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Species–area relationship and small-island effect of vascular plant diversity in a young volcanic archipelago

Alessandro Chiarucci¹ | Riccardo Guarino² | Salvatore Pasta³ | Alfonso La Rosa⁴ |
Pietro Lo Cascio⁵ | Frédéric Médail⁶ | Daniel Pavon⁶ | José María Fernández-Palacios⁷ |
Piero Zannini¹

¹BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum, University of Bologna, Bologna, Italy

²Department STEBICEF, University of Palermo, Palermo, Italy

³Institute of Biosciences and Bioresources (IBBR), National Research Council of Italy (CNR), Unit of Palermo, Palermo, Italy

⁴Cooperativa Silene, Palermo, Italy

⁵Associazione Nesos, Lipari, Messina, Italy

⁶Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE), Aix Marseille Univ, CNRS, IRD, Avignon Univ. Technopôle de l'Arbois-Méditerranée, Aix-en-Provence Cedex 4, France

⁷Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna (ULL), La Laguna, Spain

Correspondence

Riccardo Guarino, Department STEBICEF, University of Palermo, Via Archirafi, 38 - 90123 Palermo, Italy.
Email: riccardo.guarino@unipa.it

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Abstract

Aims: Aeolian islands form an active volcanic archipelago. By using updated vascular plant checklists for islands and islets, we tested four hypotheses: (i) Island species–area relationship (ISAR) of alien species has lower *c*- and higher *z*-values than native species, (ii) islands with active volcanoes have lower species richness than expected for native and alien species, (iii) ISAR of native species shows lower *c*- and higher *z*-values than ISARs of Mediterranean land bridge archipelagos and (iv) species richness of smaller islets is independent of area.

Location: Aeolian Archipelago, Mediterranean Basin.

Taxon: Vascular plants, identified and named according to the Flora of Italy (Pignatti et al., 2017–2019).

Methods: Checklists of native and alien plant species were obtained for eight islands and 24 islets. ISARs were fitted by the Arrhenius power function ($S = c \cdot A^z$) and used to test the first two hypotheses. The third hypothesis was tested by comparing ISAR of Aeolian Archipelago to those from other central and eastern Mediterranean archipelagos. The fourth hypothesis was tested by fitting models defining the presence and limit of the small-island effect.

Results: The checklists included 894 species—749 native and 145 alien. ISARs fitted well for native and alien species and resulted in typical values of *c* and *z* parameters. The first and second hypotheses were supported by model fitting. The third hypothesis was not confirmed by the comparison of the ISAR of the Aeolian Archipelago with other archipelagos. The small-island effect predicted by the fourth hypothesis was supported using *S* versus *LogA* for both native and alien species, while for native species it was supported also using the log transformation of the Arrhenius model.

Main conclusions: We reported a first comprehensive analysis of plant species richness in the unique Aeolian Archipelago, verifying typical ISARs, no peculiarity with respect to land bridge archipelagos and a somewhat unclear signal for the small-island effect.

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KEYWORDS

biodiversity, island biogeography, Mediterranean, species richness, species–area relationships, vascular flora

1 | INTRODUCTION

Because of the environmental constraints shaping their biotic assemblages, islands and archipelagos are considered perfect model systems to investigate ecological and biogeographical patterns and processes (Whittaker & Fernández-Palacios, 2007; Whittaker et al., 2017), specifically for species colonisation and extinction (MacArthur & Wilson, 1963), species–environment interactions and evolutionary processes (Borregaard et al., 2016), and community assembly rules (Schrader, 2020). One of the fundamental patterns in ecology and biogeography that has been investigated using islands as model systems is the species–area relationship (Matthews et al., 2019). Island species–area relationships (henceforth: ISARs) have been used to understand island-related processes (Abbott, 1983) and to test theoretical topics such as the equilibrium theory of island biogeography (MacArthur & Wilson, 1967).

Several models have been used to investigate ISARs (Triantis et al., 2012), considering different numbers of parameters and different variable transformations (Yu et al., 2020). Different types of SARs have been discussed from theoretical and empirical points of view, while also focusing on the prevalent observed patterns (for a review, see Harte, 2011; Storch, 2016, and references therein). The debate on how to identify the best fitting model is still lively and has never come to a unique conclusion, but there is large agreement across comparative studies in identifying the Arrhenius' power law as the most frequently best fitting model for island systems (Matthews et al., 2016; Triantis et al., 2012). In addition, the use of this model is also supported by the capacity to perfectly include its fitted parameters into ecological and biogeographical frameworks (Martin & Goldenfeld, 2006; Rosenzweig, 1995; Triantis et al., 2012). According to the Arrhenius' power law ($S = c \cdot A^z$), S is the number of species present on the island, A is the area of the island, while c and z are empirically determined parameters, varying across archipelagos and expressing the number of species per unit area (c) and the increment of the number of species along with the increase in island area (z) (Arrhenius, 1921). The value of the c and z parameters are largely dependent on the isolation degree, with islands having lower c and higher z than continental units (Rosenzweig, 2004), and oceanic remote archipelagos having lower c and higher z than continental and close archipelagos (Connor & McCoy, 1979; Triantis et al., 2012). Additionally, small and isolated islands imply a low probability of being colonised by new species and an even lower chance of survival for newcomers, thus increasing the z -value compared to equally isolated but larger islands (Fattorini et al., 2017).

The relationship between species richness and island area often disappears below a certain size (breakpoint), with the consequence that the number of species varies independently of island size (Lomolino, 2000; Triantis et al., 2006). This stochastic phenomenon,

known as *small-island effect* (henceforth: SIE), was first applied by Woodroffe (1986), but has already been hypothesised in earlier contributions (MacArthur & Wilson, 1967; Niering, 1963; Whitehead & Jones, 1969). As SIE is considered a widespread phenomenon (Whittaker & Fernández-Palacios, 2007), the investigation on SIE has been included with increasing frequency in the analysis of ISARs (Dengler, 2010; Gao & Perry, 2016; Schrader, 2020). Island age may also influence the species richness of an island and the structure of insular communities, as predicted by the general dynamic theory of oceanic island biogeography (Whittaker et al., 2008). Young islands offer more empty niches (Simberloff & Wilson, 1969) and patterns of species co-occurrence become progressively more influenced by biotic interactions as island age increases (Badano et al., 2005). This is particularly true for volcanic archipelagos, which often are a mosaic of differently aged habitat fragments, periodically disturbed and eventually destroyed by eruptive events, if volcanoes are still active. Species diversity on volcanic islands tends to increase with island age till a period of geological maturity is reached, and then starts to decrease after the cessation of volcanic activity, when island erosion or subsidence take over (Whittaker et al., 2008). Substantially, older and inactive volcanic islands are expected to be richer in species, but if too old they undergo a long-term process of community disassembly or 'relaxation' (Diamond, 1972) in which extinction is the dominant population process.

Generally, since both c - and z -values largely depend on the isolation and age of a given insular system, these two parameters are expected to differ between native and alien species, with the ISAR for alien species having lower c - but higher z -values than that for native species, since the insular systems have a shorter connection history, and thus are more isolated, for the alien species (Blackburn et al., 2016). However, some exceptions may occur, because for many alien species, connectivity is generally associated with human movement rather than geographical proximity (Russell et al., 2017) and the habitat suitability for alien species is far from being homogeneous (Guarino et al., 2021).

The study of ISARs has been particularly developed for oceanic archipelagos, which have never been connected to the mainland, with the consequence that their biotas have been exclusively assembled through long-distance dispersal and in situ evolutionary processes. However, only few oceanic archipelagos significantly contributed to the development of biogeographical and ecological theories, the most famous ones being Hawaii, Galápagos, Canary Islands and Azores (see e.g. Borregaard et al., 2016; Chiarucci et al., 2011; Fernández-Palacios et al., 2011; Otto et al., 2020; Price, 2004; Schaefer et al., 2011; Whittaker et al., 2008). All these model systems are located in oceanic areas and issue from the volcanic activity of tectonic hotspots (Whittaker et al., 2008). On the other hand, there is a much higher number of islands and archipelagos that are

continental fragments or continental shelf islands, which became islands because of tectonic deformation and sea level changes (Whittaker & Fernández-Palacios, 2007). This is the case for most of the thousands of islands occurring in the Mediterranean Basin, which host a relevant part of the regional biodiversity (Médail, 2017, 2021; Vogiatzakis et al., 2016).

Few Mediterranean islands are volcanic, and very few archipelagos are composed exclusively by volcanic islands. This is the case of the Santorini-Christiana and Milos in the South Aegean Volcanic Arc, the Columbretes islands in eastern Spain, the small Chafarinas island group north of Morocco and the Aeolian Archipelago. The latter archipelago is the largest in terms of area and is very famous for its magnificent volcanic activity, but it is poorly recognised in the modern biogeographical literature. This is especially true for plants, while for animal taxa, some quantitative studies have been already published (Fattorini, 2009, 2010, 2011; Schär et al., 2020; Vodă et al., 2016). To our knowledge, the only paper using plant diversity data from the Aeolian Archipelago to explore its biogeographical patterns is a study on the general dynamic model (GDM) of island biogeography, aiming to test the role of island age and area as predictors of species richness (Carey et al., 2020). By analysing raw data regarding the total species richness of various biota (vascular plants, birds, bryophytes, arthropods, molluscs) from eight volcanic archipelagos (Azores, Galapagos, Hawaii, Marquesas, Society Islands, Cape Verde Islands, Canary Islands and Aeolian Archipelago), Carey et al. (2020) concluded that both species–area relationships and species–time relationships ‘should always be considered as potentially more parsimonious options’, supporting the value of this type of investigation even in the context of volcanic archipelagos, for which a more advanced theoretical framework (GDM) is available (Borregaard et al., 2016; Whittaker et al., 2008). In addition, the role of time in affecting the environmental and biological processes that can control the community assembly in insular systems has been conceptualised (Flantua et al., 2020) and Aeolian Islands, with their different ages, offer an opportunity to disentangle the role of time, specifically expecting lower species richness in islands with ongoing volcanic activity.

While only few data—and usually the same—have been used to test biogeographical theories on the Aeolian Archipelago, these islands have been recently subjected to a fairly high amount of botanical and ecological studies. Some of them refer to single species, such as the narrow endemic *Cytisus aeolicus*, a small tree that is perfectly adapted to life on active volcanoes (Zaia et al., 2020). Many others are floristic, phytosociological or bryologic contributions (Lo Cascio & Pasta, 2004 and references therein, Puglisi et al., 2006; Troia, 2012; Troia et al., 2012). As a consequence, an extensive amount of plant species occurrence data is available across the seven larger islands and a number of smaller islands and islets. Most of these data have been published in regional journals or are not published yet, thus hindering their comprehensive use for investigation on a hypothesis-driven approach. Now, the availability of a robust and comprehensive plant checklist for each island and islet (Lo Cascio & Pasta, 2020; Pasta et al. in prep.) offers the opportunity to use the

Aeolian Archipelago as a model system for testing biogeographical models in the youngest and most active volcanic archipelago of the Mediterranean Basin.

This paper aims to use the vascular plant species records from the Aeolian archipelago to test the following hypotheses: (i) ISAR for alien species has lower *c* but higher *z*-values than ISAR for native species, (ii) islands with active or recent volcanic activity show lower species richness than expected by ISAR for both native and alien species than islands with older volcanic activity, (iii) ISAR of native species of Aeolian Archipelago shows lower *c*- and higher *z*-values than the ISARs of other Mediterranean archipelagos composed of land bridge islands and (iv) because of the SIE, species richness values of smaller islets and island fragments are independent of island area.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area includes the whole Aeolian Archipelago, a group of polygenetic volcanic islands ranging between 38°49'–38°22' N and 15°15'–14°20' E. The archipelago is located 19.5 km north of Sicily and 54.3 km west of peninsular Italy (Calabria).

This study is based on data assembled from 32 insular units (Table S1 for details) that have originated as volcanic bodies or by the disruption of previous volcanic islands (Figure 1). Although the Aeolian Archipelago is traditionally considered as composed of seven major islands, ranging in surface area from 37.2 to 3.34 km², the islet Basiluzzo may also be included among the ‘large’ islands, since it is 0.281 km², that is about one order of magnitude smaller than the smallest major island (Panarea, 3.34 km²) but also one order of magnitude larger than the second largest islet (Lisca Bianca, 0.031 km²). Through historical times, Basiluzzo has also been inhabited and it housed agro-pastoral activities. Because of these geographical and historical features, we decided to include Basiluzzo among the large islands, obtaining a set of eight islands and 24 islets.

The Aeolian volcanism entirely occurred during the Quaternary, as demonstrated by the oldest radiometric age of 1.3 Ma (Beccaluva et al., 1985), and the subaerial activity of the Aeolian Islands developed from around 270–250 ka BP up to nowadays, with the following timing: Lipari (267 ka BP to 801 years BP; Forni et al., 2013 and ref. therein), Filicudi (246 ka to 29 ka BP; Lucchi, Santo, et al., 2013, and ref. therein), Salina (244 ka to 15 ka BP; Lucchi, Gertisser, et al., 2013 and ref. therein), Panarea (155 ka to 24–8 ka BP; Lucchi, Tranne, et al., 2013 and ref. therein), Vulcano (127 ka BP to 143 years BP; De Astis et al., 2013 and ref. therein), Alicudi (106 ka to 28 ka BP; Lucchi, Peccerillo, et al., 2013 and ref. therein) and Stromboli (85 ka BP to present, Strombolicchio = 204 ka BP; Francalanci et al., 2013 and ref. therein). The abrasion platforms around all the islands suggest the occurrence of significant quiescence periods in the Aeolian volcanism, which occurred about 200/180 ka and 20 ka ago (Favalli et al., 2005). Even if the Aeolian orogenic volcanism includes many

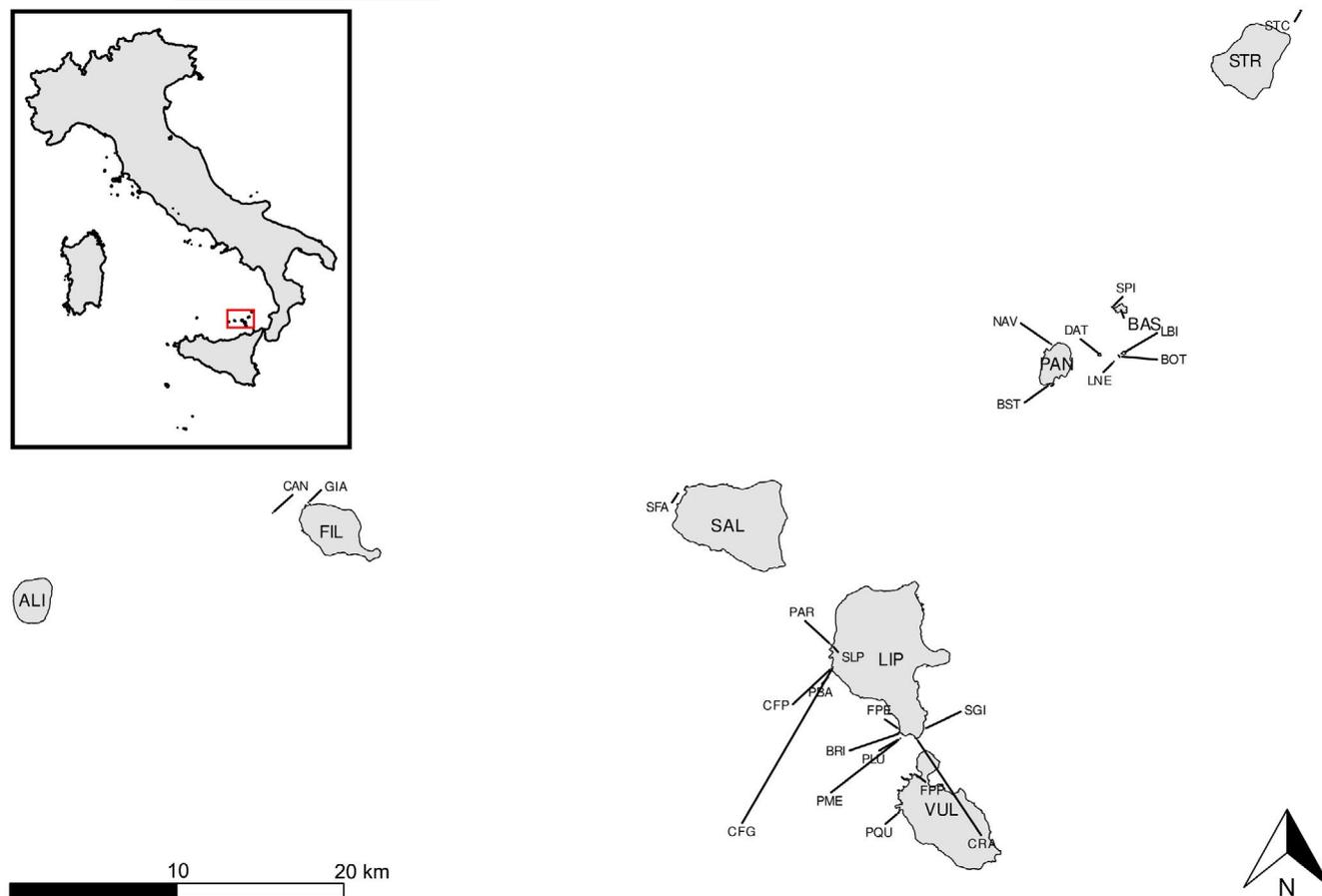


FIGURE 1 The Aeolian Archipelago, with the eight major islands and the 24 islets used in the present study. The acronyms identifying each island and islet are reported on Table S1

seamounts located west and north-west off the currently emerged Aeolian Islands, there is no evidence of the occurrence of other islands in the past (Beccaluva et al., 1985). Indeed, the Pleistocene sea level changes did not significantly affect the configuration of the archipelago with respect to the actual pattern, with Vulcano and Lipari being the only large islands which were connected during the glacial maxima.

The availability of obsidian, a precious raw material for ancient human communities and the strategic position on prehistoric trade routes triggered the early human colonisation of the Aeolian Archipelago since Neolithic times (about 7500 years ago, see Pasta et al., in press). Nowadays, the archipelago bases its economy almost exclusively on seasonal tourism. The resident population consists of ca. 15,500 people (mainly concentrated in Lipari and Salina), whose number increases by an order of magnitude during the summer months (King & Young, 1979).

Despite its relatively young age, the archipelago hosts a rich vascular flora, consisting of 879 species (Pasta et al., in prep.), including seven endemic taxa (*Anthemis aeolica*, *Centaurea aeolica* subsp. *aeolica*, *Cytisus aeolicus*, *Dianthus rupicola* subsp. *aeolicus*, *Bituminaria basaltica*, *Erysimum brulloi* and *Silene hicesiae*) and other rare species such as *Eokochia saxicola*, *Helichrysum litoreum* and *Limonium minutiflorum* (Troia, 2012).

2.2 | Data assembly

The checklists of the infrageneric plant *taxa* (species + subspecies, hereinafter named 'species') were compiled by reviewing and assembling all the existing published data and by including original collections resulting from field surveys carried out in the last three decades (Table S3; Pasta et al. in prep.). The checklists include every vascular plant species that have been recorded in the 32 insular units considered in this study, with each species classified as native (N) or alien (A) on the basis of national and regional data (Pignatti et al., 2017–2019). Due to the extremely long human presence in the Aeolian Archipelago, it is sometimes difficult to know which species have been introduced on each island. We considered as alien those species which are reported as 'casual' or 'naturalised' in Table S3. These include species having native ranges outside the Mediterranean Basin plus a number of Mediterranean or wide-ranging species whose alien status is well documented, as in the case of *Arundo donax* (Hardion et al., 2014), or fairly presumable, as in the case of archaeophytes (Brullo & Guarino, 2007).

The checklists were assembled by using different criteria for islands and islets. For the eight major islands, much more explored and most exposed to the arrival of alien species, only the species

observed in the last three decades were considered. For the 24 islets, some of which are hardly accessible, the data collected in the last century were considered. The application of this 'cumulative' criterion seeks to achieve reliable data for islets whose exploration is extremely challenging and uneven, due to landing difficulties and terrain instability.

2.3 | Analytical methods

We fitted the archipelago ISARs by the Arrhenius power function through the nonlinear modelling procedure of the *sar_power* function contained in the 'sars' R package (Matthews et al., 2019). We modelled ISARs separately for native (*N*) and alien (*A*) species. The first hypothesis was tested by comparing the *c* and *z* parameters of the ISAR models fitted jointly and separately for the data sets of islands ($n = 8$) and islets ($n = 24$) as well as for the full data set of islands and islets ($n = 32$).

To test the second hypothesis, we quantified the standardised residuals of the ISARs of native and alien species by dividing the residuals by the expected values. Then, to verify the hypothesis that the two currently active volcanic islands (Stromboli and Vulcano) have the largest negative values, we ranked the islands by their standardised residuals. We expected this hypothesis to be confirmed at least for native species within the set of larger islands, since smaller islets are likely subjected to the SIE. A similar expectation was stated for alien species, despite being less likely, as these plants have been less exposed to the geological history of the archipelago.

To test the third hypothesis, we compared the *c* and *z* parameters of the models fitted on the native species of the Aeolian Archipelago with those from other archipelagos and groups of islands located in the Mediterranean but made up of land bridge islands. For this comparison, we used the power function model, fitted first by using nonlinear modelling on original data (*S* and *A*) as previously described, and then by using linear modelling on Log_{10} transformed data (*LogS* and *LogA*). The land bridge archipelagos used for comparison were the Tuscan Archipelago (Chiarucci et al., 2017), the Dalmatian islands of Croatia (Nikolić et al., 2008), the Greek Ionian Archipelago in West Greece (Valli et al., 2019), the Northern Sporades (Iliadou et al., 2020) and the East Aegean Archipelago (Panitsa et al., 2010). A comparison with the Santorini-Christiana, a volcanic archipelago within the Cyclades (Raus et al., 2019), was also included. For all these archipelagos, we refitted the models using the original data provided in the cited papers. However, to avoid overrating the weight of the small islets included in some data sets but not in all, we considered in this analysis only the data for islets and islands larger than 0.1 km².

To test the fourth hypothesis, we fitted the number of native and alien species per island to its area by different models defining the threshold of the SIE (see e.g. Schrader et al., 2020; Wang et al., 2018; Yu et al., 2020). Species richness data of native and alien species for the whole set of islands and islets were fitted to

models with one threshold and a left horizontal segment or two slopes (Dengler, 2010; Gao & Perry, 2016; Lomolino & Wisser, 2001), based on *S* or *LogS* as a function of *A* or *LogA*. Then, we compared them to their analogous models with a single slope, that are the untransformed Arrhenius power function (*S* as function of *A*), the Gleason model (*S* as function of *LogA*; Gleason, 1922) and the log-transformed Arrhenius power function (*LogS* as function of *LogA*). One-threshold models were fitted using the *sar_threshold* function from the 'sars' R package (Matthews, Triantis, et al., 2019), whereas the Gleason and the log-transformed Arrhenius models were fitted using the *sar_loga* and *lin_pow* functions, respectively, from the same package. While the models based on *S* were fitted to both native and alien species, the models based on *LogS* were fitted only to native species, since most of the small islands did not have alien species and zero values are problematic for model fitting and interpretation. Model selection was carried out based on Akaike information criterion corrected for small sample sizes (AICc, Hurvich & Tsai, 1989; Sugiura, 1978) and the comparisons across different models were done using its difference (ΔAICc) within the groups of models using the same variables (namely *S* and *A*, *S* and *LogA*, and *LogS* and *LogA*). The most parsimonious model was chosen if the decrease in AICc when adding the next order term was small. In particular, we assumed that models in which the difference in AICc is <2 can be considered as equally supported (Burnham, 1998; Burnham et al., 2011).

3 | RESULTS

3.1 | Native and alien species and ISAR fitting

The checklists of vascular plants recorded in the Aeolian Archipelago included 894 species, 749 of them being native (seven of which endemic to one or more islands). Also, a total of 145 alien species was found to occur in the archipelago (16.7% of the total flora), with some of them being particularly invasive (*Opuntia ficus-indica*, *Carpobrotus edulis*, *Cenchrus ciliaris* and *Saccharum biflorum*).

ISARs based on the Arrhenius power function fitted quite well both for native and alien species of the Aeolian Archipelago, with relatively high R^2_{Adj} values and quite typical values for the *c* and *z* parameters (Figure 2a,b). As expected, the ISAR for native species shows a higher *c*-value and a lower *z*-value than the ISAR for alien species. This pattern is consistent across the different sets used for model fitting, namely those including all islands and islets (Figure 2a,b) and those split between islets (Figure 2c,e) and islands (Figure 2d,f). Therefore, the first hypothesis (lower *c*- and higher *z*-values for alien species) is confirmed for the whole data set, as well as for the subsets of islets and islands. Separate model fitting for islets and islands (Figure 2c-f) also shows consistently higher estimated *z*-values for islets than islands both in the case of native and alien species. Finally, model fitting for the whole data set of islets and island shows much higher explained variance than for the subsets.

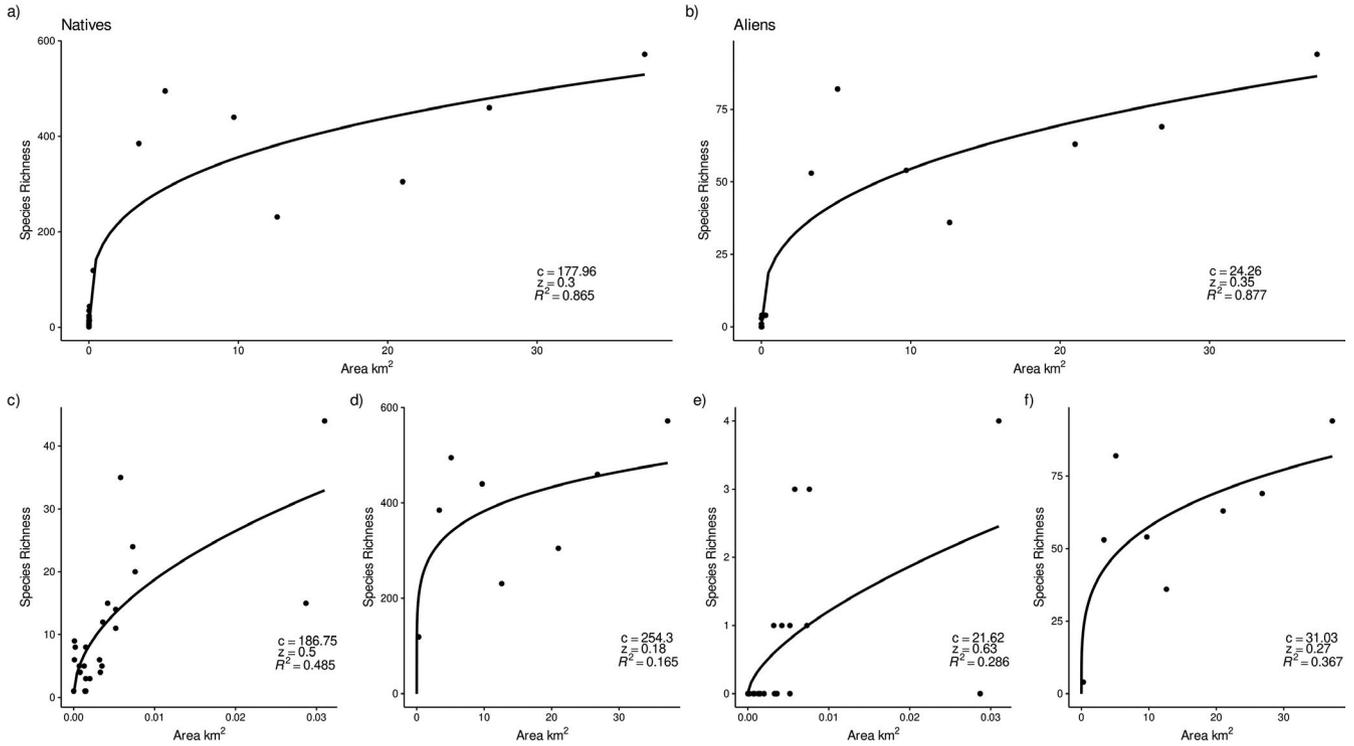


FIGURE 2 Island species–area relationship (ISAR) for native and alien species of the Aeolian Archipelago. Upper panels show the ISARs for the whole set of islands and islets for native (a) and alien (b) species. Lower panels show separate ISARs for islets and islands for native species (c and d) and for alien species (e and f). Model fitting and parameters are shown within each panel

3.2 | Species richness in volcanically active islands

In the fitting of ISAR for native species across the whole data set of 32 islets and islands, the two volcanically active islands (Stromboli and Vulcano, i.e. the third and fourth largest islands respectively) are those with the largest negative deviation from model expectations among the eight large islands (Figure 2a; Table S2), but some of the islets show remarkable negative deviations as well (Table S2). When the ISAR fitting is done only using the eight largest islands (Figure 2d), Stromboli and Vulcano still show large negative deviation from model expectations (Figure 2d), but Basiluzzo (the smallest among the large islands) shows the second largest negative deviation after Stromboli. The hypothesis of a lower native species richness in the most volcanically active islands is largely confirmed; however, because of the small numbers of species involved, some smaller islets show larger negative deviations.

In the ISAR fitting for alien species using the full data set (islands and islets), the two volcanically active islands remain those with the second and third largest negative deviations among the eight largest islands, with Basiluzzo having the largest negative deviation. Some smaller islets show larger negative deviations (Figure 1b, Table S2). When the ISAR fitting is done using only the eight largest islands, Stromboli and Vulcano still show the second and third largest negative deviations, while Basiluzzo showed the largest one (Figure 2f, Table S2). This test confirms the hypothesis of a lower species richness in the most volcanically active islands even for alien species.

3.3 | ISAR comparisons between Aeolian Islands and other archipelagos

The ISAR fitted using the normal form of the Arrhenius power function ($S = c \cdot A^z$) shows that the Aeolian Archipelago has the lowest proportion of variance explained with respect to the other Mediterranean archipelagos used for comparison (Table 1, Figure 3a), suggesting that the area effect is there less predominant than in other archipelagos. The Aeolian Archipelago shows a lower c-value than that of the Tuscan Archipelago, that is also located in the Tyrrhenian Sea, but higher than those of the Adriatic Sea, Ionian Sea and eastern Mediterranean. In addition, the z-value of the Aeolian Archipelago is lower than the z-values of all other archipelagos. The comparison across archipelagos done by using linear fitting on the log transformation of the Arrhenius power function ($\text{Log}(S) = \text{Log}(c) + z \cdot \text{Log}(A)$) still shows the smallest value of explained variance but values of the c and z parameters that are within the range of the parameters of the other archipelagos (Table 1, Figure 3b). So, the third hypothesis, expecting a lower c-value and a higher z-value in the Aeolian Archipelago with respect to the other Mediterranean archipelagos, is not supported by model fitting.

3.4 | Small-island effect

Model fitting for native species shows quite different outcomes depending on the group of models. In the comparison with the Arrhenius

TABLE 1 Model fitting of the Arrhenius species–area relationship by using the linear values of A and S ($S = c \cdot A^z$) and their log-transformed values ($\text{Log}S = k + z\text{Log}(A)$) for the native plant species of the Aeolian Islands in comparison with analogous data retrieved from literature on other Mediterranean archipelagos and sets of islands

Archipelago	Island area (km ²)	Nonlinear fitting on natural data			Linear fitting on log–log data		
		R^2_{Ad}	c	z	R^2_{Ad}	c	z
Aeolian ($n = 8$)	0.28–37.2	0.165	254.3	0.178	0.478	208	0.243
Tuscan ^a ($n = 8$)	2.26–223.2	0.796	281.9	0.219	0.721	291.1	0.205
Adriatic Islands ^b ($n = 54$)	0.1–409.9	0.725	227.7	0.25	0.663	199.2	0.267
Ionian Greek Islands ^c ($n = 17$)	1.2–406	0.956	169.9	0.326	0.925	140.17	0.366
North Sporades ^d ($n = 12$)	0.2–95.1	0.805	178.4	0.319	0.746	194.8	0.272
East Aegean ^e ($n = 20$)	1–1636	0.944	112.0	0.310	0.881	101.1	0.326
Santorini–Christiana ^f ($n = 7$)	0.13–76	0.956	143.5	0.345	0.901	145.7	0.339

^aChiarucci et al. (2017), for this paper we used the most recent data set, referring to the period 1951–2015.

^bNikolić et al. (2008).

^cValli et al. (2019).

^dIliadou et al. (2020).

^ePanitsa et al. (2010).

^fRaus et al. (2019).

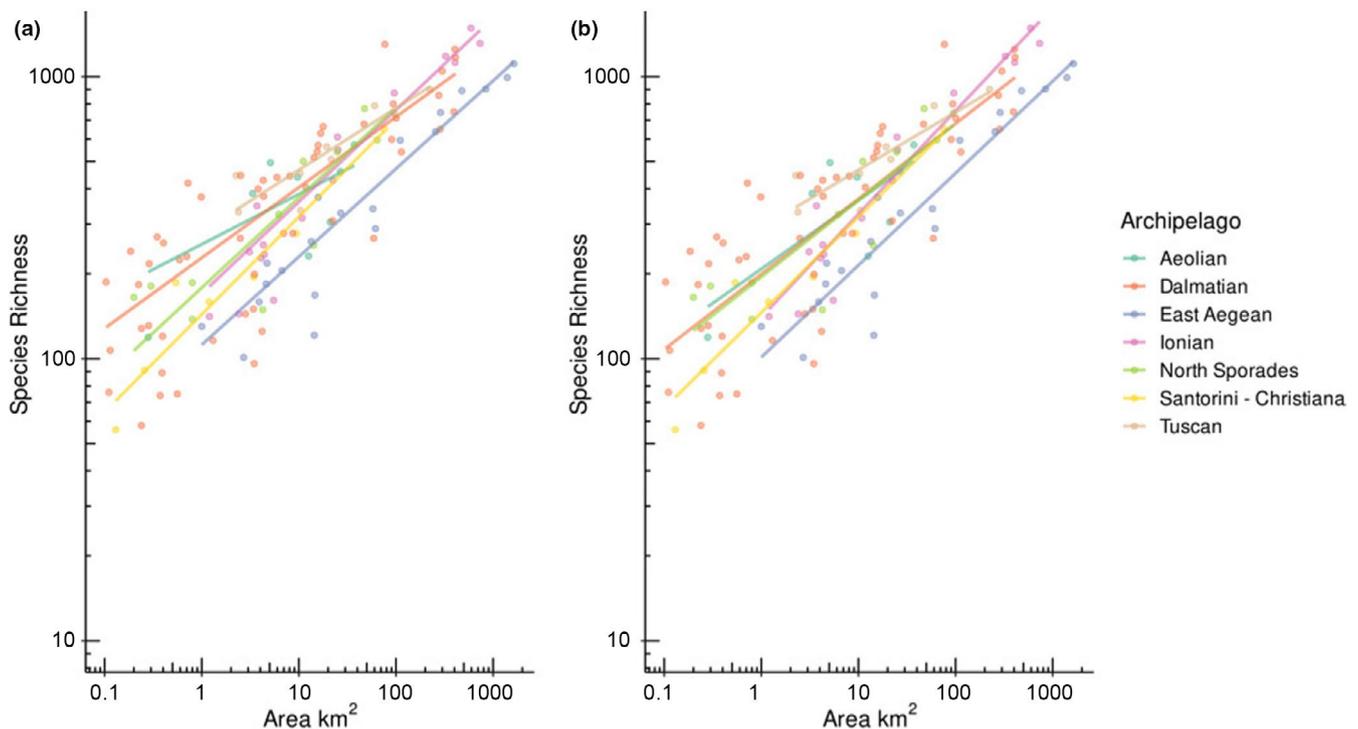


FIGURE 3 Island species–area relationship (ISAR) for native species of the Aeolian Archipelago compared with those of the Tuscan Archipelago, Adriatic Islands, Greek Ionian Islands, Northern Sporades, East Aegean archipelago and the Santorini-Christiana island group. Only islands larger than 0.01 km² have been considered in the analyses. All the graphs are shown in a log–log space, but the left-hand side panel contains the model fitted on normal form of the Arrhenius power function ($S = c \cdot A^z$), while the right hand-side panel contains the model fitted by using the log transformation of the Arrhenius power function ($\text{Log}(S) = \text{Log}(c) + z \cdot \text{Log}(A)$)

power function based on natural numbers, the *left horizontal* provides a much larger AIC_C value, while the *two slopes* model provides a remarkable improvement (i.e. a decrease) in AIC_C . However, the interpretation of the model parameters is difficult, showing a T of 1 and a Z_1 of 349.93. In the comparison with the Gleason model, both

the *left horizontal* and *two slopes* provide an improvement in AIC_C and the fitted values of T are reasonable (0.0219 km² and 0.0245 km² for the *left horizontal* and the *two slopes* respectively) and the values of Z_1 and Z_2 are also within the expected values (Table 2). In the *log-transformed* version of the Arrhenius power function, both the *left*

TABLE 2 Parameters and model fitting for the three ISAR models used to test the small-island effect on the Aeolian Islands ($n = 32$), using the Arrhenius power function, the Gleason model and the log-transformed Arrhenius power function, for the native and alien species

Group	Variable	Model	C	T	Z ₁	Z ₂	R ² _{Adj}	AIC _c	DeltaAIC _c
Native	S–A	Arrhenius	177.96	–	0.302	–	0.865	361.38	0.00
		Left horizontal	43.09	0.00001	–	16.25	0.653	392.57	31.19
		Two slopes	9.35	1.00	349.93	3.47	0.921	346.87	–14.51
	S–Log(A)	Gleason	264.73	–	38.228	–	0.772	381.58	0.00
		Left horizontal	9.12	0.0219	–	144.11	0.903	351.72	–29.86
		Two slopes	25.35	0.0245	5.65	144.13	0.9	354.23	–27.35
	Log(S)–Log(A)	Arrhenius (log)	117.75	–	0.439	–	0.835	27.34	0.00
		Left horizontal	0.66	0.00138	–	0.5	0.864	23.85	–3.49
		Two slopes	1.03	0.00141	0.12	0.49	0.863	22.88	–4.46
Alien	S	Arrhenius	24.26	–	0.351	–	0.877	240.87	0.00
		Left horizontal	4.81	0.00001	–	2.712	0.715	271.55	30.68
		Two slopes	0.44	3.00	17.47	0.855	0.930	228.55	–12.32
	S–Log(A)	Gleason	40.18	–	6.00	–	0.742	263.73	0.00
		Left horizontal	0.58	0.129	–	31.704	0.907	235.87	–27.86
		Two slopes	2.59	0.145	0.725	31.799	0.904	238.59	–25.14

For each model the normal version of the model was compared with the respective left horizontal and two slopes models. For alien species, the log-transformed Arrhenius Power Function was not used because of the presence of zero values in some islets.

horizontal and the *two slopes* provide an improvement in AIC_c and the fitted values of T are reasonable, despite very small (0.00138 and 0.00141 km² for the *left horizontal* and the *two slopes* respectively) and the values of Z₁ and Z₂ are also within the expected values (Table 2).

For alien species, in the comparison with the *Arrhenius power function* based on natural numbers, the *left horizontal* provides a larger AIC_c value, while the *two slopes* model provides an improvement in AIC_c. However, also in this case the interpretation of the model parameters is difficult, showing a T of 3 and a Z₁ of 17.47. In the comparison with the *Gleason* model, both the *left horizontal* and *two slopes* provided an improvement in AIC_c and, in this case, the values of T are reasonable, being represented by an area of 0.129 and 0.145 km² for the horizontal left and the two slopes respectively (Table 2). The values of Z₁ and Z₂ are also within the expected values (Table 2).

So, for both native and alien species, the hypothesis regarding the SIE can be verified only when using a model based on S versus LogA, despite that Gleason provided worse fitting than Arrhenius power function. In the case of native species, the SIE can be verified also using the log transformation of the Arrhenius model.

4 | DISCUSSION

4.1 | Island species–area relationship of native and alien plant species

We reported an original investigation based on high-quality floristic data for the largest set of Aeolian Islands and islets presently available (32 insular units, with respect to the seven units investigated by Carey et al., 2020). In addition, thanks to a recently assembled

data set on vascular plant species occurrence across all the eight islands (Pasta et al. in prep) and 24 islets (Lo Cascio & Pasta, 2020), the range of plant species richness that we used in the analysis was significantly larger than that used by Carey et al. (2020) for the seven larger Aeolian Islands (288–658 species) and permitted the separation between native species (1–572 species) and alien species (0–94 species).

The first hypothesis tested in this paper stated that the ISAR of alien plant species is expected to have a lower *c*-value and a higher *z*-value than the ISAR of native species, since we assume that alien species arrived later in the archipelago and are expected to have a pattern more similar to those of isolated archipelagos. This pattern emerged from the ISAR analyses performed for the whole set of islands and islets, as well as from the ISAR analyses performed for the separate subsets of islets and islands. The first research hypothesis is thus confirmed. This depends on the higher degree of rarity and the higher turnover of alien species across islands in comparison to native species, leading to stronger dependence on increasing area. Exactly the same pattern was already noticed in other insular systems, such as the Tuscan Archipelago (Chiarucci et al., 2017) and oceanic islands in general (Blackburn et al., 2016) as well as in continental systems in the United Kingdom (Hulme, 2008) and Carolinas (Tarasi & Peet, 2017). However, comparative studies using a large number of data sets did not highlight significant differences between the *c* and *z* parameters of SARs of alien and native species. In particular, Baiser and Li (2018) found that the processes driving the increase in species richness with area are similar for native and alien plant species, but not for animals. Therefore, the case that we observed in the Aeolian Islands is likely dependent on the combination of local factors depending on the specific biogeographical history of the archipelago as well as on the history of human colonisation, closeness to Sicily or Italian mainland and landscape transformation. This is coherent



with the conclusions of similar studies carried out in southern oceanic islands (Chown et al., 1998) and even in continental 'insular' ecosystems generated by different land use matrices (Dembicz et al., 2020).

The values of the c and z parameters emerging from the fitting of all models are within the typical range of Arrhenius parameters for ISARs (Matthews et al., 2016; Patiño et al., 2014). However, it emerges that the ISARs of islets have constantly higher z -values than those of the largest islands, a pattern suggesting a relatively higher degree of isolation for islets than islands, and also conflicting with the theoretical expectations of the SIE (see below).

4.2 | Plant diversity and volcanic activity

The second hypothesis we tested assumed that islands with active or recent volcanic activity should have lower species richness, for both native and alien species, than islands with older volcanic activity when accounting for the effect of area. In fact, a major peculiarity of the Aeolian Archipelago in the Mediterranean Basin is that some of the volcanoes making up the islands are still active. Such activities have occurred until quite recent historical times on Lipari (1220 AD, Forni et al., 2013) and Vulcano (1888–1890 AD; De Astis et al., 2013), while explosive eruptions, of small to medium volume and violence, are frequent (usually separated by intervals of minutes) on Stromboli (Francalanci et al., 2013), which in turn gives the name to a specific type of volcanism, namely the 'Strombolian volcanism' (Gaudin et al., 2017). Our analysis highlighted that the two islands hosting recent or ongoing volcanic activity, namely Vulcano (the eponym for all 'volcanoes' worldwide) and Stromboli, show a markedly lower plant species richness with respect to the expectations derived by the ISARs. This pattern emerges for both native and alien species, especially for the former, supporting our hypothesis. For alien species, the small negative deviation of Vulcano could also be explained by the intense urbanisation and land use transformation of this island that likely has favoured biotic invasions.

Species depauperation in islands with ongoing volcanic activity is well known for other islands and archipelagos, also in the Mediterranean basin (e.g. Karadimou et al., 2015; Raus et al., 2019). In real oceanic contexts, this is the case of the Big Island for the Hawaiian Archipelago, hosting a significantly lower number of native plant species than expected by the species–area relationship and also lower species richness than the islands of Maui, Oahu and Kauai, that are one order of magnitude smaller (Chiarucci et al., 2010, 2011). Volcanic activity can even destroy the island itself or its biota, as it was the case of Krakatoa in historical times (Whittaker et al., 2000) or the case of a larger island of the Aeolian Archipelago which underwent gradual disruption and currently is represented by few scattered fragments, the largest of them being Basiluzzo. The recolonisation process after island sterilisation takes decades or even centuries, as in the case of Krakatoa (Whittaker et al., 1989). More frequently, volcanic activity affects the island biota by temporarily sterilising part of the island with lava flows or other geochemical or

geophysical processes which make plant persistence impossible (Thornton, 2007). In the case of the Aeolian Islands, most of the currently active volcanic cone of Vulcano is devoid of vegetation because of the recent age of the substrates and the continuous emission of toxic gases (Granieri et al., 2017), while c. 20%–25% of Stromboli's surface is constantly affected by several forms of natural disturbance (e.g. rockfalls triggered by local earthquakes, extensive wildfires, accumulation of ashes, frequent fall out of burning debris and huge lava bombs) linked with active volcanism (Marsella et al., 2012). Basically, plant diversity on these islands is negatively affected by volcanism, but at the same time, volcanism may be considered a key trigger and driver of local-scale plant evolutionary processes, so that some species were able to develop specific adaptations to live on active volcanoes, as in the case of *Cytisus aeolicus* (Zaia et al., 2020).

4.3 | ISAR of Aeolian Archipelago and other Mediterranean archipelagos

The comparison of the ISAR for vascular plants of the Aeolian Archipelago with those of other Mediterranean archipelagos did not allow us to detect any clear or striking differences between this young volcanic archipelago and the other island systems used for comparison, as expected by our third hypothesis. Therefore, we cannot confirm that the ISAR of native species of the Aeolian Archipelago has lower c - and higher z -values than those from other Mediterranean archipelagos composed of land bridge islands. This expectation was based on major reports showing a reduction of the c -value and an increase of z -value passing from continental units, to continental islands and to oceanic islands (see e.g. Patiño et al., 2014).

The failure to find a clearly distinctive pattern probably just underlines something that needed to be confirmed: although having an extremely young origin and being volcanically very active and dynamic, the Aeolian Islands are not far enough from the continental coastline of Italy (Sicily and Calabria in particular) to show a typically oceanic ISAR pattern. As remarked by Matthews, Rigal, et al. (2019), intra-archipelago processes have a major role in determining the shape of the ISAR, also obscuring the diversity patterns predicted by theoretical expectations as a function of archipelago isolation. The Mediterranean archipelagos here investigated do not show relevant differences in the shape of ISAR, likely because of the closeness to the mainland, the complex biogeographical history of this area in the Pleistocene and also because of the millennial history of human activities (Martinelli & Lo Cascio, 2018).

4.4 | Small-island effect

Our fourth hypothesis stated that below a certain threshold, plant species richness was not related at all to the island areas, with species richness of smaller islets and island fragments independent of island area (namely SIE). The results of the analyses here performed

did not permit to clearly confirm the existence of a SIE in the Aeolian Archipelago, despite the presence of many small islets in the data set. In particular, we found evidence for the presence of a SIE in terms of model fitting and parameters plausibility in the case of S versus $\text{Log}A$ and $\text{Log}S$ versus $\text{Log}A$.

Despite a general consensus on SIE is recently emerging (Dengler, 2010; Gao & Perry, 2016; Schrader, 2020), many authors observed that the interpretation of this phenomenon is not simple, since other factors interact with island area in controlling species richness in small islands. Triantis and Sfenthourakis (2012) highlighted that in small islands, the effects of habitat diversity (e.g. elevation, exposure to wind and sea salt spray, presence of bird colonies) can be prevalent with respect to area. Schrader et al. (2020) stated that SIE is a widespread phenomenon more complex than generally described, with different functional groups having different responses to this phenomenon. They concluded that the complexity of SIE is often masked and not easily inferred by using only plant species richness. On the basis of comparisons across 278 data sets, Wang et al. (2016) demonstrated that the SIE is largely generated by the presence of empty islands in the data set. They concluded that to perform a more robust detection of the SIE, the empty islands should not be excluded from the analysis. In the Aeolian Archipelago, no single islet in the data set was empty and the lowest observed value of native species richness was 1 for four islets (whereas many islets did not host any alien species), the smallest of which being 'U Brighghiu with an area of only 10 m². In a methodological investigation based on null models to test for non-random variability in the capacity of island area to predict species richness applied to island plant communities in Canada and New Zealand, Burns et al. (2009) concluded that 'commonly used regression techniques can generate spurious small-island effects and that alternative analytic procedures are needed to detect non-random patterns in species richness on small islands'. So, to date, there is no general consensus on the recognition of the SIE pattern nor in the processes that are supposed to generate it and large variability exists across archipelagos and island systems. Also Tjørve and Tjørve (2011), after subjecting the SIE theory to Ockham's razor, concluded that it should be abandoned, since there is no reason to assume that the ecological factors or patterns that affect the shapes of ISARs cause two distinct patterns depending on island size thresholds.

Another peculiarity that we wish to highlight is that, for both native and alien species, the ISARs calculated for islets (area <0.1 km²) show higher slope (z -value) than the ISAR calculated for larger islands, indicating a stronger dependence of species richness on area for smaller islets than for larger islands. This result is particularly interesting, if we consider that the 24 islets considered in our data set include very different land morphologies, ranging from almost flat islets to others rising tens of metres above the sea, surrounded by steep rocky cliffs.

5 | CONCLUSIONS

We tried to disentangle ISAR patterns for vascular plants from the Aeolian Archipelago compared to other Mediterranean

archipelagos, while accounting for different island sizes and differences in native and alien floras. Our results demonstrate that the ISAR patterns of the Aeolian Islands are more similar to those of Mediterranean land bridge archipelagos than to those of typical oceanic islands. Future research should bridge the gap between plant and animal biogeography of the archipelago, likely integrating and comparing the different data sets and results, in order to account for differences in the colonisation speed rates by different biotas. Moreover, the large amount of available data (both in terms of floristic and faunistic species lists, but also geological and geographical knowledge) makes the archipelago very appealing for testing several biogeographical hypotheses. As such, the Aeolian Archipelago could become a model system to explore intra-archipelago beta diversity patterns and drivers, phylogenetic polarisation of island floras in respect of past and present isolation, responses of plant communities to climate change on islands and biological invasions.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All the data used in this study and supplemental tables regarding the absolute and relative residuals of the fitting of the Arrhenius species–area relationship (Tables S1–S3) are available at the following links: doi.org/10.5061/dryad.j6q573nf9 (Geographic and descriptive data on the Aeolian islands and islets) and doi.org/10.5061/dryad.n02v6wwxs (Checklist of the vascular plant taxa recorded from all the insular units of the Aeolian Archipelago).

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BIOSKETCH

Alessandro Chiarucci is interested in biogeography and macroecology of plant assemblages with a special focus on the implications for biodiversity conservation planning.

Author contributions: A.C. ideated the project, organised the research group and developed the first theoretical framework; P.Z. contributed to setting the theoretical framework and made all the statistical analyses; R.G. and S.P. contributed to setting the general framework and to write down a first draft of the discussions; S.P. reviewed the plant occurrence data, assembled and standardised the checklists. The manuscript was drafted by AC and subsequently developed by all the authors.

SUPPORTING INFORMATION

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

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