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Habitat type and island identity as drivers of community assembly in an archipelago

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Abstract

Aim: Ecoinformatics offer new opportunity to test islands as biogeographic and ecological models. In this paper we predicted three hypotheses: (1) plot-based data issuing from vegetation surveys can be used to predict Island Species-Area Relationships (ISARs) or island similarity; (2) the habitat area is an independent predictor of species richness patterns within island; (3) species richness and composition are more dependent on habitat type than island identity in land-bridge islands.

Area: Tuscan Archipelago, Italy.

Methods: We assembled a database of all the vegetation plots available for the archipelago. For the first hypothesis we calculated ISARs, using Arrhenius model, and Beta Diversity, using Jaccard dissimilarity, on both published floras and cumulative plot data. For the second hypothesis, we modelled Habitat Species-Area Relationships (HSARs), using Arrhenius model. For the third hypothesis, we used additive partitioning of species richness, NMDS and PERMANOVA.

Results: Island Species-Area Relationships based on plot data mirrored those on published floras, but absolute values of c and z parameters were different. Beta diversity based on plot data resembled those of published floras, but was higher. Species richness was significantly related to the habitat area. The total species richness of the archipelago was linked to large scale drivers, such as island identity, while plot species composition was driven by both habitat type and island identity.

Conclusions: Data assembled issuing from vegetation surveys are useful to describe biogeographic patterns. Species richness in the archipelago is driven by spatial factors such as the amount of habitats and the differences among islands, while the species composition of local assemblages is largely driven by habitat filters rather than by island identity, as expected in land-bridge islands.

KEYWORDS

biogeographic patterns, islands, plot data, species-area relationships



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1 | INTRODUCTION

Islands and archipelagos represent one of the most attractive study models in biogeography and ecology. Indeed, they are often regarded as natural laboratories, since their evolutionary and ecological processes are shaped by the geographic limits constraining their biotic assemblages (Whittaker et al., 2017). Islands have provided a fertile environment to develop theories and test specific hypotheses, and their potential contribution to the advancement of scientific knowledge is far from exhausted (Warren et al., 2015; Santos et al., 2016; Losos, 2017).

One of the most studied patterns in island ecosystems is the species–area relationship (Rosenzweig, 1995), typically referred to as ISAR (Island Species–area Relationship: Triantis et al., 2012). ISARs and the parameters affecting them have been widely investigated for a variety of taxa and insular systems (e.g., Sfenthourakis, 1996; Panitsa and Tzanoudakis, 2001; Hamilton et al., 2009; Rabosky and Glor, 2010; Chiarucci et al., 2011; Fattorini, 2011; Triantis et al., 2012; Furness et al., 2016). The general shape of ISARs and the ecological and biogeographic significance of the statistical parameters emerging from ISAR modelling have been debated and are now quite well elucidated, also thanks to the use of large data sets and global analyses (Triantis et al., 2012; Patiño et al., 2014; Matthews et al., 2019a, 2019b).

The relation between the number of species and island area is affected by the degree of isolation (Ding et al., 2006; Peay et al., 2010; Spengler et al., 2011), but also by the habitat diversity on the island (Hannus and Numers, 2008; Triantis and Sfenthourakis, 2011; Whittaker and Triantis, 2012; Cazzolla Gatti et al., 2018; MacDonald et al., 2018; Craven et al., 2019; Schrader et al., 2019a, 2019b). The number of species reported for a habitat or an island is also dependent on the sampling effort used to build up the data set (see e.g., Chase et al., 2019a, 2019b). The importance of habitat diversity in controlling the plant diversity on islands has been highlighted in several studies (Nilsson et al., 1988; Kohn and Walsh, 1994; Hortal et al., 2009; Stein et al., 2014; Keppel et al., 2016; Schrader et al., 2019a, 2019b). These studies made evident that habitat diversity plays a primary role in controlling the species diversity on islands. Studies on functional traits (e.g., Ottaviani et al., 2020) have increasingly become important in recent investigations on island biogeography and provided new insights on islands' species assemblages and their habitat filtering. For instance, on oceanic islands, such as the Galápagos islands, habitat filtering proved to be more important than dispersal limitation in determining the species composition of plant assemblages (Carvajal-Endara et al., 2017). Thus, habitats within each island can differ in species composition (e.g., Cutts et al., 2019) and have also been referred to as “habitat islands” (Kontopanou and Panitsa, 2020). Since the species–area relationship predicts that larger habitats support higher species richness, the species richness of each habitat within an island is controlled by the area, by a Habitat Species–Area Relationship (HSAR).

While biogeography made extensive use of island ecosystems for testing theories and models, vegetation science has not yet deeply

exploited the opportunity of using island ecosystems to investigate community assemblage patterns and processes in peculiar and well-delimited model ecosystems. Community ecology in general, and plant community ecology in particular, can significantly benefit from studies focused on islands, since these simplified systems are ideal for studying the interplay of ecological and evolutionary processes in community assembly (Kueffer et al., 2014). Significant progress in the interface between vegetation science and island biogeography can be expected with the recent advent of large regional and global databases of vegetation plots (Bekker et al., 2007; Chytrý et al., 2015; Bruelheide et al., 2019). The availability of such databases permits analysing huge amounts of data across large spatial and temporal scales, by using data sets from a variety of different resources. The resources and approaches offered by ecoinformatics on vegetation data (Dengler et al., 2011; Wilson et al., 2012) open new possibilities for investigating the assembly patterns in the plant communities typical to island ecosystems. Despite these databases nearly always collecting plot data recorded with different protocols and approaches, the amount of information they contain has been used to answer large-scale questions (Dengler et al., 2011; Chytrý et al., 2015; Bruelheide et al., 2019).

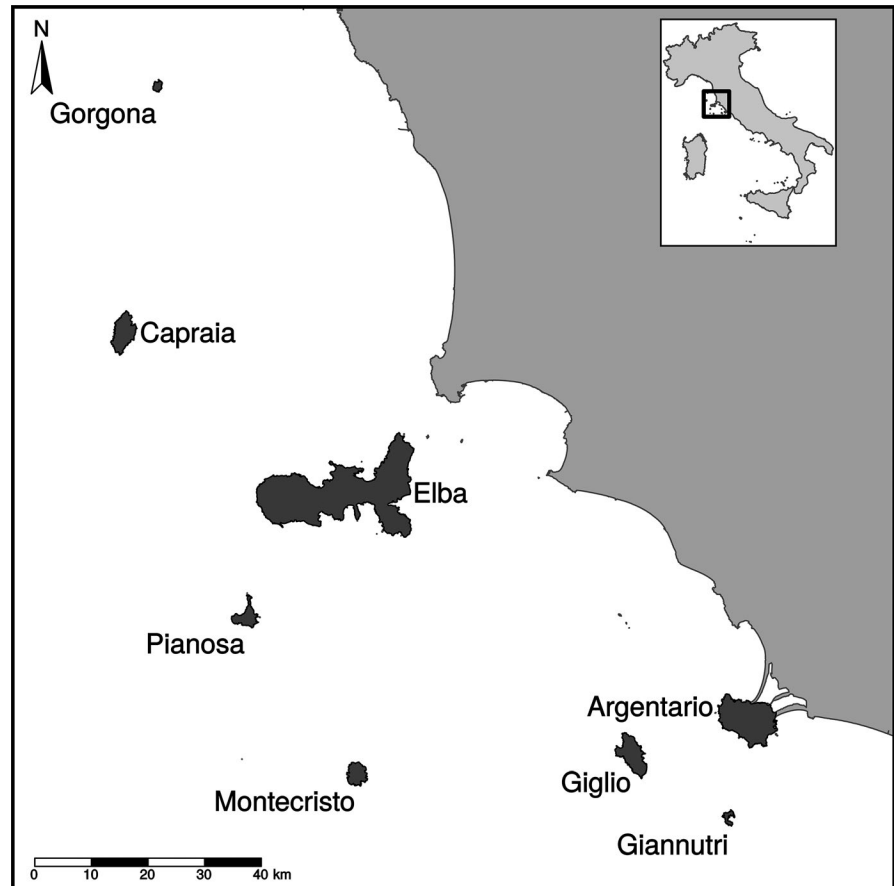
This paper aims to test the possible use of vegetation plot data in island biogeography and to verify the insularity effect on plant communities, by using a study system whose vascular flora and vegetation are well known after two centuries of thorough and repeated botanical investigations, i.e. the Tuscan Archipelago (see Chiarucci et al., 2017). In particular, here we predict and test three hypotheses: (1) plot data obtained by vegetation surveys can be used to predict traditional island biogeographic patterns, such as ISAR or beta diversity among islands; (2) the habitat area is an independent predictor of species richness within island or, in other words, the Habitat Species–Area Relationship (HSAR) is independent from the ISAR; (3) species richness and composition are more dependent on the habitat type than island identity on land-bridge islands.

2 | METHODS

2.1 | Study area

The Tuscan Archipelago is a typical land-bridge system, including seven major islands, the “fossil” island of Monte Argentario, currently connected to the Italian Peninsula through two sand ayres, and several smaller islets (Figure 1). The oldest island, Capraia, emerged during volcanic eruptions between 9 and 5 Mya, the other islands emerged between 7 and 5 Mya and the most recent, Pianosa, emerged about 3 Mya. Some islands were repeatedly connected to the continent due to the Pleistocene sea-level oscillations (Barbato et al., 2018). Pianosa is almost flat, with a maximum elevation of 29 m a.s.l., while all the other islands and Argentario are mountainous, the maximum elevation of 1,017 m a. s. l. being reached at Monte Capanne on Elba Island. Small perennial water courses occur on Elba and Argentario, while natural permanent

FIGURE 1 The seven major islands of the Tuscan Archipelago, and the former island of Argentario, currently connected to the Italian mainland through two narrow strips of sand



ponds are present on Capraia, Giglio and Montecristo. The climate of the archipelago is Mediterranean, with mild winters, hot and very dry summers, low annual rainfall, and summer drought. Geographic features and land use vary significantly across islands (Table 1).

Despite its small overall surface, the Tuscan Archipelago hosts an extremely rich vascular flora, including more than 1,500 sub-generic taxa, and a huge amount of floristic data, collected from 1830 onward, is available (Chiarucci et al., 2017). This flora is a subset of that of the Italian Peninsula but it also includes several taxa that are endemic to one or a few islands (e.g., *Centaurea aetaliae*, *Linaria capraia*, *Crocus ilvensis*, *Viola corsica* subsp. *ilvensis*) or to the Sardinian-Corsican biogeographic domain. The flora of the archipelago has undergone major changes during the last two centuries, with a general reduction of native species (−10.7%) and an increase of alien species (+132.1%); a dramatic reduction of annual species was also remarkable. All these effects – mostly due to land-use change and habitat transformation – were caused by the switch from extensive agro-pastoral activities to a tourism-based economy (Chiarucci et al., 2017). The vegetation of the archipelago has been deeply investigated for descriptive and/or mapping purposes (e.g., Foggi et al., 2006, 2008, 2011; Foggi and Pancioli, 2008; Viciani et al., 2011, 2016, 2018). The data source for the calculation of habitat areas was the habitat map of “Map of Nature Informative System” (<https://www.isprambiente.gov.it/it/servizi/sistema-carta-della-natura/carta-della-natura-alla-scala-1-50.000/toscana>).

2.2 | Data assembly

We assembled a database including all the vegetation plot data that we retrieved from published and unpublished sources, most of which were recorded during the last four decades for phytosociological description of the local vegetation. These plots were sampled from 1975 to 2010 and had a large variation in grain size (from less than 1 m² to 900 m²). Almost all the plots were sampled with phytosociological goals, using opportunistically located units and the Braun-Blanquet cover scale. We geolocated all the plots for which it was possible to find geographic information, while the others were simply referred to the island. Each plot was referred to a habitat type according to the second level of EUNIS classification (Appendix S1), on the basis of original plot descriptors and dominant plant species (Angelini et al., 2009). Species nomenclature was standardised following Bartolucci et al. (2018) for native species and Galasso et al. (2018) for alien species.

2.3 | Data analyses

From the plot database, we retrieved only the species occurrence data. To test if the plot data were suitable for the analysis of biogeographic patterns, we compared the cumulative number of species per island recorded by the plot data with those known from the island floras as estimated by the most recently published floras



TABLE 1 Basic geographic and ecological information for the seven islands of the Tuscan Archipelago and Argentario

Island	Area (km ²)	Elevation (m a.s.l.)	Isolation (km)	Inhabitants (n)	Prevalent land use		
					Urbanization	Agricultural	Natural
Elba	223.5	1,017	9.21	32,090	Relevant, mainly coastal but also in the interior	Relevant, but decreasing. Mainly vineyards	Woods, large and widespread shrublands and open rocky areas, and coastal habitats
Argentario	60.23	634	0	12,462	Relevant, mainly coastal but also in the interior	Present, but poorly significant	Woods, shrublands, open rocky areas and coastal habitats
Giglio	21.21	496	14.32	1,399	Relevant, mainly coastal	Formerly relevant (mainly vineyards and cultivated terraces), but mostly abandoned nowadays	Woods, shrublands, open rocky areas and coastal habitats
Capraia	19.72	445	27.05	407	Small settlements	Formerly relevant (mainly vineyards and cultivated terraces), but mostly abandoned nowadays	Shrublands, open rocky areas and coastal habitats
Montecristo	10.40	645	40.51	2	Absent	Absent	Shrublands, open rocky areas and coastal habitats
Pianosa	10.24	29	13.30	10	Small settlement and abandoned prison structures	Formerly relevant overall, nowadays entirely abandoned	Anthropic pine plantations, shrublands, open old-field in rapid evolution and coastal habitats
Giannutri	2.32	88	11.46	27	Small settlement in the central area	Absent	Mainly shrublands and coastal habitats.
Gorgona	2.23	255	33.41	147	Small settlements (prison structures)	Present but non-significant	Woods (mainly pine plantations), shrublands, open rocky areas and coastal habitats
Total	349.85			46,544			

Note: Isolation corresponds to the smallest distance of the considered island from the Italian mainland or — in the case of small islets — from the nearest larger island. Additional data concerning the whole archipelago are provided.

TABLE 2 Data illustrating the final plot assembly for each island, showing the number of plots, the proportion of plots, the number of species per island recorded in the plots and by the published floras, and the ratio between the island's species richness recorded by the plots and that recorded in the published floras. Data for the whole archipelago are also given

Island	Area (km ²)	Area (%)	Plots (n)	Plots (%)	Plot density (n/km ²)	Island species richness (plots)	Island species richness (published floras)	Island species richness by plots/ Island species richness by published floras
Elba	223.50	63.9	633	40.6	2.8	557	1,016	0.548
Argentario	60.23	17.2	170	10.9	2.8	343	835	0.411
Giglio	21.21	6.1	100	6.4	4.7	155	579	0.268
Capraia	19.72	5.6	195	12.5	9.9	247	630	0.392
Montecristo	10.40	3.0	88	5.6	8.5	124	373	0.332
Pianosa	10.24	2.9	147	9.4	14.4	222	515	0.431
Giannutri	2.32	0.7	142	9.2	61.6	112	380	0.295
Gorgona	2.23	0.6	85	5.4	38.1	155	495	0.313
Total	349.85	100	1,561	100	4.48	865	1,831	0.472

(Chiarucci et al., 2017). Then, we compared the ISAR fitted on the plot data with those fitted on the published floras. In particular, we fitted the Arrhenius (1921) ISAR ($S = cA^z$), where S is the number of species, A the island area, and c and z are two fit parameters) on the cumulative number of species per island from plot data and on published floras, by using the “*SSarrhenius*” function of the *vegan* R package (Oksanen et al., 2019). Then, we compared the standardised residuals of the two models under the assumption of a perfect correlation. Subsequently, we compared the beta diversity across islands from using plot data with that calculated by using the published island floras. In particular, we calculated the beta diversity across all the possible pairs of islands ($n = 28$) based on the Jaccard (1901) index of dissimilarity ($1 - \text{Jaccard similarity}$), as well as its turnover and nestedness components (Baselga, 2009), by using both the plot data and published floras. Lastly, we compared the results by linear regression under the assumption of a perfect relation. Beta diversity was calculated using the “*beta.pair*” function of the *betapart* R package (Baselga and Orme, 2012).

To detect the role of the specific habitat on species richness, we calculated the Habitat Species–Area Relationships (HSAR) based on the Arrhenius (1921) model, by using the surface area of each habitat type on each island as independent variable, and the cumulative number of species recorded by the plots sampled in each habitat type of each island as dependent variable. The area of each habitat on each island was calculated in a GIS environment by using the previously mentioned habitat maps. In addition, to exclude rare habitats that are present on one or a few islands only and can have extremely specific features, we fitted the same model to a subset including only the data from the habitats that were present on at least six islands. The positive or negative deviation of each island from the HSAR was measured by using the standardised residuals of the habitats belonging to each island, under the assumption that larger islands host larger species pools and thus have higher species richness per habitat. As a consequence, the larger islands should show positive deviation from the HSAR model and smaller islands a negative one. To test this, we applied ANOVA on standardised residuals with island as grouping factor.

To detect the dependence of species richness on habitat type and island identity, we used multiplicative partitioning on species richness. Multiplicative partitioning of diversity across scales is appropriate for the numbers equivalent (as a measure of the effective numbers of elements) of all diversity indices (Jost, 2007). The scales that we considered in the diversity partitioning were plot, habitat type and island identity. The plot scale was based on the original sampling units adopted for collecting the data; despite not being sampled according to a standard scheme (Chiarucci, 2007), they represent the best possible estimate of the local species assemblage. The habitat type was used to represent the ecological and management unit and corresponded to the same habitat type to which the plot was assigned. In order to obtain a hierarchical structure, the same habitats within different islands were considered as distinct entities. Finally, the island represented a natural biogeographic unit. At each scale, the alpha diversity is given by

the mean number of species per sample unit, gamma diversity is given by the mean number of species in the sample unit immediately above the one considered, and beta diversity is given by the effective number of distinct sample units within larger ones. Beta diversity was calculated relative to the gamma value of the same level (function “*multipart*” in R package *vegan*: see Suurkuukka et al., 2012; Oksanen et al., 2019). To test the significance of each component of diversity, we used the deviation of observed values from expected values by using individual-based randomisations. To do this, occurrences of each species were randomly assigned to samples at each level, while preserving the original species occurrences and sample size distributions. We repeated this process 999 times to obtain the null distributions of species richness to be used to test the statistical significance of each diversity component by counting the proportion of null values greater or smaller than the observed value.

To detect the dependence of species composition on habitat type and island identity, we performed a multivariate analysis to assess variation in species composition among the eight islands and the 13 habitat types, by using *non-metric multidimensional scaling* (NMDS) based on the Jaccard dissimilarity index calculated from the species presence–absence matrix. NMDS is a highly robust unconstrained ordination method that can be used in ecology and biogeography (Minchin, 1987). For our purpose, we ran 1,000 three-dimensional NMDS solutions based on random starts, and selected for mapping the solution with the lowest stress value. In order to improve visualisation, NMDS was performed on a subset of the original dataset: we removed one plot that had no species in common with the other plots and two plots that acted as outliers. To test for significant differences in species composition among island and habitat types, we ran a two-factors PERMANOVA (Anderson, 2001; Anderson and Walsh, 2013), by using the eight islands and 13 habitat types as permutation strata, i.e. permutations occur only within each group (function “*adonis*,” R package *vegan*; Oksanen et al., 2019).

3 | RESULTS

3.1 | Plot assembly and species richness data

The assembly of the database resulted in 23,627 occurrences of 865 vascular plant species in 1,561 plots (Table 2). Despite the methodological limitations, due to the lack of a specific sampling design and the opportunistic plot location, the amount of data contained in the database appeared to be abundant and well balanced across islands (Table 2). The number of plots sampled per island was strongly related to the island area ($r = 0.97$, $p < 0.001$), with a tendency of smaller islands to have a higher density of plots (Table 2). The cumulative number of species recorded per island by the plots was strongly related to the island area ($r = 0.94$, $p < 0.001$) and also to the number of sampled plots ($r = 0.92$, $p = 0.001$).

3.2 | Biogeographic patterns

The biogeographic patterns obtained using plot data closely mirrored the patterns obtained from the published floras. The cumulative species richness per island obtained from plot data was well related to the richness known from the published floras ($S_{\text{plot}} = -147.3 + 0.641S_{\text{flora}}$; $R^2 = 0.905$; $p < 0.001$, Figure 2a), with the intercept and slope values of the regression indicating that plot data detected a number of species significantly lower than that recorded on each island by the published flora.

The Arrhenius ISAR model based on island plot data fitted very well ($S = 74.8A^{0.368}$; $R^2 = 0.91$, $R^2_{\text{adj}} = 0.87$), but provided different parameters with respect to those obtained by fitting the same model with the published island floras ($S = 316.7A^{0.216}$; $R^2 = 0.87$, $R^2_{\text{adj}} = 0.82$). The standardised residuals of the ISAR model based on plot data matched quite well with those obtained by the published floras, providing a regression line with the intercept being almost zero. However, two islands showed relatively high deviation in comparison with the two ISAR models ($R^2 = 0.632$; $p < 0.001$; Figure 2b): the flora of Giglio island resulted to be undersampled by the plot data (less than 27% of the species listed in the published flora were detected in the plots, Table 2), while Pianosa island was well sampled (>43% of the species listed in the published flora were detected in the plots).

The beta diversity patterns among pairs of islands detected by the plot data were strongly related to the beta diversity patterns based on the published island floras (Figure 3). However, some differences emerged: in particular, the beta diversity between pairs of islands from plot data was about one third higher than the beta diversity from floras, as shown by the regression slope of 1.3 (Figure 3a); similarly, the turnover and nestedness components of beta diversity from plot data were both higher than those measured using published floras (Figure 3b, c).

3.3 | Effects of habitat type and island identity on species richness

The HSAR model using plot data fitted on habitat area on each island showed a statistically significant but limited capacity of the habitat area to predict the number of species per habitat ($R^2 = 0.34$; $p < 0.001$; Figure 4a). In contrast, the model based on the subset of habitats present in at least six islands (namely B3 – Rock cliffs, ledges and shores, E1 – Dry grasslands, F5 – Maquis, arborescent matorral and thermo-Mediterranean brushes) was able to fit the data quite well ($R^2 = 0.63$; $p < 0.001$; Figure 4b). No significant differences in the standardised residuals per island were found in the two models ($p > 0.05$; data not shown).

3.4 | Effects of habitat type and island identity on species diversity

Multiplicative partitioning of species richness (Figure 5) revealed a lower beta diversity within habitats, supporting a homogeneous

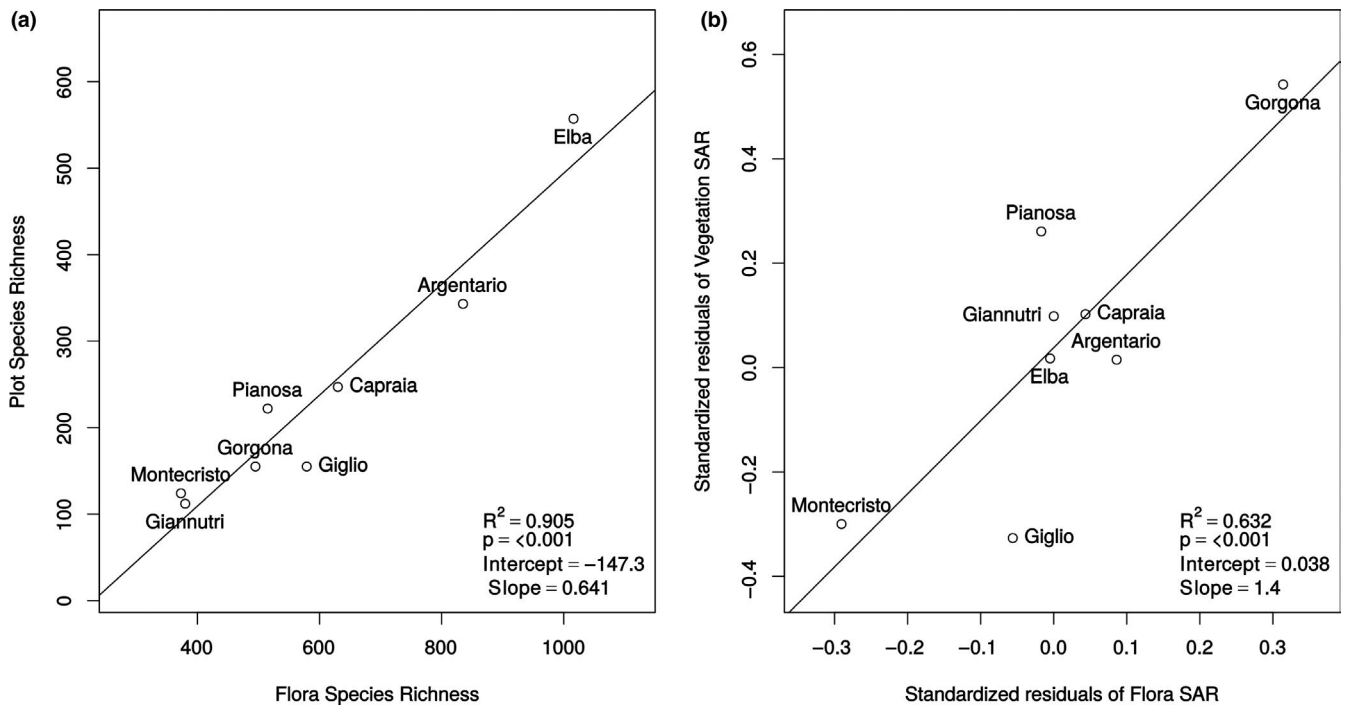


FIGURE 2 Comparison of the species richness patterns obtained by plot data with respect to those known from the floras: (a) Cumulative number of species per islands by plot data versus those by floras; (b) standardised residuals of the Arrhenius ISARs based on plot data versus those based on floras

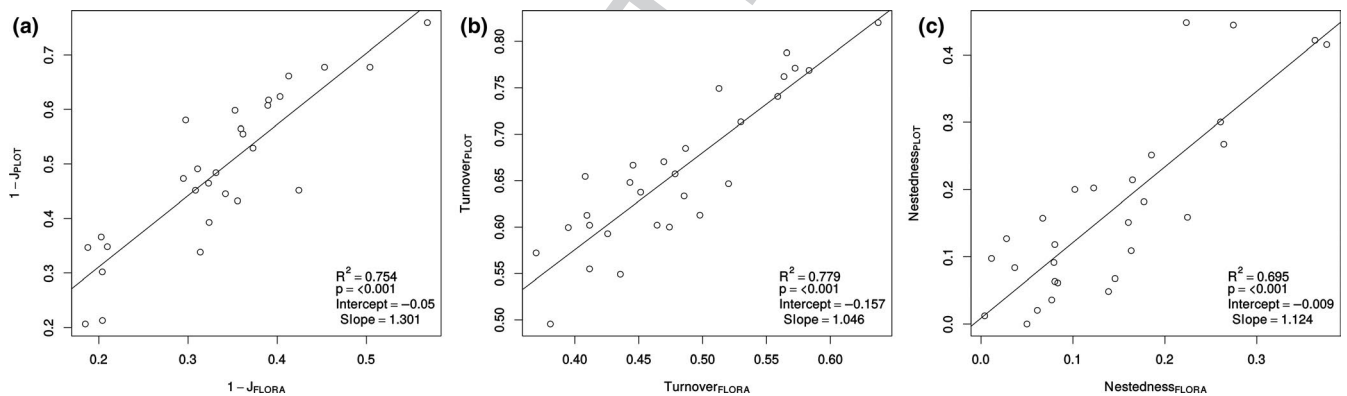


FIGURE 3 Beta diversity patterns among pairs of islands ($n = 28$) measured by plot data (y axis) with respect to the same patterns measured by floras (x axis); (a) total beta diversity measured by Jaccard dissimilarity; (b) turnover component of beta diversity; (c) nestedness component of beta diversity

species composition of all plots classified with respect to island and habitat type. On the other hand, beta diversity across habitats was significantly higher than random expectation, suggesting a certain degree of composition variability across habitats. Also, we found a much higher beta diversity across islands, indicating the major role of island identity in controlling species diversity within the archipelago.

The NMDS ordination of the 1,558 plots classified per island and habitat types had a stress value of 0.183, and the stress versus dimensions plot indicated that three dimensions were best suited for representing our results. The visual interpretation of

the first two axes of the NMDS plot (Figure 6) indicated a large overlap among the plant communities of the different islands, with the size of the island clouds largely corresponding to the island sizes. The habitat types showed some clear differences in species composition. Accordingly, the PERMANOVA analysis (Table 3) showed the role played by island identity and habitat type, with the latter explaining a higher proportion of variance in species composition than the former (0.18 vs. 0.13). The interaction term between island identity and habitat type was also significant, indicating that some habitat types were exclusively linked to some islands.

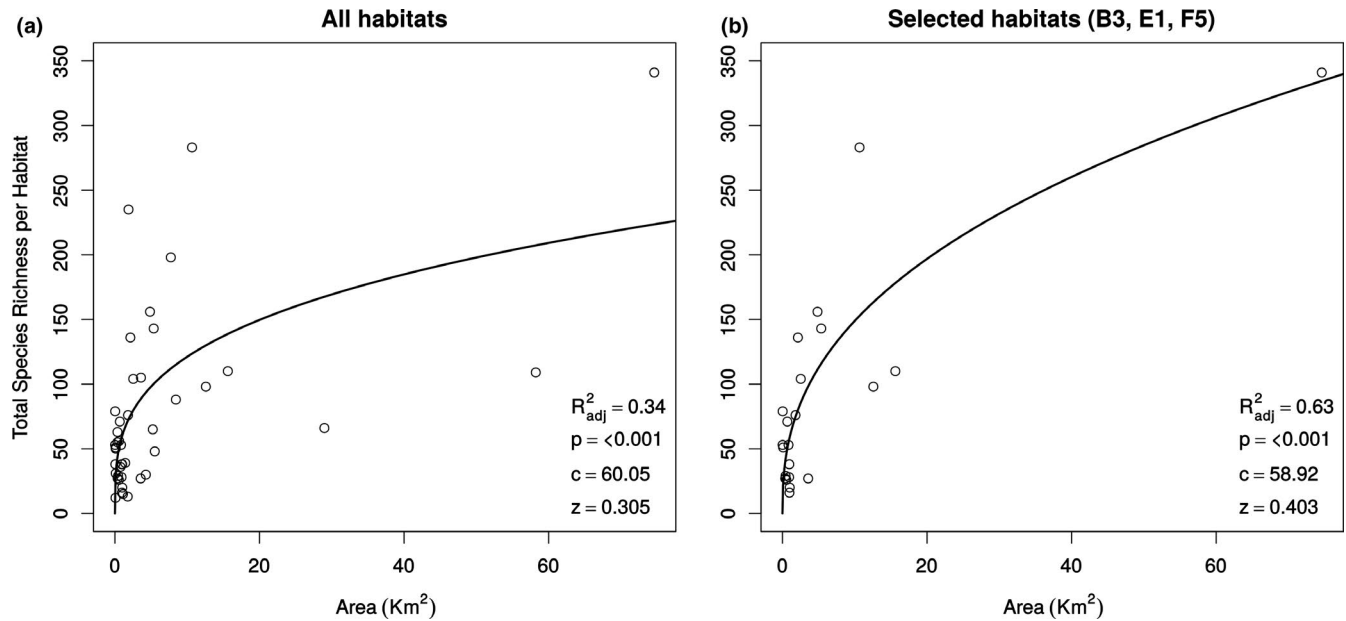


FIGURE 4 ISAR model based on cumulative species richness obtained by plot data and area of each habitat on each island (a) and only for those habitats that are present in at least 6 islands (b)

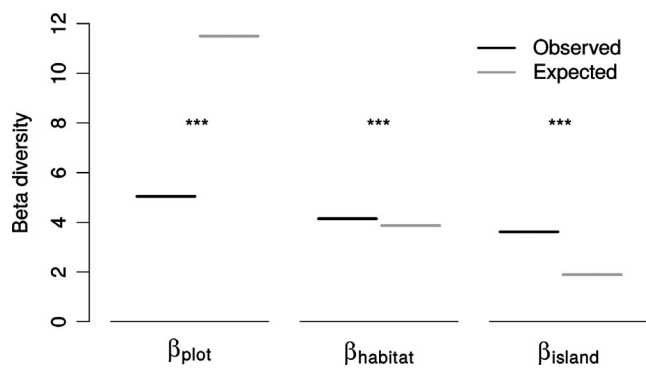


FIGURE 5 Multiplicative partitioning of species richness across scales (plots, habitats and islands) for the vascular plants recorded in the island of the Tuscan archipelago by the 1,561 plots

4 | DISCUSSION

4.1 | Biogeographic models

The first hypothesis we tested addressed the possibility of using assembled plot data, that had been opportunistically collected to survey plant communities, to predict traditional island biogeographic patterns, such as Island Species–Area Relationships (ISARs) or island beta diversity patterns. The results showed that large assemblages of vegetation plot data can detect fundamental biogeographic patterns, such as ISARs and beta diversity among islands, even if the resulting values of the model parameters differ from those obtained by data on complete assemblages. Substantially, biogeographic patterns extracted by large and well-distributed plot data are significant.

Island Species–Area Relationship shapes are naturally affected by the sampling approach used to build up the list of species within

each island (Schrader et al., 2019a, 2019b; Gooriah and Chase, 2020). It is well known that recording species richness is affected by the effort dedicated to the sampling or recording process, effort in terms of duration of the field survey, number of scientists involved and other factors (see, e.g., Sastre and Lobo, 2009; Petřík et al., 2010). Different concepts have been used to describe sampling-effort effects on species richness data. One of the simplest concepts, namely the “botanist effect,” predicts that places where scientists are more present or connected tend to have more species than others (Moerman and Estabrook, 2006; Ahrends et al., 2011). The islands investigated have been the focus of many floristic studies, from at least 1830 (Chiarucci et al., 2017), and can be considered places with high intensity of data collecting, despite which some new species occurrences continue to be recorded (e.g., Gonnelli et al., 2019). The intensity of local botanical studies is mirrored by the remarkably high number of floristic records as well as by the number of vegetation plots, making this archipelago a perfect system for comparing models with different data (sources and types).

The completeness of the survey, in terms of number of recorded individuals or number of sampling units, determines the number of species detected on an island, and several studies have investigated the impact of sampling design and scale on diversity estimates on islands (e.g., Sfenthourakis and Panitsa, 2012; Gillespie et al., 2013; Chase et al., 2019a, 2019b). As a consequence, the completeness of the surveying process is expected to directly affect ISAR model fitting and parameters (Turner and Tjørve, 2005). Species–area relationships are one of the fundamental patterns in ecology and their parameters have been discussed and interpreted from both the statistical and ecological points of view (Connor and McCoy, 1979; Lomolino, 2000; Dengler, 2009). Our comparison of ISARs based on plot data and on published floras supported the dependence of the parameters c and z on data completeness. In fact, despite the general

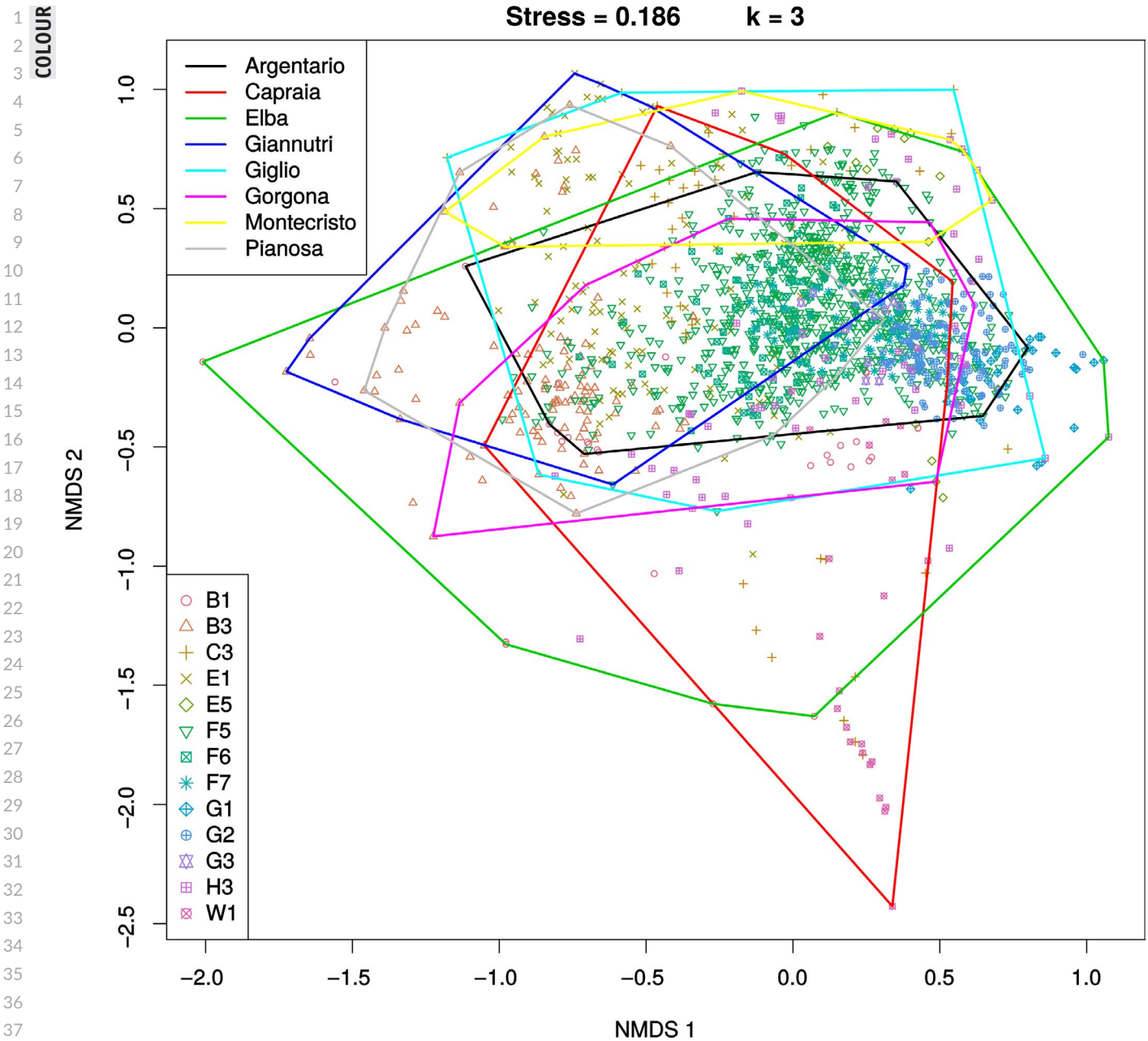


FIGURE 6 NMDS ordination of the 1,558 vegetation plots classified according to the island (cloud polygons) and habitat type (symbols)

TABLE 3 Statistics of the PERMANOVA analysis on the effects of island identity and habitat type on species composition at the plot scale

Factor	df	Sums of Squares	Mean Squares	F.Model	R ²	Pr(>F)
Island	7	60.77	8.68	26.22	0.087	0.001
Habitat	12	81.98	6.83	20.63	0.118	0.001
Habitat * Island	36	53.69	1.49	4.5	0.077	0.001
Residuals	1,505	498.32	0.33	NA	0.717	NA
Total	1,560	694.76	NA	NA	1	NA

Note: We used a vegetation plot database to perform island biogeography tests on the Tuscan Archipelago, showing the potential of such data to model the Island Species–Area Relationship and beta diversity patterns. In such a land-bridge system, species richness is driven by the number of habitats and differences among islands, while local species composition is driven by habitat filters rather than island identity.

1 goodness of fit of the ISAR on the plot data, the resulting parameters
2 were quite different from those achieved by using published floras.
3 In particular the c value, which is an estimate of species richness on
4 an island of unit area (1 km^2), is lower in the plot data (74.8) than in
5 the flora data (316.7), since plot data do not sample all the species on
6 the islands. On the other hand, the z parameter estimated on ISAR
7 from plot data (0.368) is a bit higher than that based on flora data
8 (0.216), but it is well within the range of z values for plants on island
9 ecosystems (Triantis et al., 2003, 2012). It should be noticed that the
10 model based on checklists or floras may also contain biases, since
11 published lists often include extinct, cultivated and/or occasional
12 species. In fact, the completeness of species lists affects biogeo-
13 graphic and ecological results and can depend on the amount of data
14 collection (Sastre and Lobo, 2009; Aranda et al., 2010) but also on
15 the taxonomic treatment (e.g., Bagella et al., 2020).

16 Despite the general agreement of the ISAR model fitting by
17 plot data, the standardised residuals of some islands deviated more
18 markedly from the model, with the two most deviating islands being
19 Pianosa and Giglio (Figure 2). The first is the flattest and ecologically
20 most homogeneous island, with a low disturbance regime (no wild
21 goats, 10 resident people, limited number of visitors), while the sec-
22 ond is mountainous and has a relatively intense disturbance regime
23 (relatively dense population of mouflons, 1,399 resident people, in-
24 tense seasonal tourism). Giglio island has a more species-rich pub-
25 lished flora, but has been surveyed with lower plot density (Table 2),
26 while Pianosa was intensively surveyed in terms of plot density, mak-
27 ing the former a negative outlier and the latter a positive outlier. This
28 type of bias is likely to depend more on plot location rather than on
29 plot density. As demonstrated by Sfenthourakis and Panitsa (2012),
30 a limited number of plots located with a specific sampling design
31 can be used to predict biogeographic patterns, such as insular diver-
32 sity and/or species–area relationship. The evidence reported above
33 highlights the caution needed when using incomplete sampling in
34 estimating ISAR models and parameters. It should be remarked
35 that incomplete data, such as those arising from plots, are the only
36 possible approach for some taxa which cannot be completely sur-
37 veyed (e.g. soil fauna). Therefore, the comparison of assembled plot
38 data versus published floras is particularly useful to understand the
39 changes affecting ISAR models. As also demonstrated in islands by
40 Sfenthourakis and Panitsa (2012) or in protected areas network by
41 Chiarucci et al. (2012), species–area relationships can be modelled
42 without complete data, by using a sampling design with sample in-
43 tensity proportional to the area size and a spatially representative
44 distribution.

45 As for ISAR fitting, the estimation of beta diversity among islands
46 was affected by the type of data, with values being higher in the plot
47 data than in the published floras. Similarly to other measures of bio-
48 diversity, beta diversity is affected by sampling completeness (e.g.,
49 Qian et al., 2018). The subjective nature of sampling and its degree
50 of incompleteness may change the results concerning macroecolog-
51 ical patterns, such as the beta diversity across regions, as was found
52 when using data from herbarium specimens versus plot data (Guerin
53 et al., 2018). The problems associated with the use of incomplete lists

of species have been widely investigated using data from herbar-
ium and/or species occurrence databases such as GBIF (e.g., Guerin
et al., 2018; Qian et al., 2018), but not much investigation has been
dedicated to the use of opportunistic plot data such as those arising
from vegetation plot databases. If resources are limited (a frequent
issue in many conservation projects), when calculating beta diver-
sity it is crucial to extract significant patterns from incomplete data.
This has been clearly pointed out for palaeontology (Forcino et al.,
2015), but it can similarly be applied in ecology and biogeography.
Beta diversity is affected by the completeness of the species lists,
but reliable data and a correct ranking of the beta diversity measures
can be achieved by using data on the most abundant species per site,
a standard procedure in palaeobiology (Roden et al., 2018). In the
case investigated here, the beta diversity patterns achieved by plot
data matched those obtained from complete data, even if the latter
were higher in terms of absolute values. Plot data that have been op-
9 portunistically collected to describe the structure and composition
of vegetation are likely to include the most abundant species on a
site, an island in the present study, and thus, if available in quantity,
they are good enough to describe beta diversity patterns. A recent
proposal of collecting data with a standardised sampling scheme on
islands (Borges et al., 2018) can contribute to improving the use of
plot-based data to disentangle island biogeographic patterns.

4.2 | Habitat effects on species richness

The second hypothesis we tested focused on the possible effect of
habitat area as an independent predictor of species richness within
island, through a Habitat Species–Area Relationship (HSAR) and in-
dependently from island identity. Our results supported this hypoth-
esis rather well, even if they showed a reduced predictive capacity
when tested on all the habitat patches, while the tested hypothesis
fitted quite well when applied to a set of habitats spread across most
of the islands.

Unambiguously, the area of each habitat type within each island
is a driver of the richness for those species which are directly or indi-
rectly associated to the habitat itself. This pattern can be predicted
by HSAR, with the total species richness of an island resulting from
the combination of the number of habitats and their size (Tjørve,
2002). Our results demonstrated that the species richness within
the types of habitats present in the archipelago is predictable by the
size of the area of the habitat, as shown by the relatively good fitting
of the HSAR. However, it is known that habitat specialist species on
islands can be more linked to the past than to the current habitat
area (e.g., Otto et al., 2017). This is also a cause of future habitat-
and taxon-specific extinction debts for the species strongly linked to
specific habitat types (Otto et al., 2017). In the studied archipelago,
major land-use changes have happened during the last century, in
particular the abandonment of traditional agro-pastoral practices,
with the consequent reduction of some groups of species, such as
the annual plants linked to anthropogenic disturbance (Chiarucci
et al., 2017).

Besides of the area of occupancy, HSAR can be influenced also by the intensity of biotic relationships among the islands, related to the topographic position of each island within the archipelago (Torre et al., 2018). The modularity of habitat networks and the topological role of habitat patches among the islands can change (Trøjelsgaard et al., 2013), thus influencing the prediction accuracy of HSAR based only on the size of the area of a given habitat, particularly if that habitat is linked to one or few islands (Figure 4a).

4.3 | Habitat type or island identity effects

The third hypothesis we tested was to disentangle the role of the habitat type and island identity in controlling species richness and composition. The effects on species richness were tested by using multiplicative partitioning of species richness, to provide independent components of species diversity (Baselga, 2009). Habitat type and, especially, island identity contributed more than expected to the total species richness. Similarly, species composition was significantly controlled by both habitat type and island identity, but with a different ranking with respect to that observed for species richness. Thus, island identity is the most relevant factor driving species richness, while habitat type is the one controlling species composition.

The dominant role of macroscale ecological drivers, such as the case of island identity here, in controlling the total species richness of a system is a well-known process, that also emerges in continental units such as ecoregions (e.g., Gering et al., 2003), nature reserves (e.g., Chiarucci et al., 2012), or grassland patches within a forest landscape (e.g., Crist and Veech, 2006). Thus, the broadest spatial scale controls the total number of species in a biological assemblage, and this is particularly important in insular systems, where isolation controls local evolutionary and ecological processes (Whittaker et al., 2017). In a land-bridge system, as is the Tuscan Archipelago, the large-scale process is represented by the differences among islands in terms of paleogeography, topography and land-use history. The complexity of such drivers explains the extremely high species richness of this archipelago observed not only for plants (Chiarucci et al., 2017) but also for terrestrial molluscs (Barbato et al., 2018) and butterflies (Dapporto et al., 2017).

On the other hand, on the local scale, the habitat type was the major driver of the species composition of plant communities, with island identity showing a significant albeit minor role. The role of habitat size and diversity in controlling island species diversity is well known in many insular systems (Tjørve, 2002; Sfenthourakis and Panitsa, 2012; Otto et al., 2017) and this is clearly evident at the scale of local species assemblages, such as those recorded in the plot data. However, the PERMANOVA analysis demonstrated that a signal of island identity was present in the plot data and contributed to a significant amount of the variance in species composition. Island plant communities are thus peculiar in having a specific species composition driven by island identity, even in an archipelago that is close to the mainland. This pattern is very evident on oceanic islands, where each island has its own set of exclusive species in the same

archipelagic habitat (Zobel et al., 2011), but a similar pattern has also been observed here.

5 | CONCLUSIONS

With the present study we demonstrated that large assemblages of vegetation plot data that have been opportunistically collected to describe or monitor local plant communities, can be used to describe fundamental biogeographic patterns. Although the numerical values of the resulting parameters are different, patterns such as Island Species–Area Relationships (ISARs) and beta diversity among islands calculated from vegetation plot assemblages results are concordant with those emerging from complete floras. We also pointed out that, within each island in an archipelago composed of land-bridge islands, the species richness is governed by the amount and size of habitat types, suggesting that changes in the habitat area within one island can deeply affect the species diversity. Additionally, we showed that the total species richness of an archipelago is governed by broad-scale drivers, such as the differences among islands, that control the beta diversity at broader scales; on the other hand, local species composition is more dependent on the type of habitats, even if a significant signal of island identity can be observed. Therefore, vegetation plot data assembled from various sources represent a potentially valid source of information for testing classical biogeographic theories.

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AUTHOR CONTRIBUTIONS

AC conceived the research idea; PZ coordinated and performed the data analyses; RG, MC, BF, DV, LL, BELC and SP provided plot data; FB, ME and MC assembled the database; LC and PA assembled the habitat data. AC drafted the first version of the paper and all the authors contributed to the development of the paper.

DATA AVAILABILITY STATEMENT

The plot data are permanently stored in the database AMS-VegBank (EU-IT-021 – <http://www.givd.info/ID/EU-IT-021>), partner of the European Vegetation Archive (<http://euroveg.org/eva-database>). The dataset used for the analyses is also permanently stored in the Zenodo data repository (<http://doi.org/10.5281/zenodo.4005595>).

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SUPPORTING INFORMATION

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

Appendix S1. Habitat types occurring on the islands of the Tuscan Archipelago

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Graphical Abstract

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We used a vegetation plot database to perform island biogeography tests on the Tuscan Archipelago, showing the potential of such data to model Island Species–Area Relationships and beta diversity patterns. In such a land-bridge system, species richness is driven by the number of habitats and differences among islands, while local species composition is driven by habitat filters rather than island identity.