



# Climatic and biogeographic factors show contrasted effects on continental and volcanic ISARs

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Received: 8 February 2024 / Accepted: 21 April 2024  
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## Abstract

**Aim** The study of islands biotas is fundamental to understand biodiversity patterns and process, both on evolutionary and ecological time scales. This study explores the influence of biogeographic and climatic factors on island species–area relationships (ISARs) in volcanic and continental islands, aiming to detect differences in slopes and intercepts between these island origins.

**Methods** Data from 5049 vegetation plots on 58 Central Mediterranean Sea islands were collected from various sources. Islands were categorized as volcanic or continental based on their geological origin. area, isolation, maximum elevation, eccentricity, mean annual temperature and annual precipitation were calculated for each island. By using a moving window, we created groups of islands, and ISARs were fitted to each group using the Arrhenius power functions. Linear models and a permutation test were employed to examine how ISAR model parameters varied with the above-mentioned variables.

**Results** While ISAR intercept values did not differ between island origins, volcanic islands showed higher ISAR slopes than continental islands. Whereas increasing island isolation and mean annual temperature increased ISAR intercepts on continental islands groups, it decreased on volcanic ones. Increasing annual precipitation decreased ISAR intercept on continental islands groups and increased on volcanic islands groups. Increasing island isolation, eccentricity and mean annual temperature increased the ISAR slope on volcanic islands groups while increasing annual precipitation decreased it. Increasing maximum elevation increased ISAR slope on continental islands groups.

**Main conclusions** Our study provides evidence about the importance of island geological origin in determining the observed ISAR patterns. Biogeographic and climatic factors are pivotal in shaping species richness patterns on islands, exerting varying influences on both volcanic and continental islands.

**Keywords** Biodiversity data · Island biogeography · Island species–area relationship

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## Introduction

Islands are a natural test bed for studying long-term evolutionary processes and formulating ecological theories. As a matter of fact, they constitute unique natural experiments where ecological and evolutionary processes are bounded by clear physical limits, constraining local biotic assemblages (Whittaker et al., 2017). Moreover, islands exhibit a large variability in terms of ecologically and evolutionary relevant features such as geological origin, geographic setting, biogeographic history and isolation through time. Such features have endowed biogeographers, evolutionary biologists and ecologists of a strong attraction and interest for island systems (Fernández-Palacios et al., 2015).

One of the best known patterns in island ecology and biogeography is the island species–area relationship (ISAR hereafter; Rosenzweig, 1995; Whittaker and Fernández-Palacios 2007), which describes the nonlinear increase in species richness with increasing area. Since its formulation by Watson in 1835, it has been widely used to develop and support ecological and biogeographical investigations (Chiarucci et al., 2017; Lomolino, 2000; MacArthur & Wilson, 1967; Preston, 1962; Rosenzweig, 1995; Triantis et al., 2008, 2010). The most widely adopted model to describe the ISAR is the Arrhenius power function ( $S = c \cdot A^z$ ), with easily understandable meaning and interpretable parameters. The interpretation of ISAR parameters and predictions of their patterns started with Preston (1962), who estimated a canonical value of 0.262 for the  $z$  parameter, often reported as slope. He predicted the slope value for true islands to be from 0.2 to 0.4 and that less isolated areas could result in values lower than 0.2. Subsequently, MacArthur and Wilson (1967) complemented Preston's prediction and formulated the equilibrium theory of island biogeography (ETIB), according to which patterns of island species richness could be predicted based on island area and isolation.

Following the ETIB, larger islands are normally characterized by a greater resource base, reducing extinction rates and supporting more species (*i.e.*, higher ISAR intercept) than smaller islands. Conversely, more isolated islands are harder to reach, leading to lower immigration rates and fewer species (*i.e.*, lower ISAR intercept) than less isolated islands. As for ISAR slopes, MacArthur and Wilson (1967) highlighted that values may vary depending on the degree of isolation of smaller islands. When the ISAR is estimated for less isolated islands, the smaller islands of these sets are influenced by higher immigration rates and higher number of transient species that, in turn, inflate their species richness and may lead to flatter slopes. Conversely, in more isolated islands, the immigration rates approach zero, leading to overall lower species richness, hence a steeper slope (Patiño et al., 2014; Rosenzweig, 1995).

The previous studies analyzing ISAR parameters suggest that island isolation is one of the most important factors explaining species richness patterns and is tightly connected to island origin. Indeed, volcanic islands are isolated since their emergence and generally show steeper ISAR slopes and lower ISAR intercepts than continental islands (Kreft et al., 2007; Martin, 1981; Matthews et al., 2015; Patiño et al., 2014; Rosenzweig, 1995; Triantis et al., 2012). Although this is a widely recognized pattern previous work showed contradictory results (*e.g.*, Chiarucci et al., 2021b; Connor & McCoy, 1979; Drakare et al., 2005), and empirical evidence on how ISAR parameters may vary as a function of other biogeographic and ecological factors (*e.g.*, island altitude, island shape, temperature and precipitation) is still scarce. Furthermore, most of the existing literature focuses on animal species (*e.g.*, Rahbek, 1997 and Kalmar & Currie, 2006, for birds; Fattorini et al., 2016, for land snails, isopods, centipedes, tenebrionids and reptiles; Ohyama et al., 2021, for ants and Franzén et al., 2012, for butterflies and moths), with fewer studies analyzing ISAR patterns for plants. In this context, it has been shown that the ISAR slopes are also influenced by climate, with more temperate islands exhibiting higher slopes than colder islands (Chown et al., 1998), while wetter islands showed lower slopes and higher intercepts than drier islands (Iliadou et al., 2014). Nevertheless, to our knowledge, other biogeographically relevant factors such as altitude and island shape were not accounted for when analyzing ISAR of plant species richness (but see Moraldi et al. 2020 for an analysis of nested SARs), nor was the interaction between such factors and island origin. Given the correlation between island area and elevation (Weigelt et al., 2013), islands with higher maximum elevation may exhibit higher ISAR intercepts and lower slopes. As for island shape, rounder islands may exhibit higher ISAR intercepts and lower slopes than more elongated islands, because of the increased core-to-edge ratio in the former. Overall, contrasted patterns between volcanic and continental ISAR as a function of environmental variables are to be expected.

ISARs are also dependent on the sampling scheme used to collect species occurrences (Scheiner, 2003, 2011; Dengler, 2009) and by the adopted fitting approach. It is usually assumed that the figures used for fitting ISARs are based on lists of species which are complete for each area, but this is not always true due to undersampling or undetected rare species (Daru et al., 2018) or due to other factors that trigger different floristic richness across different authors (Bagella et al., 2020). The survey intensity, in terms of number of observed individuals or sampling units, determines the completeness of the list of species detected on an island, and several studies investigated the role of sampling design and scale on diversity estimates on islands (*e.g.*, Chase et al., 2019a, 2019b; Gillespie et al., 2013; Sfenthourakis & Panitsa, 2012). Recently, Chiarucci et al. (2021a) showed that

large vegetation databases represent a reliable source of information to estimate island plant species richness and fit ISARs, even if the resulting parameters are not identical to those obtained using floristic lists. Similarly, vegetation plot data have been used to identify island hotspots and coldspots, as well as information about species rarity (Testolin et al., 2023).

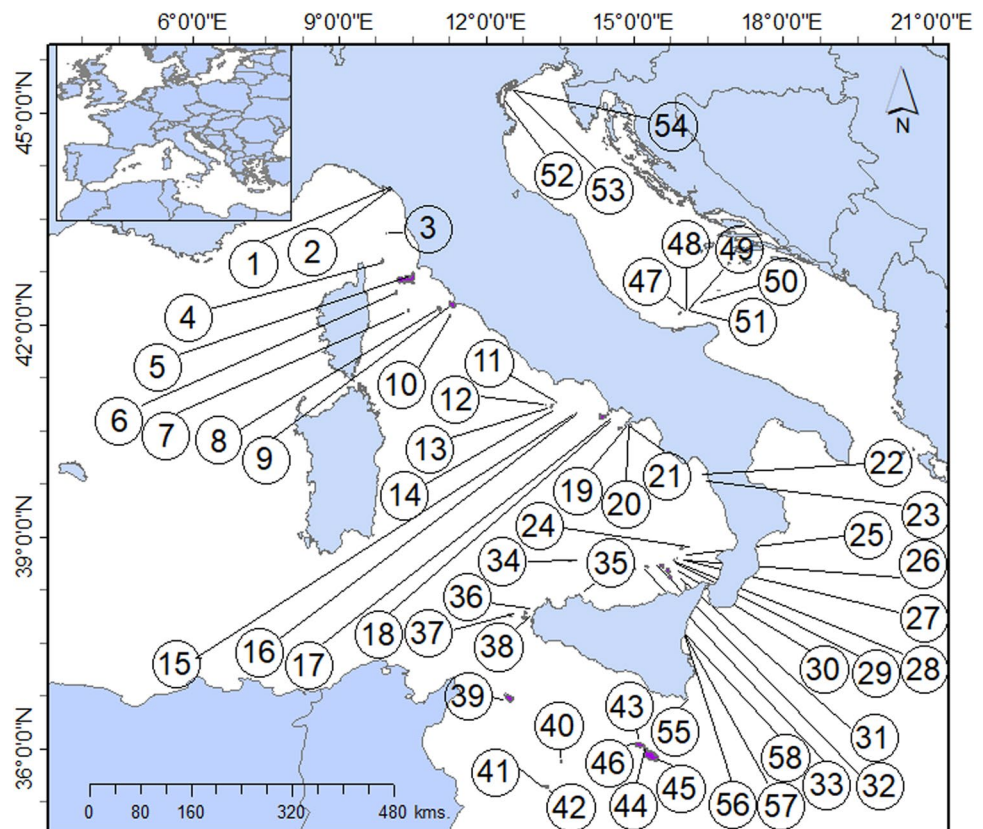
In this study, we focus on island species–area relationship curves (ISARs; type IV curves sensu Scheiner, 2003) applying the framework by Chiarucci et al. (2021a) and fitting the log–log Arrhenius’ power function. We analyzed the ISAR patterns based on plant occurrence data obtained by vegetation plots sampled in 27 islands of volcanic origin and 31 continental islands located in the Central Mediterranean Sea, with the aim to uncover biogeographical patterns related to island features, namely, island area, geographic isolation, elevation, island shape, precipitation, temperature and geological origin. Specifically, our research aims were: 1) to explore differences on ISAR slopes and intercepts between volcanic versus continental islands and 2) to detect ISAR slopes and intercepts changes along biogeographic and climatic gradients on volcanic versus continental islands.

## Methods

### Study area

The Mediterranean Sea covers an approximate area of  $2.51 \times 10^6$  km<sup>2</sup>; it is enclosed between the African and Eurasian continents and connected to the Atlantic Ocean across the strait of Gibraltar. A large number of islands and archipelagos with outstanding biodiversity and endemism are present in the basin, with the exact number of islands and islets ranging between 5000 (Vogiatzakis et al., 2016) and 10,000 (Médail, 2022; Sfenthourakis & Triantis, 2017), depending on definitions and area thresholds. The MEDIS geodatabase reported that the islands larger than 10,000 m<sup>2</sup> in the Mediterranean basin are 2214 (Santi et al., 2024). Yet, only 157 of these islands are larger than 10 km<sup>2</sup> (Médail, 2017). The basin experienced long-term anthropogenic changes started by ancient civilizations, triggering ecosystem transformation, biotic homogenization and biodiversity loss (Médail, 2017). From the conservation perspective, this area has been considered one of the most important global hotspots of biodiversity (Médail, 2022; Médail & Quézel, 1997; Myers et al., 2000). Our study system consists of a set of 58 islands located in the Central Mediterranean Sea, around peninsular Italy but not exclusively Italian (Fig. 1).

**Fig. 1** Map of the study area. The 58 islands included in the analyses are represented by progressive numbering. Islands represent 12 archipelagos and six solitary islands: Spezzino Archipelago (1 and 2), Tuscan Archipelago (3–10), Pontine Archipelago (11–16), Campanian Archipelago (17–19), Li Galli Islands (20 and 21), Isola di Cirella (22), Dino Island (23), Aeolian Archipelago (24–33), Ustica Island (34), Isola delle Femmine (35), Egadi Islands (36–38), Pantelleria Island (39), Pelagie Islands (40 and 42), Maltese Archipelago (43–46), Tremiti Islands (47–51), Venice Archipelago (52–54), Isola di Capo Passero (55) and Cyclops Archipelago (56–58). Detailed island features are given in Appendix S1.1



## Data assembly

We obtained island species lists based on the plant occurrence data retrieved from vegetation plot data stored in the database AMS VegBank (Alessi et al., 2022) which contains published and unpublished vegetation surveys dataset (list of data sources in Appendix S2). The plots were sampled between 1950 and 2022, mostly for descriptive purposes, using opportunistically located units, the Braun–Blanquet cover scale and heterogeneous grain sizes (from less than 1 to 900 m<sup>2</sup>). Plot data have been recorded over a quite long time period, introducing some possible bias. However, this is the only possible way to obtain list of species for large areas lacking dedicated intense surveys, and it is normally adopted in biogeographical studies (e.g., Cao Pinna et al., 2021; Testolin et al., 2021). Taxa were standardized at species level, according to the Global Biodiversity Information Facility (GBIF) taxonomic backbone by means of the “taxadb” package (Norman et al., 2020).

## Data analyses

### Islands species richness estimation

For each island, we estimated the total number of vascular plant species using the Chao2 estimator on the basis of plot data. Such estimator derives from the Cauchy–Schwarz inequality, which has been applied to obtain a non-parametric estimation of species richness of an assemblage based on species incidence (detection/non-detection) data in multiple sampling units. The results are nearly unbiased when very rare/infrequent species have approximately the same detection probabilities (Chao & Colwell, 2017). As most of the other nonparametric estimators of species richness, Chao2 underestimates the total number of species in real communities and can be considered as a lower bound estimator (see, e.g., Xu et al., 2012; Chiarucci et al., 2018). The Chao2 estimator was calculated using the iNext package (version 3.0.0) in *R* (Hsieh et al., 2022).

### Island features

For each island, we obtained data about surface area, geographical isolation, geological origin, maximum elevation, mean annual temperature, annual precipitation and shape eccentricity. The latter, calculated as the ratio between the longest and the shortest sides of the smallest rectangle enclosing the island, is a measure of island shape. Geographic isolation was calculated as the minimum distance to the mainland and maximum elevation as the elevation of the highest point of the island. Mean annual temperature and annual precipitation were derived from CHELSA 2.1 (Karger et al., 2017, 2018) as the mean of the values

extracted within each island polygon. The geological origin was used to divide the total data ( $n = 58$  islands) into volcanic ( $n = 27$ ) and continental ( $n = 31$ ) islands.

Variables with a skewed distribution were transformed as follows: Island area, species richness and maximum elevation were  $\log_{10}$  transformed; geographic isolation and precipitation were root squared transformed; eccentricity was transformed to its inverse and mean annual temperature was not transformed. We then analyzed the differences between volcanic and continental islands as follows: For area, geographical isolation, eccentricity and annual precipitation, we employed two-sample *t*-tests, whereas for mean annual temperature and maximum elevation, we used two-sample Wilcoxon rank-sum tests due to the violation of normality assumptions.

### Fitting island species–area relationship

We calculated ISARs separately for volcanic and continental islands by fitting the Arrhenius power function in an log–log transformed space:

$$\log_{10}(S) = c + z \log_{10}(A) \quad (1)$$

where “*S*” is species richness, “*A*” island area and “*c*” and “*z*” are two fitted parameters.

Then, we investigated how the *c* (intercept) and *z* (slope) parameters of the fitted models vary as a function of the above-mentioned variables by performing an iterative analysis (moving window) to highlight the variation of ISAR parameters with increasing biogeographic and climatic gradients. For this purpose, we systematically analyzed two datasets, defined by the geological origin of the islands (continental,  $n = 31$ ; and volcanic,  $n = 27$ ). The moving window approach involved the arrangement of the islands in ascending order based on the target variable (e.g., area and island isolation). At each step, a group of nine islands was selected, representing those with the minimum values of the biogeographic or climatic variable under consideration at that specific point in the process. Subsequently, we calculated the mean of the target variable and fitted an ISAR model to this island group. In the following step, another set of nine islands is chosen. This selection excludes the first two islands from the previous iteration and introduces two new islands. We obtained 10 and 12 ISAR models fitted for volcanic and continental islands, respectively, as a function of each biogeographic and climatic variable. To our first aim, we performed a permutation test due the dependence of the sample. In this context, we evidenced whether slopes and intercept were significantly different between continental and volcanic islands. To our second aim, we fitted simple linear models to the resulting ISAR intercepts and slopes as a function of each biogeographic and climatic variable

to evidence significant tendencies. All of our analyses were performed using *R* (R Core Team, 2022).

## Results

### Island features and plant species richness

The 58 islands included in the study have different geologic origins, 27 of them being volcanic and 31 being continental or land-bridge islands. Details about each island are given in Supporting Information Appendix S1.1. Cavallino-Treporti is the northernmost island ( $45.46^\circ N$  latitude, 54 in Fig. 1) whereas Isola dei Conigli is the southernmost island ( $35.51^\circ N$  latitude, 42 in Fig. 1). The island located nearest to the mainland is Monte Argentario (connected to the mainland by two strips of sand, so 0 km away; 9 in Fig. 1), whereas the farthest island from the continent is Linosa Island (162 and 173 km away from Tunisia and Sicily, respectively; 40 in Fig. 1). Malta is the largest island with  $245.8 \text{ km}^2$  (45 in Fig. 1), whereas Faraglione di Mezzo (56 in Fig. 1; Cyclops Archipelago) is the smallest with just  $0.0004 \text{ km}^2$ . Despite a huge range of variation for all the considered biogeographic and climatic variables, the volcanic and continental islands did not show statistically significant differences for all the variables, except for mean annual temperature, which resulted slightly higher in volcanic than in continental islands (see Appendix S1.3 for details).

In the 5717 vegetation plots, we assembled in the 58 islands, we collected 81,093 occurrence records for a cumulative number of 1604 vascular plant species (see Appendix S1.1 and Appendix S1.2 in Supporting Information). The number of species recorded per island averaged 156

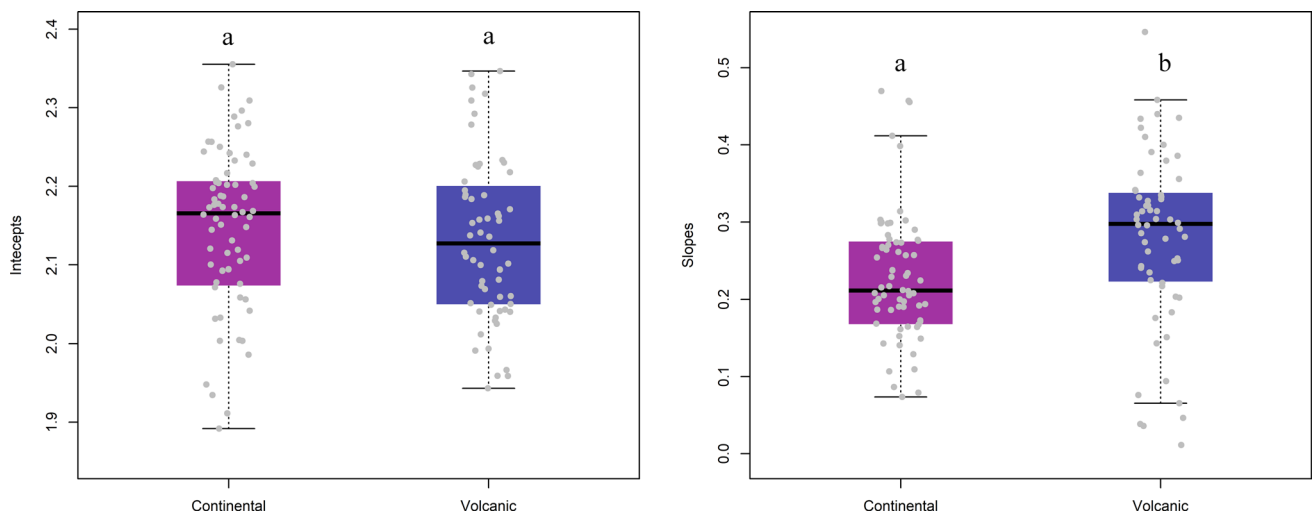
and ranged from a minimum of 10 species in Faraglione di Mezzo to a maximum of 524 species in Elba, while the estimated number of species per islands averaged 195 and ranged from 12 in Faraglione di Mezzo to a maximum of 603 species in Elba (Appendix S1.2).

### ISAR parameters between volcanic and continental islands

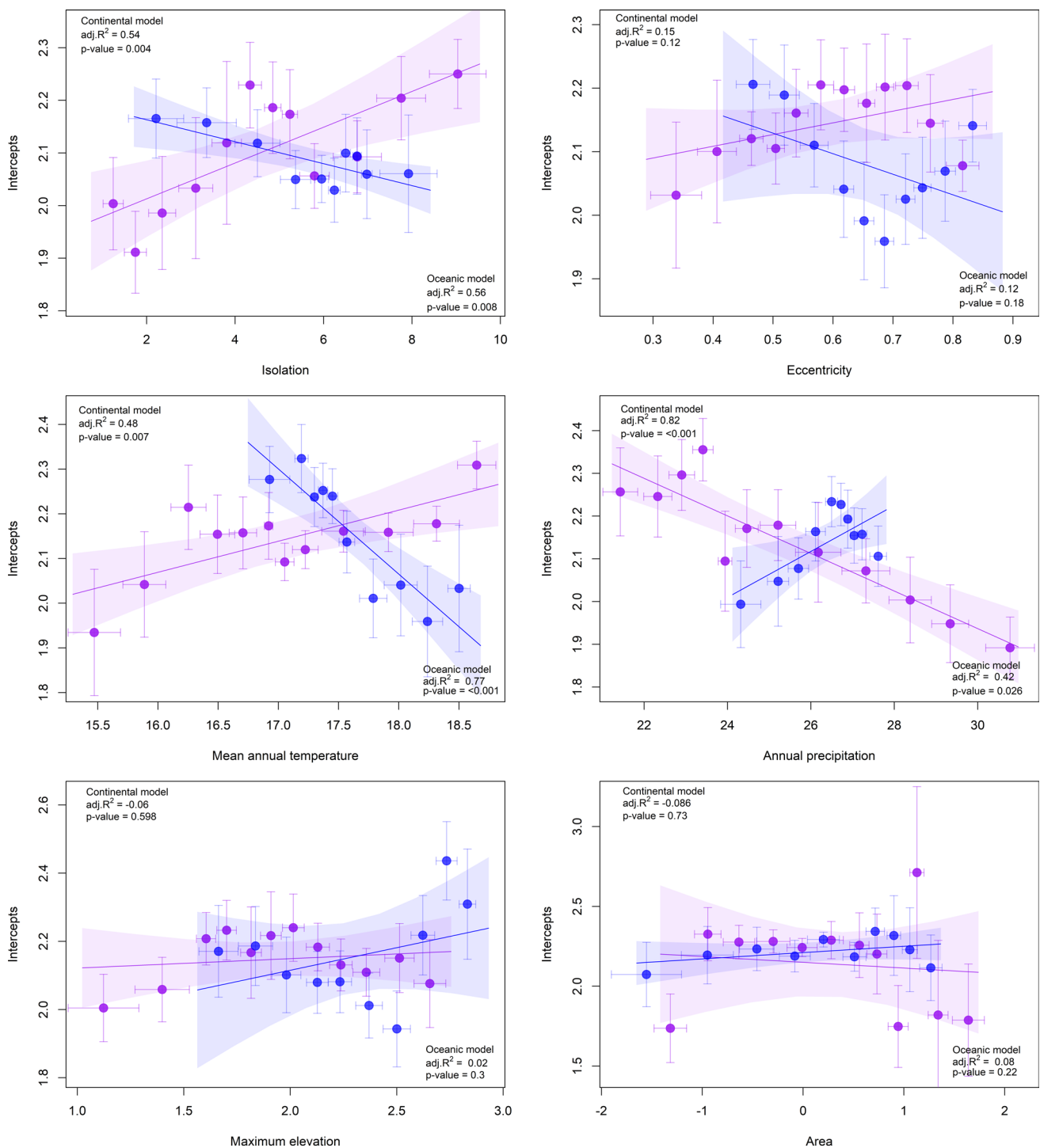
Overall, ISAR intercepts did not show a statistically different value between volcanic and continental islands ( $p$ -value  $> 0.05$ ; Fig. 2). Contrary, the slope of the ISAR was significantly higher for volcanic than for continental islands ( $p$ -values  $< 0.05$ ; Fig. 2).

### Patterns of ISAR parameter variations on different island origins throughout biogeographic and climatic variables

We evidenced significant variation in ISAR intercepts between volcanic and continental islands along gradients of isolation, mean annual temperature and annual precipitation. Specifically, intercepts significantly decreased for volcanic islands and significantly increased for continental islands with increasing isolation ( $p$ -value = 0.008 and 0.004 for volcanic and continental model, respectively; Fig. 3a) and mean annual temperature ( $p$ -value  $< 0.001$  and 0.004 for volcanic and continental model, respectively; Fig. 3c). On the other hand, intercepts significantly increased for volcanic islands and significantly decreased for continental islands with increasing annual precipitation ( $p$ -value  $< 0.021$  and  $< 0.001$  for volcanic and continental model, respectively; Fig. 3d). We did not detect significant



**Fig. 2** ISAR intercept and slope results based on the Arrhenius model in a log–log space ( $\log S = \log(c) + zA$ ) calculated for continental ( $n = 31$ ) and volcanic islands ( $n = 27$ ). Different letters among island origins **a**, **b** show significant differences ( $p$ -value  $< 0.05$ )



**Fig. 3** ISAR intercepts resulted for continental (violet) and volcanic islands (blue) in a gradient of **a** island isolation, **b** eccentricity, **c** mean annual temperature, **d** annual precipitation, **e** maximum elevation and **f** island area. Blue circles and regression lines correspond

to volcanic islands. Purple circles and regression lines correspond to continental islands. Bands represent the 95% confidence interval for volcanic and continental linear regressions. Error bars represent the variable standard errors

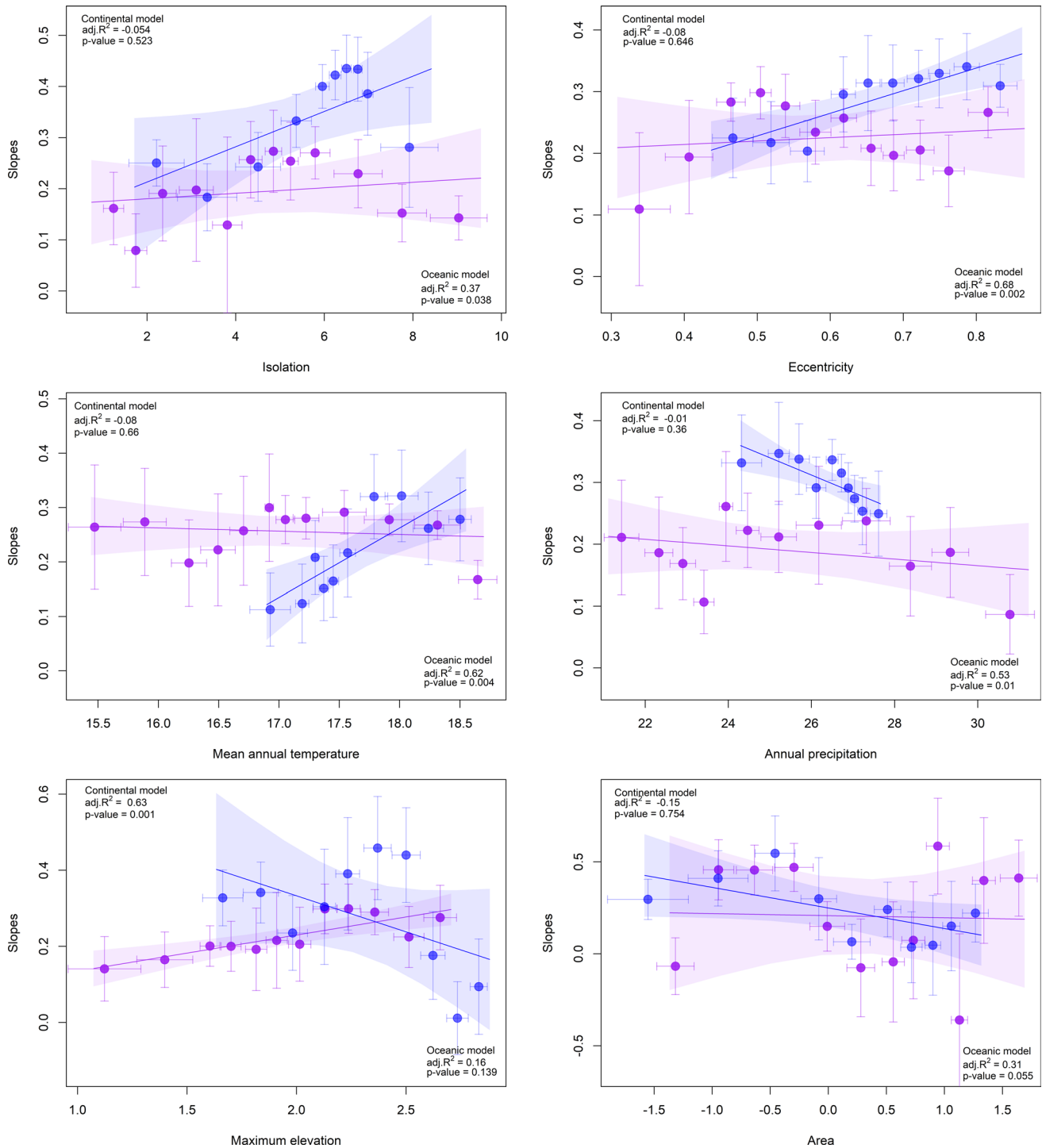
intercept variation on volcanic and continental islands for eccentricity, maximum elevation and area variables.

We detected significant contrasted variation of the slopes between volcanic and continental islands in the

majority of the environmental gradients. While the slope on volcanic islands significantly increased with increasing isolation ( $p$ -value = 0.038; Fig. 4a), eccentricity ( $p$ -value = 0.002; Fig. 4b) and mean annual temperature

( $p$ -value = 0.032; Fig. 4c), and decreased with annual precipitation ( $p$ -value = 0.01; Fig. 4d), the slopes of

continental islands significantly increased with increased maximum elevation ( $p$ -value = 0.001; Fig. 4e).



**Fig. 4** ISAR slopes resulted for continental (violet) and volcanic islands (blue) in a gradient of **a** island isolation, **b** eccentricity, **c** mean annual temperature, **d** annual precipitation and **e** maximum elevation and island area. Blue circles and regression lines correspond

to volcanic islands. Purple circles and regression lines correspond to continental islands. Bands represent the 95% confidence interval for volcanic and continental linear regressions. Error bars represent the variable standard errors

## Discussion

Several hypotheses have been tested seeking a deeper biogeographic meaning of the ISAR slopes and intercepts (Matthews et al., 2021; Triantis et al., 2012). By using 81,093 occurrence data on 1604 vascular plant species in 5717 vegetation plots from 58 Mediterranean islands, we confirmed the hypothesis that ISAR slope is higher in volcanic than continental islands (Kreft et al., 2007; Matthews et al., 2015; Patiño et al., 2014; Triantis et al., 2012), while the expected lower intercept in volcanic than continental islands was not supported by statistical evidence. We also confirmed a contrasted response of the ISAR slope and intercept values for several biogeographic and climatic gradients on volcanic versus continental islands. In this context, we showed that ISAR slopes were more influenced by biogeographic and climate variables on volcanic islands than on continental islands while ISAR intercepts were inversely influenced by island isolation, annual precipitation and mean annual temperature on both islands origins.

It has been described that steep SAR slopes could be generated by speciation-dominated systems, such as island systems (McArthur and Wilson 1967; Brown, 1971). While the dominance of speciation processes can be true in oceanic islands, situated in the middle of the oceans and very distant from the continents, this is hardly the case of volcanic islands in the Mediterranean basin, which are quite close to the coastline (range of distances 0.15–163.7 km) and have experienced periods with even lower isolation during the Quaternary sea level variations (see Whittaker and Fernández-Palacios et al. 2007). The smaller relevance of speciation processes in controlling species diversity and ISARs in Mediterranean volcanic islands is supported by the lower degree of endemism in these islands compared to real oceanic islands, such as Juan Fernández, Canarys, Hawaii or Galápagos (Caujapé-Castells et al., 2010; Vargas et al., 2014).

Differences in island isolation and geological origin have been described as the main factors that influence steeper ISAR slopes on oceanic than on continental islands (Kreft et al., 2007; Matthews et al., 2015; Patiño et al., 2014; Triantis et al., 2012). In the case of the Mediterranean volcanic islands, the geographic isolation is limited if compared with real oceanic islands, but the lack of pre-existing species pool at the moment of islands formation is certainly true, and while the speciation process can be limited because of the closeness of species pools and the easy immigration, the colonization process is likely lower in volcanic than in continental islands. In fact, volcanic islands are characterized by a lower immigration but also by lower colonization rates, since few species of those

that arrive on volcanic islands survive and establish vital populations (MacArthur & Wilson, 1967). This also has the consequence of relaxing species competition, triggering adaptive radiations and species turnover (Patiño et al., 2014; Triantis et al., 2012). In this context, even in a frame of lower speciation in comparison with real oceanic islands, our results were in line with our expectations evidencing higher slopes for volcanic than for continental islands and increasing slopes with increasing isolation.

The ISAR intercepts, which can be interpreted as the number of species per area unit, is expected to be lower in volcanic than in continental islands, as well as with increasing isolation (MacArthur & Wilson, 1967). Yet, we did not evidence a significant difference between volcanic and continental islands. Moreover, the ISAR intercept increased with increasing isolation on continental islands. We hypothesized that these increases could be determined by the interplay of two processes: (1) area is positively correlated with island isolation allowing more species on continental islands with increasing isolation and/or (2) isolated islands host more endemic species formed from adaptive radiations or genetic drifts (Stuessy et al., 2006; Takayama et al., 2018). The first statement is supported by the significant positive correlation between the mean area and mean isolation of the continental islands grouped on each ISAR model (see Appendix S1.4 for further details). As for the second statement, it has been described that isolation and island area (also island elevation, positive and significantly correlated) influence speciation rates that combined with relaxed competition pressure could trigger adaptive radiations on islands (Givnish, 2010) generating, by consequence, higher ISAR intercepts. Nevertheless, this last claim requires a deeper analysis of our study area. In contrast, ISAR intercepts on volcanic islands were decreasing with increasing isolation, in line with our expectation and with the previous studies (Matthews et al., 2015; Triantis et al., 2012).

We expected higher slopes for round islands because they could contain greater habitat diversity than elongated islands (Blouin & Connor, 1985). In contrast with elongated islands, round ones could contain wider environmental gradients given by their diametric form and differences on sea, winds and sun exposure. We also expected this last pattern to be more pronounced on volcanic islands because they generally contained greater habitat diversity than continental islands (Whittaker & Fernández-Palacios, 2007). We rejected in part our hypothesis because only ISAR slopes on volcanic islands responded to the influence of eccentricity evidencing the opposite expected pattern, *i.e.*, higher slopes with increasing eccentricity. However, this trend could be influenced by the isolation effect. As we showed, the mean eccentricities were positively correlated to the mean isolations resulting from the analyzed groups of islands on the sensitivity analysis (see Appendix S1.5 for further details). Other studies have

described the challenges encountered when analyzing patterns of island shapes because these could be obscured by other variables that influence species richness such as isolation and habitat heterogeneity (Blouin & Connor, 1985). Despite species richness trends have been assessed by at least four different island shape measures finding contrasting patterns, the analysis has been carried out on mixed islands origin (Blouin & Connor, 1985), and these could have hidden the trends for strictly volcanic and/or continental islands (Cáceres-Polgrossi et al., 2023). Thus, our results suggest the need for further analysis, for example, on strictly volcanic islands for a deeper understanding of this trend.

According to Kreft et al. (2007), harsh climates may constrain the number of potential immigrant species that are able to tolerate the specific conditions and are thus able to successfully colonize an island. So, the intercepts could decrease, and the slopes increase when climatic conditions are unfavorable. Conversely, when climate is favorable, ISAR intercepts could increase, and the slopes decrease. In our study, we evidenced different dynamics of species richness between continental and volcanic islands along climate gradients. Following the hypothesis of Kreft et al. (2007), we could evidence that while vascular plant species richness on volcanic islands tends to decrease with increasing mean annual temperature and decreasing annual precipitation, we observed the opposite pattern on continental islands. Additionally, we attributed the absence of slope variation on continental islands to the fact that most plant species arrived when continental islands were connected to the mainland (Whittaker & Fernández-Palacios, 2007), so no climatic barriers had to be overcome. Although these interpretations need to be tested in depth and in a more global perspective, our study contributed to the existing knowledge gap on ISAR parameters variation as a function of climate variables.

Finally, we hypothesized that the general non-significant trends evidenced for the ISAR slopes on continental islands are suggesting a low influence of immigration and colonization dynamics in the majority of these islands (Brown, 1971). It would be interesting to investigate if continental islands often show difficulty in reflecting patterns on ISAR slopes. However, the significantly higher slopes with increasing island elevation on continental islands are also suggesting that islands with higher elevation presented some grade of speciation dynamics in their flora. For example, Illiadou et al. (2014) evidenced steeper slopes for Aegean islands that have higher elevations and a larger proportion of in situ speciation than Ionian Islands. In this context, our results suggest that some biogeographic variables could influence stronger ETIB dynamics on volcanic than on continental islands. At the same time, some biogeographic variables other than area and isolation (e.g., elevation, temperature and precipitation) could exclusively influence ETIB dynamics and that these could be easily evidenced by means

of their ISAR even on systems with lower ETIB dynamics (e.g., continental islands of this study).

## Conclusions

Using a large amount of vegetation plot data sampled on 58 Mediterranean islands, our study disentangled the contribution of different biogeographic and climatic variables on vascular plant species richness dynamics in continental and volcanic islands. Overall, ISARs reflected higher immigration and colonization dynamics for volcanic than for continental islands. Further research is needed to confirm and expand upon these findings in a broader context.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s42974-024-00195-5>.

**Acknowledgements** We would like to thank Marcelino J. Del Arco Aguilar for his kindness and expertise in the field of phytosociology. His invaluable insights and mentorship have greatly enriched our understanding. We would like to express our gratitude to the Carolina Foundation for providing opportunities for students from Central and South America to study in Spain. AC and RT were funded by the European Union—NextGenerationEU, under the National Recovery and Resilience Plan (NRRP), Project title “National Biodiversity Future Center -NBFC” (project code CN\_00000033) CUP J33C22001190001. Finally, we thank to the ERASMUS program for facilitating and promoting European cooperation and knowledge exchange.

**Author's contribution** L.C.-P. and A.C. conceived the ideas; L.C.-P., A.C., P.Z., V.B., F.B. and M.C. collected the data; L.C.-P. and R.T. analyzed the data and L.C.-P. and A.C. led the writing, with major contributions by J.M.F.-P. and R.T. All authors checked, improved and approved the manuscript.

**Funding** Open access funding provided by Alma Mater Studiorum - Università di Bologna within the CRUI-CARE Agreement.

## Declarations

**Conflict of interest** The authors have no competing interests to declare that are relevant to the content of this article. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript. The authors have no financial or proprietary interests in any material discussed in this article.

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