gould's prediction (1979), that the general homogeneity of slopes not only eases the investigation of variations in the *c* parameter, but also emphasizes how the intercept could be a very distinctive property of different SARs. In fact, comparisons between different archipelagos indicate that the Tyrrhenian islands host more species of land snails, tenebrionids and centipedes per unit area than the Aegean islands, but approximately the same number of isopod and reptile species. Three, not mutually exclusive hypotheses can be formulated to explain this pattern: (1) a higher extinction rate on the Aegean Islands; (2) a higher colonization rate on the Tyrrhenian islands; and (3) similar colonization rates, but a higher success of establishment on the Tyrrhenian islands.

As regards the tenebrionids, all these hypotheses can be supported by the high number of endemic species existing in the Aegean islands. Tenebrionid colonization of the Aegean islands mainly occurred via Pleistocene land-bridges (Hausdorf & Hennig, 2005; Fattorini, 2007; Papadopoulou *et al.*, 2009). After the Last Glacial Maximum, tenebrionid populations on different islands remained substantially isolated from one another, and from the mainland. This led to faunal relaxation and to the evolution of neo-endemic taxa (Hausdorf & Hennig, 2005; Fattorini, 2007; Papadopoulou *et al.*, 2009). More than 32% of the tenebrionid currently inhabiting the Aegean islands are endemic, whereas the percentage of endemic tenebrionids on the Tyrrhenian islands is less than 20% (Fattorini, 2006b and unpublished data), which indicates that the latter were subject to a more recent colonization. Compared to the Aegean Islands, Tyrrhenian islands are, in general, closer to the mainland coast, which suggests a major role for over-sea dispersal as a route for their colonization. Most of them can be considered at equilibrium, and their populations are probably enriched by regular species arrivals (rescue effect) (Fattorini, 2009, 2011a, b). The same reasoning applies also to centipedes and land snails.

In general, it has been observed that *c* values tend to decrease progressively from inland to continental shelf to ocean islands (Triantis *et al.*, 2012), i.e. in relation to system isolation. Our results for tenebrionids, centipedes and reptiles support this conclusion, with higher *c* values in the less isolated (Tyrrhenian) islands.

Our analyses indicate that SAR intercepts are also influenced by organisms' ecology. In the Tyrrhenian area, *c* values, i.e. the number of species per km^2, increased in the order reptiles < centipedes < tenebrionids ≈ isopods ≈ land snails. In the Aegean area, we found the same pattern with number of species per km^2 increasing in the order reptiles < centipedes ≈ tenebrionids < isopods ≈ land snails. These consistent results suggest that c values, which area measure of species density, reflect the population abundances of the respective taxa.

Reptiles are the largest animals considered in our study, and it is reasonable to assume that the same area can sustain a lower number of species than that of the other groups (Brown, 1995). A survey conducted in an Italian coastal site using pitfall traps revealed that, among the investigated arthropods, isopods were the most abundant group, followed by tenebrionids and centipedes (Pitzalis *et al.*, 2005; Trucchi *et al.*, 2009; Fattorini, 2010b). A study conducted in Greece confirmed these results, finding that abundance of soil arthropods decreased in the order isopods > tenebrionids > centipedes (Gkisakis *et al.*, 2014). Although, to the best of our knowledge, there is no research comparing the abundance of arthropods with that of land snails, the latter are known to be extremely abundant (Cameron *et al*., 2003). Thus, it appears that *c* values may reflect the abundances of taxa, being therefore indicative of the realized carrying capacity of the populations of all species of a given group in a given area per unit area, as hypothesized by Triantis *et al.* (2012). Thus, the groups that are more abundant are those for which the carrying capacity per unit area is higher. Under the assumption of random distribution of individuals and species, we expect that a unit area that hosts larger populations (i.e that samples more individuals from the whole community) tends to host also more species, leading to the relation between c values and species abundance.

Because of the non-linearity of the power function, the number of species per unit area does not vary linearly, i.e. the ratio species number/area is not constant. For this reason, to compare species richness of areas of different size, Ovadia (2003) and Brummitt & Nic Lughadha (2003) proposed the use of the *c* parameter of the power function as a measure of species richness standardized by area. A relevant problem with this method is, however, that neither the *c* value nor the *z* value represent the magnitude of species diversity, because both parameters are responsible for the regression. Thus, some authors (e.g., Veech, 2000; Ulrich & Buszko, 2005; Fattorini, 2006b) propose to use regression residuals to compare the species densities of different area sizes. Likewise, Hobohm's (2003) α index, defined as $\alpha = \log S - (z \log A + \log c)$, is, for a given area, exactly its residual from the linearized power function regression line. Because the number of species per unit area expressed by *c* varies according area size, *c* values cannot be used to compare different areas, but they can be legitimately used to compare different systems, provided comparisons are done by using always the same unit of measurement.

CONCLUSIONS AND FUTURE CHALLENGES

In this study we aimed at exploring if *c* values can provide ecological information complementary to that provided by *z* values. Indeed, we got more insights from SAR intercepts than from slopes, not only because intercepts had higher variability, but also because they showed interesting relationships with important ecological characteristics of the target taxa. To the best of our knowledge, no effort has been previously spent to compare the SARs of different taxa within the same area, under the 'old' claim that only few areas have been sampled for multiple taxa (Gould, 1979). A few studies have compared the slope of the SARs for the same taxonomic group in different archipelagos, but all of them were based on very small sample sizes. Moreover, they mixed islands with very different geological histories and contemporary ecology, and/or compared completely unrelated archipelagos (see, for example, Sfenthourakis, 1996; Simaiakis *et al.*, 2012). Thus, our study represents the first detailed analysis comparing SARs for different taxa in the same island groups, and that simultaneously tested if a given taxon has different SARs in different island groups.

Our approach can be replicated in other archipelagos benefiting, for example, from the availability of a large number of datasets for Macaronesia. A larger comparative framework could represent a unique opportunity to understand the eco-evolutionary forces regulating the variation of *z* and *c* values across different taxa and archipelagos (see e.g Aranda *et al.*, 2013; Patiño *et al.*, 2014). Moreover, the unique data on the abundance of several arthropod groups now available for the Azores (Borges *et al.,* 2005, 2008; Ribeiro *et al.,* 2005) could be an extremely valuable resource for testing how population abundances affect *z* and *c* values of SARs modelled for different taxa within the same archipelago.

Our findings demonstrate that, despite the wide breadth of literature focusing on the SAR in island systems, rigorous analyses based on robust datasets can still provide new interesting insights. We do not mean our results to be conclusive or groundbreaking, but we do hope that they could keep the debate on these points open.

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SUPPORTING INFORMATION

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

Appendix S1 Values of species richness and island area for the various taxa in both island groups.

BIOSKETCH

Members of the research team are actively engaged in island biogeography, conservation and macroecology, with emphasis on the factors regulating species-area relationships, species-abundance distribution patterns and colonization processes in Mediterranean and Macaronesian archipelagos.

Author contributions: S.F. conceived the ideas and collected the data; S.F., L.D. and G.S. analysed the data. S.F. and P.B. led the writing; all authors contributed in the form of discussions and suggestions, and approved the final manuscript.

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Appendix 1 Data sources. Literature used to assess species richness of land snails, isopods, centipedes, tenebrionids and reptiles on the Tyrrhenian and the Aegean islands.

Values of species richness for the land snails of the Tyrrhenian islands were taken from Giusti (1973, 1976) and Piantelli et al. (1990). For the Aegean Islands, we used values of land snail richness reported by Welter-Schultes & Williams (1999). For the Tyrrhenain isopods, we referred to Gentile & Argano (2005), whereas species richness values for the Aegean islands were taken from Sfenthourakis et al. (1996). Data on centipede species richness were extracted from Simaiakis et al. (2012) for both the Tyrrenian and the Aegean islands. For the tenebrionid beetles of the Tyrrhenian islands we used data reported in Luigioni (1923, 1929), Gridelli (1950), Cerruti (1954), Canzoneri (1972, 1976), Gardini (1976, 1979), D'Antonio & Fimiani (1988), Marcuzzi (1988), Leo (1998), Fattorini & Leo (2000), Lo Cascio et al. (2000), Aliquò et al. (2006), Fattorini (2009a, 2009b, 2010a, 2010b, 2011a, 2011b), plus a few new records from the Pontine Ilsands. For the tenebrionid beetles of the Aegean islands, we used data reported in Fattorini (2002), Soldati & Soldati (2003), Fattorini & Fowles (2005), Hausdorf & Hennig (2005), Trichas (2008), Trichas et al. (2008), Soldati & Kakiopoulos (2010), Kaltsas et al. (2012), Papadopoulou et al. (2009, 2011) and Soldati (2012). For the reptiles of the Tyrrhenian islands we used data reported by Parlanti et al. (1988) updated and supplemented with data reported in Balletto (2005), Sindaco et al. (2006), Cipolla & Nappi (2008) and Fattorini (2010). For the reptiles of the Aegean islands we used distributional data reported in Foufopoulos et al. (1999) supplemented and revised using Angelici et al. (1990), Dimitropoulos (1990), Ionnides et al. (1994), Cattaneo (2001, 2003, 2005, 2006, 2007, 2008, 2009, 2010a, 2010b) and Hausdorf & Hennig (2005).

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TABLES

Table 1. Values of the parameter *c* of the species-area relationships for the same animal groups in the Tyrrhenian and the Aegean islands calculated at different area units. Numbers in parentheses indicate the rank sequence of *c* values from the lowest (1) to the highest (5).

	Area unit (km^2)						
	0.001	0.01	0.1	1	10	100	1000
Tyrrhenian Islands							
Land snails	2.594 (5)	4.355 (5)	7.311 (5)	12.274 (5)	20.606 (5)	34.594 (5)	58.076 (5)
Centipedes	0.748 (1)	1.521 (1)	3.090 (2)	6.281 (2)	12.764 (2)	25.942 (2)	52.723 (2)
Isopods	1.510 (4)	2.761 (4)	5.047 (4)	9.226 (4)	16.866 (4)	30.832 (4)	56.364 (4)
Tenebrionids	1.334 (3)	2.483 (3)	4.624 (3)	8.61 (3)	16.032 (3)	29.854 (3)	55.59 (3)
Reptiles	1.268 (2)	1.754 (2)	2.427 (1)	3.357 (1)	4.645 (1)	6.427 (1)	8.892 (1)
Aegean Islands							
Land snails	2.685 (5)	4.102 (5)	6.266 (5)	9.572 (5)	14.622 (4)	22.336 (4)	34.119 (4)
Centipedes	0.721 (3)	1.262 (3)	2.208 (3)	3.864 (2)	6.761 (2)	11.83 (2)	20.701 (2)
Isopods	2.301 (4)	3.673 (4)	5.861 (4)	9.354 (4)	14.928 (5)	23.823 (5)	38.019 (5)
Tenebrionids	0.637 (2)	1.18 (2)	2.188 (2)	4.055 (3)	7.516 (3)	13.932 (3)	25.823 (3)
Reptiles	0.398 (1)	0.755 (1)	1.432 (1)	2.716 (1)	5.152 (1)	9.772 (1)	18.535 (1)

Table 2. Results (*F*-values) of ANCOVAs for differences in *z* and *c* values of species-area relationships for the same animal groups between the Tyrrhenian and the Aegean islands. *P*-values: *<0.05; ***<0.001.

	F-tests for *z*	*F*-tests for *c*
Land snails	1.626	13.740***
Centipedes	1.619	28.390***
Isopods	2.503	0.374
Tenebrionid beetles	0.0004	18.470***
Reptiles	8.036*	0.226

Table 3. Results (*F*-values) of ANCOVAs for differences in *z* and *c* values of species-area relationships for different animal groups in the Tyrrhenian and Aegean islands. *F*-values above the diagonal refer to differences in *z*, those below the diagonal refer to differences in *c*. *P*-values : *<0.05; **<0.01; ***<0.001.

	Land snails	Centipedes	Isopods	Tenebrionid beetles	Reptiles
Tyrrhenian Islands					
Land snails	-	2.288	0.338	0.702	4.042
Centipedes	16.630***	-	0.679	0.757	9.198**
Isopods	2.329	5.312*	-	0.029	3.696
Tenebrionid beetles	4.282*	4.920*	0.204	-	5.226*
Reptiles	258.000***	56.190***	78.740***	77.480***	-
Aegean Islands					
Land snails	-	3.149	1.146	3.280	16.840***
Centipedes	95.520***	-	1.573	0.154	0.629
Isopods	0.140	116.800***	-	1.982	8.052**
Tenebrionid beetles	28.590***	2.405	28.640***	-	0.025
Reptiles	184.600***	6.512**	182.600***	9.743*	-

FIGURES

Figure 1. Tyrrhenian (a) and Aegean (b) islands. Investigated islands are in black. The inset shows the location of the two study areas in southern Europe.

Figure 2. Regression lines of log-transformed species richness (log *St* for the Tyrrhenian islands – black diamonds, log *Sa* for the Aegean islands – gray squares) against log-transformed island area (log*A*). The following animal groups are modelled: land snails (a), centipedes (b), isopods (c), tenebrionid beetles (d) and reptiles (e). Regression statistics: (a) Tyrrhenian land snails: R^2 = 0.761, $F_{1,16}$ = 50.817, p < 0.0001; Aegean land snails: R^2 = 0.819, $F_{1,63}$ = 285.660, p < 0.0001, n = 18; (b) Tyrrhenian centipedes: R^2 = 0.700, $F_{1,30}$ = 70.034, p < 0.0001; Aegean centipedes: R^2 = 0.546, $F_{1,41}$ = 49.397, p < 0.0001, n = 43; (c) Tyrrhenian isopods: R^2 = 0.577, $F_{1,26}$ = 35.439, p <0 .0001, n = 28; Aegean isopods: R^2 = 0.898, $F_{1,41}$ = 360.049, p < 0.0001, n = 43; (d) Tyrrhenian tenebrionids: R^2 = 0.764, $F_{1,44}$ = 142.160, p < 0.0001, n = 46; Aegean tenebrionids: R^2 = 0.407, $F_{1,30}$ = 20.575, p < 0.0001, n = 32; (e) Tyrrhenian reptiles: R^2 = 0.493, $F_{1,26}$ = 25.251, p < 0.0001; Aegean reptiles: R^2 = 0.751, $F_{1,54}$ = 161.537, n = 56, p < 0.0001. Errors refer to standard errors.

625 Figure 1

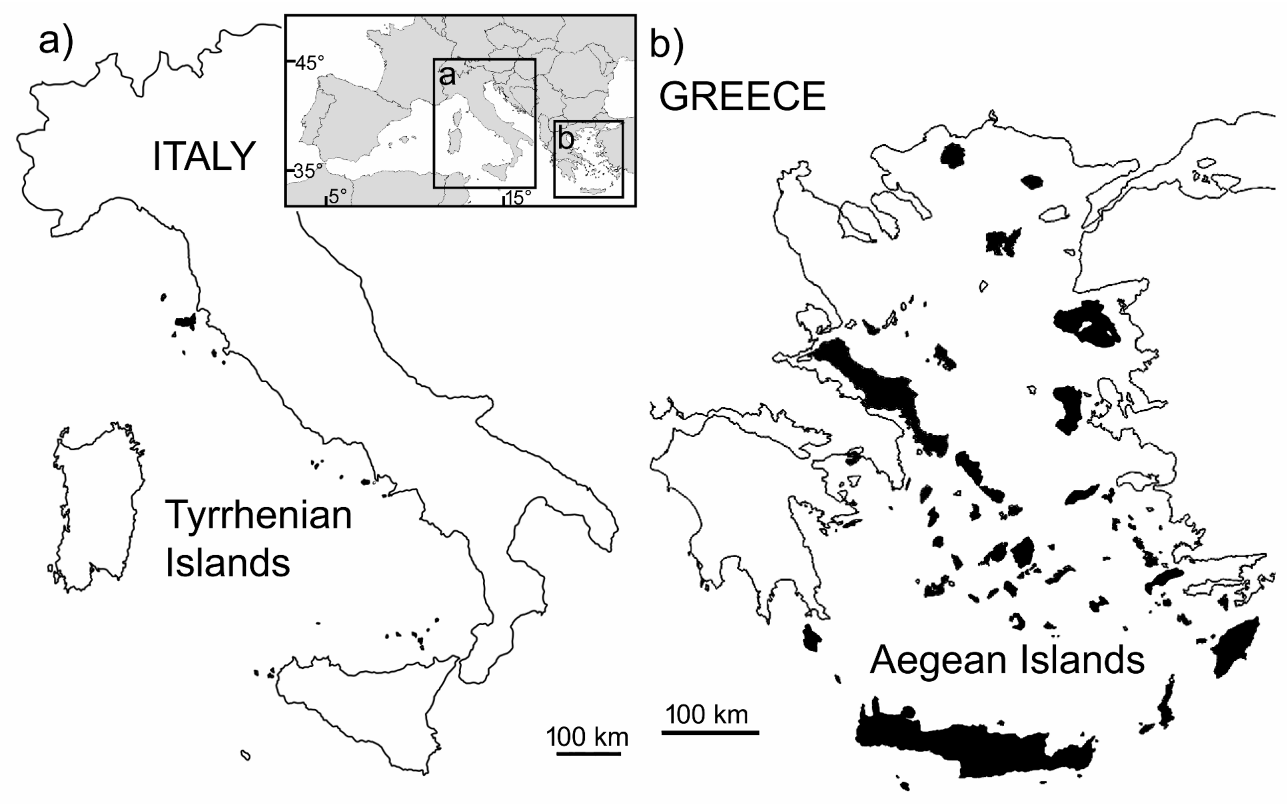

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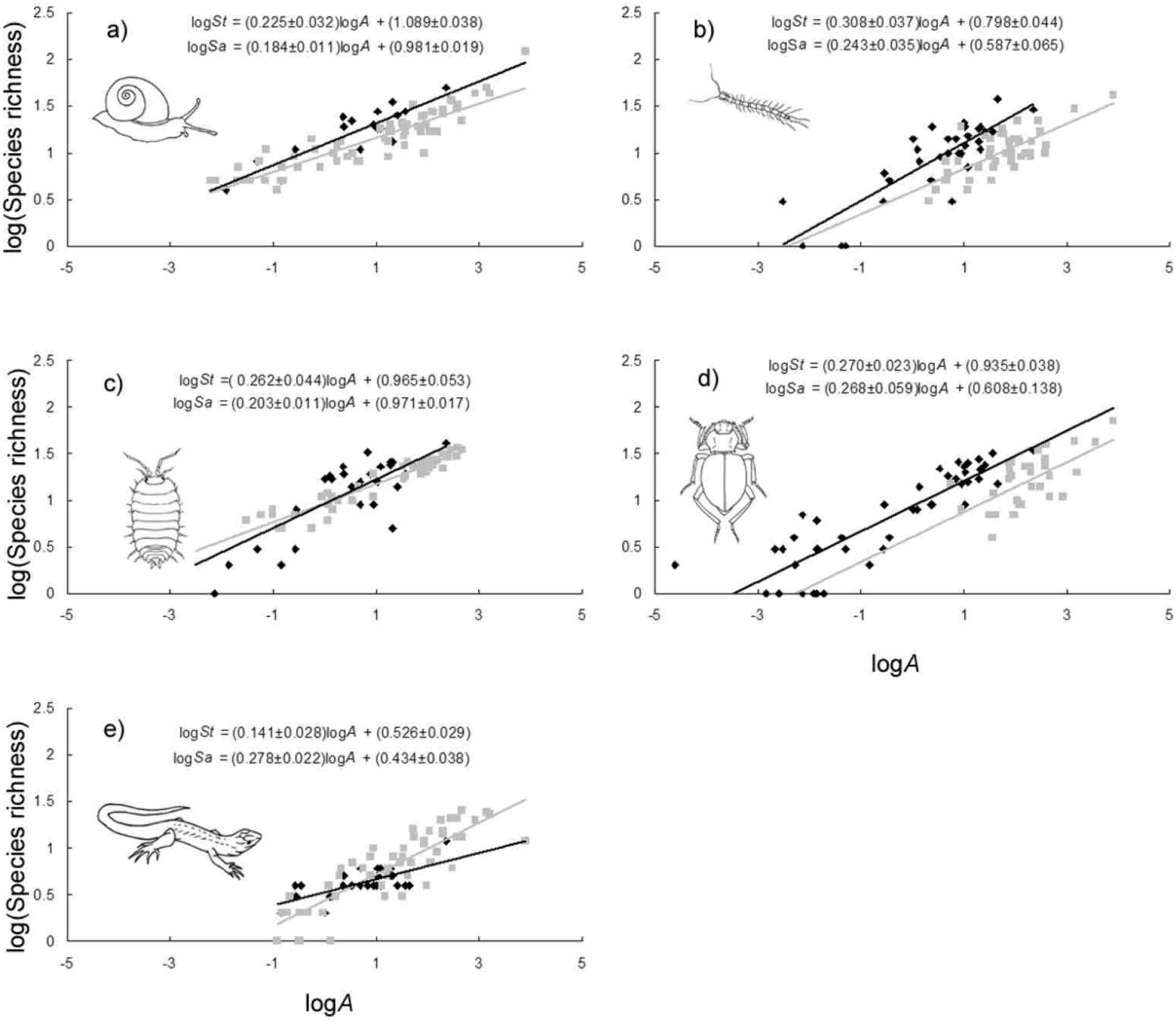
Figure 2


a)
logSt = (0.225±0.032)logA + (1.089±0.038)
logSa = (0.184±0.011)logA + (0.981±0.019)
b)
logSt = (0.308±0.037)logA + (0.798±0.044)
logSa = (0.243±0.035)logA + (0.587±0.065)
c)
logSt =(0.262±0.044)logA + (0.965±0.053)
logSa = (0.203±0.011)logA + (0.971±0.017)
d)
logSt = (0.270±0.023)logA + (0.935±0.038)
logSa = (0.268±0.059)logA + (0.608±0.138)
e)
logSt = (0.141±0.028)logA + (0.526±0.029)
logSa = (0.278±0.022)logA + (0.434±0.038)
log(Species richness)
logA