Research Article

Plant species richness hotspots and related drivers across spatial scales in small Mediterranean islands

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Abstract Small islands represent a common feature in the Mediterranean and host a significant fraction of its biodiversity. However, the distribution of plant species richness across spatial scales—from local communities (alpha) to whole islands (gamma)—is largely unknown, and so is the influence of environmental, geographical, and topographical factors. By building upon classic biogeographic theory, we used the species–area relationship and about 4500 vegetation plots in 54 Central Mediterranean small islands to identify hotspots of plant species richness and the underlying spatial determinants across scales. To do so, we fitted and averaged eight species–area models on gamma and alpha richness against island area and plot size, respectively. Based on positive deviations from the fitted curves, we identified 12 islands as cross-scale hotspots. These islands encompassed around 70% of species and habitat richness, as well as almost 50% of the rarest species in the data set, while occupying less than 40% of the total island surface. By fitting generalized linear mixed models, we found that gamma richness was mainly explained by island area and was weakly related to mean annual temperature (positively) and annual precipitation (negatively). As for alpha richness, after accounting for the idiosyncratic effect of habitats and islands, plot size and gamma richness remained the only significant predictors, showing a positive relationship. This work contributes to the understanding of the patterns and drivers of plant diversity in Central Mediterranean small islands and outlines a useful methodology for the prioritization of conservation efforts.

Key words: biodiversity hotspots, conservation biogeography, species–area relationship, vascular plants, vegetation plots.

1 Introduction

The Mediterranean Basin is one of the global biodiversity hotspots (Myers et al., 2000; Mittermeier et al., 2004). This region occupies less than 2% of the Earth's land while hosting 10% of global plant diversity, that is, ~25 000 species, many of which are endemic (Cowling et al., 1996). This huge biodiversity, partly explained by the considerable environmental heterogeneity and complex geological and biogeo- graphic history of the area (Médail, 2022), is not evenly distributed across the Basin. In fact, it is possible to identify several sub-regional hotspots (Médail & Quézel, 1997) and, within these, even finer-scale hotspots of a few km² in size (the so-called nano-hotspots; see Cañadas et al., 2014). The identification of these 'hotspots-within-hotspots' is key to prioritize conservation actions that maximize the number of species protected when resources are limited (Cañadas et al., 2014).

Within the different subregions, islands contain an outstanding fraction of Mediterranean biodiversity, with the notable presence of many narrow-ranging species and characteristic vegetation types (Médail, 2022). Islands provide habitat for specific plant and animal species and sometimes represent the only refuge for species that have disappeared from continental areas (Petit et al., 2022). At the same time, islands are among the areas most exposed to anthropogenic pressures, like species invasion, seasonal tourism, and climate change, with the latter linked to increased fire frequency and sea-level rise (Médail, 2017; Petit et al., 2022).

While most ecological studies focused on large and medium islands, small islands represent the most common element within the Mediterranean Basin. Small islands encompass a large set of environmental and biogeographic situations (Médail, 2017) and are even more sensitive to exogenous disturbances and environmental stochasticity (Greuter, 1995). Moreover, these islands are essential stepping stones for migratory birds during their journey across the Mediterranean Sea, offering habitats for shelter and fuel replenishment during stopovers (Barboutis et al., 2022). Yet, the vegetation patterns of small islands have been less investigated compared to those of larger islands (Médail, 2017, 2022), and floristic inventories are often incomplete, even if small islands are known for hosting many endemic or specialist species (Greuter, 1995). Furthermore, drivers of plant diversity in small islands usually differ from those of larger ones, with unidentified scale dependencies. Although plant diversity in small islands is largely linked to local environmental features like topography, substrate composition, and exposure to salt spray (Médail, 2017), the relative contribution of these factors against macroclimate and stochastic processes is still unknown. It is therefore necessary to identify biodiversity patterns and their underlying drivers on small islands, whose protection should maximize the effectiveness of conservation investments in the Mediterranean region.

Hotspot identification is one of the main concepts supporting systematic conservation planning (Kukkala & Moilanen, 2013), that is, a structured decision analysis approach for the design and implementation of conservation actions based on the application of mathematical methods for the spatial allocation of protected areas (Margules & Pressey, 2000; Langford et al., 2011; Villarreal-Rosas et al., 2020). In this respect, conservation biogeography, that is, the application of biogeographic principles, theories, and analyses to optimize strategies for the conservation of biodiversity (Whittaker et al., 2005), may contribute to the prioritization of conservation efforts in small islands. In fact, the species–area relationship—one of the few laws of ecology (Lomolino, 2000a)—can be applied to identify biodiversity hotspots: when fitting a species–area model to empirical data, regions located above the curve can be considered as hotspots because they contain more species than expected by their area (Fattorini, 2021). Previous studies already used species–area curves to identify biodiversity hotspots in different island (or island-like) systems and considering distinct taxonomic groups, for example, birds (Temple, 1981), insects (Werner & Buszko, 2005; Fattorini, 2006), plants (Jiménez-Alfaro et al., 2021), benthic invertebrates (Guilhaumon et al., 2012), and vertebrates (Guilhaumon et al., 2008; Mazel et al., 2014). Yet, most

studies generally focused on the total number of species (counted or estimated) for each island (i.e., gamma diversity), thus neglecting the actual co-occurrences within local plant communities (i.e., alpha diversity). However, areas with low gamma diversity might still host local assemblages with high species richness and vice versa (Wilson et al., 2012; Sabatini et al., 2022). To be effective, conservation strategies should account for the multiscale nature of plant biodiversity and ensure that it is maintained at all levels (Devictor et al., 2010).

Species occurrence data emerging from large data sets of vegetation plots can help unveil biogeographic patterns and investigate drivers of biodiversity across spatial scales (e.g., Chiarucci et al., 2021; Testolin et al., 2021), disentangling the different contributions of environmental, geographical, and topographical factors. While allowing analyses at the level of local plant communities, vegetation plot data are often used to estimate the size of local species pools (Gotelli & Colwell, 2011; Bruelheide et al., 2020), overcoming the lack of complete species lists. This is particularly relevant on islands whose floras are not well known (Borges et al., 2016). Yet, most collections of fine-grained vegetation plot data have limited spatial extent, limiting their usefulness in conservation biogeography research. The recent establishment of large vegetation plot databases, aggregating and standardizing data across collections, has paved the way for a new wave of biodiversity research spanning across spatial scales (Testolin et al., 2021; Sabatini et al., 2022). The AMS-VegBank database (Alessi et al., 2022) represents a unique source of vegetation plot data in island regions surrounding the Italian peninsula, some of which (i.e., the large Tyrrhenian islands) were already identified as a biodiversity hotspot in the Central Mediterranean (Médail & Quézel, 1997).

In this work, we used vegetation plot data and built upon classic biogeographic theory to investigate the patterns and drivers of plant species richness across different spatial scales in small islands in the Central Mediterranean. Specifically, we aimed to (i) identify gamma and alpha species richness hotspots and coldspots using the species–area relationship and (ii) understand the effect of environmental, geographical, and topographical factors on gamma and alpha species richness.

2 Material and Methods

2.1 Study area and data set
The study area encompasses islands and islets surrounding the Italian peninsula, Sicily, and the Maltese archipelago (Table 1). Our data set included differently sized islands, ranging between 0.0004 and 245.8 km², located between 8°–15° longitude and 35.5°–45.5° latitude. The islands differ in terms of shape, maximum elevation, and distance from the mainland and geological origin (i.e., continental vs. volcanic). The climate of the study area is typically Mediterranean, characterized by hot and dry summers and cool, rainy winters. The mean annual temperature and annual precipitation in the islands range between 15 and 19 °C and between 380 and 1200 mm, respectively, representing half-way conditions along the basin's temperature and dryness

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Table 1 Biogeographic characteristics of 54 Central Mediterranean islands included in the study

Archipelago	Island	Area (km²)	Isolation (km)	Origin	MAT	AP	Elev	S	PT	EA	EU	EM	SM	E	O
Aegadian	Favignana	20.5524	12.61	Continental	18.2	558	314	271	3	3	2	23	55	5	7
	Levanzo	6.0477	13.64	Continental	17.9	575	278	282	4	2	1	26	55	5	6
	Marettimo	12.2141	36.39	Continental	16.8	780	686	173	3	2	2	18	51	10	13
Aeolian	Alicudi	4.8933	54.48	Volcanic	17.2	688	675	197	7	3	2	28	43	4	19
	Basiluzzo	0.246	44.63	Volcanic	18.4	615	165	18	6	0	0	33	44	6	12
	Filicudi	9.1119	47.81	Volcanic	17.3	714	773	273	7	3	2	28	46	3	12
	Lipari	37.2447	32.75	Volcanic	17.3	773	602	366	8	2	3	28	40	3	16
	Panarea	3.1553	42.9	Volcanic	17.7	628	421	196	6	3	2	23	46	8	15
	Salina	25.8914	41.56	Volcanic	17.4	731	962	291	6	2	3	28	40	5	13
	Scoglio Faraglione	0.0044	44.11	Volcanic	18.4	649	35	14	0	0	0	7	64	29	0
	Stromboli	10.3969	56.78	Volcanic	16.6	730	926	134	6	1	2	27	37	9	17
	Vulcano	20.7178	22.94	Volcanic	17.3	812	499	213	9	2	3	30	34	4	16
Campanian	Capri	10.3498	8.63	Volcanic	16.5	824	589	102	9	1	5	22	35	11	18
	Procida	4.0681	4.39	Volcanic	17.3	748	91	104	6	1	3	34	34	2	22
	Vivara	0.3281	6.76	Volcanic	17.3	749	110	117	9	3	3	28	41	3	15
Single island	Isola di Capo Passero	0.3184	0.82	Volcanic	18.8	572	21	224	5	1	1	26	52	1	13
Single island	Isola di Cirella	0.071	0.73	Continental	17.1	1156	40	50	12	0	0	34	44	2	8
Cyclopes	Faraglione di Mezzo	0.0004	0.15	Volcanic	18.6	718	20	10	20	20	0	0	60	0	0
	Faraglione Grande	0.0032	0.19	Volcanic	18.6	718	67	33	6	9	0	18	55	3	9
	Isola Lachea	0.0147	0.22	Volcanic	18.6	718	35	55	7	5	0	25	51	2	10
Single island	Dino	0.3334	0.76	Continental	17	1104	100	65	5	0	8	31	42	5	12
Single island	Isola delle Femmine	0.1689	0.83	Continental	18.6	675	35	79	3	3	1	29	56	1	8
Li Galli	Gallo Lungo	0.0437	2.92	Continental	17.6	869	54	46	4	4	0	22	52	7	10
	La Castelluccia	0.0101	2.67	Continental	17.6	865	51	24	8	4	0	17	58	12	0
Maltese	Comino	2.8775	85.11	Continental	19	537	74	117	2	2	1	20	59	5	13
	Fungus Rock	0.0075	86.64	Continental	19	517	60	36	6	0	0	28	47	6	14
	Gozo	66.2166	84.81	Continental	18.8	546	30	360	6	3	2	27	43	5	14
	Malta	245.8149	95.06	Continental	18.7	553	253	467	7	3	1	26	43	4	14
Single island	Pantelleria	83.9176	78.7	Volcanic	17.2	637	836	236	3	2	2	26	52	4	9
Pelagian	Isola dei Conigli	0.0338	133.35	Continental	19.1	384	26	66	2	5	0	21	59	5	10
	Lampedusa	20.286	135.82	Continental	19	381	133	317	4	2	1	23	51	3	14
	Linosa	5.6048	163.72	Volcanic	18.9	428	195	219	5	2	0	22	51	3	15
Pontine	Gavi	0.1703	32.34	Volcanic	17.6	725	101	40	8	0	2	20	60	5	4
	Palmarola	1.2361	35.9	Volcanic	17.4	712	262	110	5	0	1	27	54	5	9
	Ponza	7.5507	35.94	Volcanic	17.3	718	280	267	7	3	3	30	41	3	12
	Santo Stefano	0.3088	46.97	Volcanic	17.6	702	89	48	8	4	2	29	42	2	12
	Ventotene	1.3625	47.07	Volcanic	17.6	700	139	131	7	2	0	38	34	4	15
	Zannone	1.0635	28.12	Volcanic	17.4	753	71	142	3	0	3	25	58	0	9

Chorological spectrum (%)

Table 1 Continued

Archipelago	Island	Area (km²)	Isolation (km)	Origin	MAT	AP	Elev	S	Chorological spectrum (%)						
									PT	EA	EU	EM	SM	E	O
Spezzino	Palmaria	1.6437	1.02	Continental	15.8	956	191	126	5	3	7	26	37	2	19
Tremiti	Capraia	0.5434	24.53	Continental	16.9	468	53	129	6	2	4	28	50	1	11
	Il Cretaccio	0.0582	23.31	Continental	16.9	473	113	26	15	0	4	31	38	0	12
	San Domino	2.1956	22.61	Continental	16.7	476	116	311	7	3	4	31	39	3	11
	San Nicola	0.5021	23.3	Continental	16.9	472	75	220	6	3	3	30	42	4	10
Tuscan	Capraia	18.9445	29.51	Volcanic	15.8	613	447	225	6	5	4	26	36	5	16
	Elba	224.4408	24.01	Continental	15.5	668	1019	509	8	5	8	28	31	5	17
	Giannutri	2.4157	22.21	Continental	16.9	598	496	115	7	5	1	30	46	3	9
	Giglio	21.7385	26.69	Continental	16.2	605	254	149	8	3	3	32	40	4	9
	Gorgona	2.1517	34.32	Continental	16.1	726	190	152	9	4	5	30	40	3	10
	Monte Argentario	60.4076	0	Continental	15.6	754	635	281	6	4	8	27	38	3	14
	Montecristo	10.4202	62.09	Continental	15.9	570	645	119	8	3	3	26	33	6	21
	Pianosa	10.5436	44.93	Continental	16.9	550	29	215	10	4	2	31	42	3	6
Single island	Ustica	8.1428	54.71	Volcanic	18.1	573	244	115	8	2	1	29	44	2	16
Venetian	Lido	8.5025	7.99	Continental	14.6	888	3	94	13	10	9	33	13	1	21
	Pellestrina	3.7195	6.96	Continental	14.8	836	3	42	10	5	12	31	17	2	23

AP, annual precipitation (mm); E, endemic; EA, Eurasiatic; Elev, maximum elevation (m); EM, Euromediterranean; EU, European; MAT, mean annual temperature (°C); O, other; PT, Paleotemperate; S, observed number of species; SM, Stenomediterranean.

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gradients (Hofrichter, 2001). The initial data set of vegetation plots was extracted from the AMS-VegBank database (Alessi et al., 2022) and consisted of 5500 records distributed among 54 islands, with 1731 recorded vascular plant taxa. We proceeded by applying several pre-processing steps as follows (Fig. S1). First, species names were harmonized using the package TNRS (Maitner & Boyle, 2022) in R (R Core Team, 2022), updating the names according to the most recent nomenclature and merging subspecies and varieties to the species level by combining their cover values while accounting for possible overlaps (Fischer, 2015). When the geographic coordinates were missing but island and elevation information was available (672 plots), we estimated plot locations by randomly assigning the coordinates of raster cells with the same elevation ($\pm$10 m) as the plots in that island, using the SRTM-3 digital elevation model at 30 m resolution (Farr et al., 2007; NASA & JPL, 2013).

The data set was filtered further by removing records with incomplete taxonomic identification. When taxa identified to the genus level or higher taxonomic rank represented $\geq$10% of the plot vegetation cover, the corresponding plot was discarded (10 plots); otherwise, we removed those taxa from the plot record. Following the same criterion, we excluded plots dominated by neophytes (229 plots) using the checklist by Galasso et al. (2018) and removed the remaining neophytes from the species list. The resulting data set consisted of 5261 plots and 1574 species.

Then, we classified the plots according to the EUNIS habitat classification (Moss, 2008) using the R implementation (Bruelheide et al., 2021) of the EUNIS-ESy expert system, which is based on species composition and geographic location (Chytrý et al., 2020). The EUNIS classification is hierarchical in nature, with level 1 habitats distinguishing broad units (e.g., T: forest and other wooded land) and levels 2 and 3 habitats providing more detailed information about location and species composition (e.g., T1: deciduous forest; T1A: Mediterranean thermophilous deciduous forest; T1E: *Carpinus* and *Quercus* mesic deciduous forest). When the classification algorithm could not classify the plots into level 3 habitat types due to the lack of diagnostic species or the presence of unusual co-occurrences (1957 plots, of which 1353 were classified into level 1 habitats), we performed a supervised noise clustering of such plots based on species composition using the "vegclass" function of the package vegclust (de Cáceres et al., 2010). This step was aimed at assigning unclassified plots to the most similar EUNIS habitat based on their overall species composition—in addition to diagnostic species—while at the same time excluding outlier plots that do not resemble any identified habitat (for additional details on supervised noise clustering and practical examples, see the package documentation). First, we assigned unclassified records (604 plots) to level 1 habitats. Then, for each level 1 habitat group, we assigned the unclassified plots to level 3 habitats. After that, 4674 plots were successfully assigned to level 3 habitats, 472 plots were assigned to level 1 habitats, and 115 plots remained unclassified. Then, in order to restrict the focus to terrestrial habitats only, we excluded plots belonging to marine, wetland, and inland water habitats (EUNIS level 1A, Q, and C classes; 253 plots), which were also unevenly surveyed in our data set (42% of them were located in Malta). We further

removed nine plots belonging to markedly anthropogenic habitats, that is, V11 (arable land and market gardens) and V12 (mixed crops of market gardens and horticulture), to avoid the inclusion of species that may be exclusively associated with these environments. Finally, we removed 521 plots that we could not classify into level 3 habitats (which were either classified into level 1 habitats or remained unclassified). Despite the extensive cleaning, only 67 species out of 1574 were lost. The final data set consisted of 4478 plots between 0.04 and 900 m² located on 54 islands and belonging to 49 EUNIS habitats, with 1507 recorded plant species.

To further characterize the islands from the biogeographic point of view, information on species' chorology was derived from Pignatti (2005) and, in case of no match (316 species), from the Acta Plantarum web portal (www.actaplantarum.org). Using this information, we estimated the chorological spectrum of each island based on the vegetation plot data. Chorological types that represented less than 10% of species across all islands were grouped into a single type named "Other". The chorological spectra of the 54 islands were dominated by six chorological types: Paleotemperate (0%–20% of species in each island), Eurasiatic (0%–20%), European (0%–12%), Euromediterranean (0%–38%), Stenomediterranean (13%–64%), and Endemic (0%–29%) (Table 1). Notably, the "Endemic" type as provided in the above-mentioned sources does not refer to island- or archipelago-endemics only, but also to regional and national endemic species.

2.2 Measures of species richness

We estimated vascular plant species richness at the community and island spatial scales (Fig. S1). At the community scale, we calculated alpha richness simply as the number of species for each plot. At the island scale, we estimated gamma richness using the Chao2 asymptotic richness estimator (Chao, 1987) with the package iNEXT (Chao et al., 2014; Hsieh et al., 2020) and calculated 95% confidence intervals (CIs) of the point estimates. The use of another asymptotic richness estimator (i.e., first order Jackknife) led to similar results (not shown). These approximations did not aim to represent the total number of species per island, but rather to extract as much information as possible from the plot data and allow meaningful comparisons among islands.

Given that our data set included plots of very different sizes, we evaluated the effect of plot size on gamma richness estimates. To do so, we compared the same estimates using three subsets of different plot sizes (small, <10 m²; medium, $\geq$10 and <50 m²; large, $\geq$50 and <100 m²; and very large, >100 m²). For those islands where $\geq$25 plots of at least two different sizes were available, we compared richness estimates obtained from the different subsets (Fig. S2). We found that, regardless of the subset used, the relative differences among islands were largely preserved, with a few exceptions (i.e., Elba, Malta, Ponza, San Domino). However, discrepancies in richness estimates did not change consistently with plot size class across islands, suggesting that such differences were rather driven by distinct vegetation types being sampled with differently sized plots.

Furthermore, the islands in our data set were characterized by very different sampling intensities (Table S1),

which may have introduced some bias in the estimation of gamma richness. Thus, we analyzed the relationship of island area with the number and density of plots per island, as well as the relationship between density of plots, gamma richness estimates, and a measure of sampling completeness, namely, the percent increase of estimated gamma richness (Chao2) compared to that observed. Such relationships were assessed by calculating the Pearson correlation coefficient of log-transformed values. We found that, while larger islands generally contained more plots ($r = 0.74$), their density strongly decreased with island size ($r = 0.90$). However, contrary to expectations, higher plot densities corresponded to overall lower estimated gamma richness ($r = -0.64$), while no relationship was found between plot density and the percent increase in estimated gamma richness (Fig. S3). These analyses suggest that over- and under-sampling had little effect on the final gamma richness estimates (i.e., extensive samples are likely redundant in terms of habitats and species, while smaller ones are still capable of encompassing most of the compositional variability), confirming the good representativeness of the data set.

2.3 Hotspot identification and analysis

Plant species richness hotspots and coldspots were identified by fitting species–area curves, both at the scale of whole islands (gamma) and vegetation plots (alpha) (Fig. S1). At the gamma scale, species richness estimated using Chao2 was modeled against island area. At the alpha scale, plot species richness was modeled against plot size. To reduce the bias due to species–area model selection (Veech, 2000; Fattorini, 2006), we fitted four convex functions (i.e., power, logarithmic, negative exponential, Monod) and four sigmoidal functions (i.e., Gompertz, logistic, persistence function-2, and Weibull-3; for more details and formulas, see Triantis et al., 2012), and calculated the weighted average curve with 95% CIs using the sars package (Matthews et al., 2019), in a similar way as in Guilhaumon et al. (2008).

To identify hotspots, we adopted the methodological framework described in Fattorini (2006, 2021) based on the deviations from the empirical species–area relationship: areas located above the fitted curve (positive residuals) are considered as candidate hotspots, while areas below (negative residuals) are considered as candidate coldspots. We defined gamma hotspots as islands where more species can be found than simply expected by their area and alpha hotspots as islands where plots (i.e., local plant communities) generally host more species than expected by their size compared to those of other islands. Specifically, gamma hotspots were selected as those islands whose the lower boundary of Chao2's confidence interval (CI) was higher than the upper boundary of the average species–area curve's CI. Conversely, gamma coldspots corresponded to those islands whose upper boundary of Chao2's CI did not intercept the species–area curve's CI. Similarly, alpha hotspots (coldspots) were identified as those islands with more than (less than) a given percentage of their plots located above (below) the CI of the average species–area curve. To define such a threshold, we first calculated the percentage of plots above the CI of the species–area curve for each island. Then, we

calculated the 90th and 95th percentiles of the distribution of these percentage values across islands, thus defining two thresholds (70% and 80% of plots, respectively) for the identification of alpha hotspots and coldspots. For the final cross-scale hotspot selection, we considered both spatial scales, meaning that we excluded those islands that were hotspots at one scale (e.g., alpha) but showed negative residual values at the other scale (e.g., gamma).

To assess the effectiveness of the identified cross-scale hotspots in representing plant species diversity of the 54 Central Mediterranean islands, we quantified the proportion of species and the proportion of EUNIS habitats that were included in the selected hotspots (Fig. S1). We also calculated an empirical index of rarity for each species based on their geographical range, habitat specificity, and population size (Maciel, 2021) using the rrindex package (Everton, 2023). The index considers species as rare when they are found in a small fraction of the overall study area (based on plot coordinates), in few habitats (based on level 3 EUNIS habitats), and when they are characterized by low local abundance (based on species cover per plot). Each of these three components is used to calculate an average index of rarity that varies from 0 (abundant species) to 1 (rare species) (Maciel, 2021). After splitting the species into four quartiles based on their rarity score (Q1: very common species, Q2: common species, Q3: uncommon species, Q4: rare species), we calculated the proportion of species included in the cross-scale hotspots for each quartile and the proportion of species belonging to each quartile for each island (Fig. S1).

Finally, to contextualize our findings into the framework of existing conservation measures, we retrieved information on the current extent of terrestrial protected areas belonging to the Natura 2000 network for the islands in our data set using the latest available spatial layer provided by the European Environment Agency (Natura 2000—version 2021 revision 1, October 2022; available at https://sdi.eea.europa.eu/catalogue/srv/api/records/dae737fd-7ee1-4b0a-9eb7-1954eec00c65).

2.4 Predictors and statistical analyses

To analyze the drivers of species richness, we retrieved a set of environmental, geographical, and topographical variables from online databases (Fig. S1). We extracted mean annual temperature, annual precipitation, and potential evapotranspiration at each plot location from CHELSA V2.1 (Karger et al., 2017, 2021). Island-level values of the climatic predictors were estimated as the mean (i.e., average climate) and the standard deviation (i.e., climatic variability) of the plot-level values. Isolation from the nearest source landmass was calculated as the distance from the islands' centroid to the closest continental boundary, including large islands (i.e., Corsica, Sardinia, and Sicily). Island area was calculated as the two-dimensional surface of each island. A measure of island shape (i.e., eccentricity) was estimated as the ratio between the longest and the shortest axes of each island, with the aim of providing an indication of the relative amount of area shielded from the sea. Maximum elevation and island geological origin were derived from online sources (e.g., www.wikipedia.org) and from local experts. At the island

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level, area, maximum elevation, eccentricity, and isolation were log-transformed to reduce skewness. Next, we analyzed the correlations among the above-mentioned predictors at the island level with the Pearson correlation coefficient.

To identify the drivers of gamma richness, we tested the individual influence of each selected environmental, geographical, and topographical predictor while accounting for the additive effect of island area (Fig. S1). We used Poisson generalized linear mixed-effects models (GLMMs) with the "glmer" function of the R package lme4 (Bates et al., 2015). An area-only model was also fitted to test for the effect of island area per se and compare the goodness of the fits. To control for overdispersion and reduce the risk of Type I errors, we added an observation-level random effect (OLRE) to the models, that is, a unique level of a random effect for each data point that models the extra-Poisson variation present in the data (Harrison, 2014). The ratios between the sum of squared Pearson's residuals and the residual degrees of freedom of the fitted models with OLRE indicated no additional overdispersion. Finally, we checked for the presence of spatial autocorrelation in model residuals using Moran's I test with the Dharma package (Hartig, 2022) and found none. Models were compared using the Akaike information criterion for small sample sizes (AICc) in addition to marginal R^2 and conditional R^2 (mR^2 and cR^2), calculated using the MuMIn package (Bartoń, 2022). Given that the only random effect in the models was an OLRE, mR^2 = cR^2.

We modeled alpha richness by fitting Poisson GLMMs including mean annual temperature, annual precipitation, and potential evapotranspiration, as well as island geological origin and gamma richness estimated with Chao2, while controlling for the log of plot size (Fig. S1). Again, we controlled for overdispersion by adding an OLRE. Additionally, given that the plot-level predictors were derived from digital data sets at 1 km resolution and to reduce the effect of spatial autocorrelation, we also fitted an additional random effect for each 0.01° cell (c. 1 km^2). We also tested for habitat and island effects by fitting two more models: one with a random intercept for habitats and the other with an additional random intercept for islands. We tested for spatial autocorrelation using Moran's I test as described above. The three resulting models (with and without the random intercept for habitats and the one with an additional random intercept for islands) were compared using AICc, mR^2, and cR^2.

3 Results

The final data set of 4478 plots was classified into 49 level 3 EUNIS habitats (Table S1). The five most common habitats were V32 ("Mediterranean subnitrophilous annual grasslands"; 641 plots), S51 ("Mediterranean maquis and arborescent matorral"; 598 plots), N32 ("Mediterranean and Black Sea rocky sea cliff and shore"; 568 plots), R1E ("Mediterranean tall perennial dry grassland"; 449 plots), and S54 ("Thermomediterranean arid scrub"; 334 plots). The most widespread forest habitat, which was the sixth most common habitat in our data set, was T21 ("Mediterranean evergreen *Quercus* forest"), with 246 plots. Overall, these six

habitat types encompassed 63% of the data set, with the remaining 1642 plots classified into the residual 43 habitats. The islands with the smallest number of habitats were Faraglione di Mezzo, Fungus Rock, Gavi, La Castelluccia, and Scoglio Faraglione (two habitats), while the most habitat-rich islands were Malta (28 habitats), Elba (23 habitats), Gozo, and Lampedusa (18 habitats).

Island species richness estimated with Chao2 ranged from 12 species (Faraglione di Mezzo) to 582 species (Elba) (Table S2). The richest islands after Elba were Malta (513 species), Lipari (407 species), Gozo (402 species), and Monte Argentario (389 species). The least species-rich islands after Faraglione di Mezzo were Scoglio Faraglione (14 species), Basiluzzo (26 species), Il Cretaccio (33 species), and Faraglione Grande (36 species).

On the basis of the average species–area relationship (Fig. 1), we identified 10 gamma hotspots: Elba, Filicudi, Isola di Capo Passero, Lampedusa, Levanzo, Lipari, Ponza, San Domino, San Nicola, and Vivara. Conversely, 12 islands were identified as gamma coldspots: Basiluzzo, Gallo Lungo, Gavi, Giglio, Il Cretaccio, Lido, Montecristo, Pantelleria, Pellestrina, Scoglio Faraglione, Stromboli, and Ustica. As for alpha
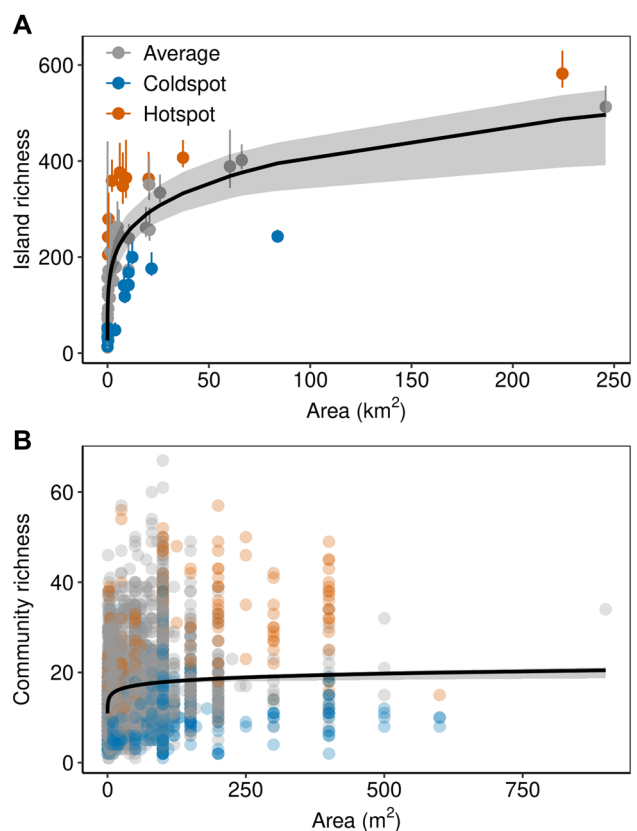

Fig. 1. Gamma (**A**) and alpha (**B**) richness hotspots and coldspots. The dots represent islands (**A**) or single plots (**B**) and are colored according to the island status (gamma/alpha richness hotspot/coldspot). Richness values are the Chao2 estimator with associated 95% confidence intervals (CIs) (**A**) and plot species richness (**B**). Black lines show the multimodel average of eight species–area functions. Shaded areas show the 95% CIs.

hotspots, when considering the threshold of 70% of plots above the species–area curve, we pinpointed six islands: Alicudi, Favignana, Levanzo, Panarea, Salina, and Ustica. On the other hand, 20 islands were classified as alpha coldspots for having more than 70% of the plots below the species–area curve: Basiluzzo, Capraia (Tremiti), Capraia (Tuscan), Capri, Faraglione di Mezzo, Faraglione Grande, Gallo Lungo, Gavi, Giannutri, Giglio, Gorgona, Il Cretaccio, Isola di Cirella, Isola Lachea, La Castelluccia, Palmarola, Pellestrina, Scoglio Faraglione, Stromboli, and Zannone (Table S2). When considering a more conservative threshold of 80% of plots above the species–area curve, only Alicudi, Favignana, Salina, and Ustica could be considered alpha hotspots. Conversely, a more conservative threshold led to the exclusion of Capraia (Tremiti), Capraia (Tuscan), Capri, Palmarola, and Zannone from the previous list of alpha coldspots.

Among the above-mentioned hotspots, we selected those with positive values of both gamma and mean alpha residuals. Our final cross-scale hotspot selection included 12 islands: the alpha hotspots Alicudi, Favignana, Panarea, and Salina, the gamma hotspots Elba, Filicudi, Lampedusa, Lipari, Ponza, San Domino, and San Nicola, as well as Levanzo, which was both an alpha and gamma hotspot. Isola di Capo Passero and Vivara were excluded from the final hotspot selection because, despite being classified as a gamma hotspot, the mean of their alpha residuals was negative. Similarly, Ustica was excluded because it was classified both as a hotspot (alpha) and as a coldspot (gamma) (Figs. 2, 3; Table S2). Carrying out the cross-scale hotspot selection based on the more conservative definition of alpha hotspots (80% of plots above the species–area curve) would lead to the exclusion of Panarea from the above list.

The 12 selected cross-scale hotspot islands hosted 1077 out of 1507 species, corresponding to 71% of the total plant species richness in our data set, while occupying 37% of the total surface area. When removing Panarea from the selection, 1070 species were included. When looking at the representativeness of EUNIS habitats in our selection, 34 out of 49 habitats were included. Among the 15 missing habitats, most of them were represented by less than 10 plots each (i.e., H34, N35, R1A, R13, R16, R55, S93, T1A, T14, T22, T3D, and V39), while 22 plots were classified as S63 ("Eastern garrigue") and 23 as S72 ("Eastern Mediterranean spiny heath"). The most common habitat not included in the selected hotspots was R36 ("Moist or wet mesotrophic to eutrophic pasture"), with 51 plots. When considering species rarity, the selection included 98% of the very common (Q1), 86% of the common (Q2), 55% of the uncommon (Q3), and 47% of the rare species (Q4) (Figs. 4A, 4B). The proportion of rare species (Q4) within each of the selected hotspot islands ranged between 2% and 14%, while the proportion outside the selection ranged between 0% and 11% (Fig. 4C).

Most islands, including all the identified cross-scale hotspots, hosted protected areas belonging to the Natura 2000 network, covering between 12% and 100% of their surface. Only Faraglione di Mezzo, Procida, and Scoglio Faraglione were not covered by Natura 2000 (Table S2).

As for the drivers of gamma richness, island area, maximum elevation, and measures of climatic variability were strongly and positively correlated with one another ($r = 0.54$–0.75). Strong negative correlations between isolation, annual precipitation ($r = -0.52$), and potential evapotranspiration were also detected ($r = -0.74$) (Fig. S4). Area explained 68% of the variance in gamma richness ($P < 0.001$; AICc = 626). When mean annual temperature was included in the model, the explained variance increased to 71% ($P < 0.05$; AICc = 622). Similarly, area and annual precipitation explained 71% of the variance in the data ($P < 0.05$; AICc = 624). Mean annual temperature showed a positive relationship with gamma richness, while annual precipitation showed a negative relationship (Table 2). The other candidate predictors were not significant ($P > 0.05$).
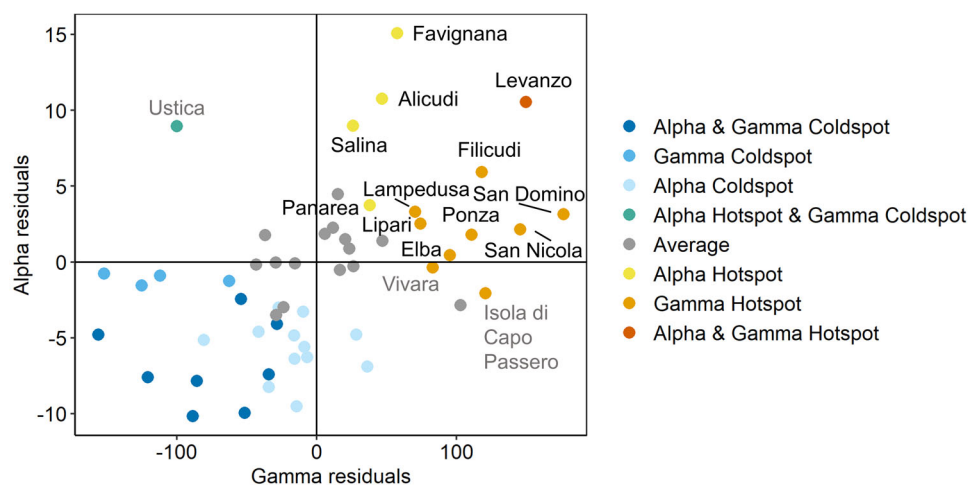

Fig. 2. Gamma and alpha (70% threshold, see Section 2) hotspots and coldspots in the regression residuals' space. Each point represents an island. Gamma residuals are the regression residuals of the gamma species –area relationship (Fig. 1A). Alpha residuals are the island-level mean of the regression residuals of the alpha species richness–area relationship (Fig. 1B). Selected cross-scale hotspot islands are labeled with their name in black. Islands that were identified as hotspots at one scale but had negative residuals at the other scale are labeled in gray.
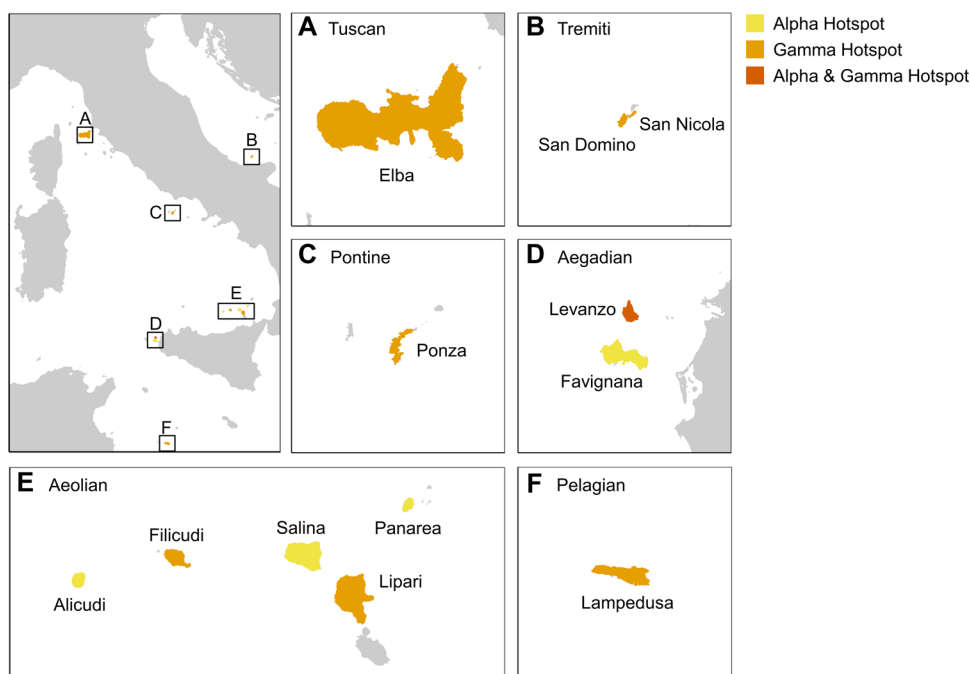
Fig. 3. Geographical location of 12 cross-scale hotspot islands, belonging to the Tuscan (**A**), Tremiti (**B**), Pontine (**C**), Aegadian (**D**), Aeolian (**E**) and Pelagian (**F**) archipelagos. The colors indicate the scale at which the hotspots were identified (alpha, gamma, or both).

4 Discussion

In this work, we identified several hotspots and coldspots of plant richness within a set of 54 Central Mediterranean islands by analyzing the species–area relationship at two spatial scales, namely, the local plant community (alpha) and the whole island (gamma). Furthermore, we investigated potential environmental, geographical, and topographical

As for the drivers of alpha richness, potential evapotranspiration, gamma richness, volcanic origin, and plot size showed a positive relationship ($P < 0.001$), while mean annual temperature ($P < 0.01$) and annual precipitation ($P < 0.05$) showed a negative relationship. Overall, the fixed effects explained 11% of the variance. The inclusion of a random effect accounting for the spatial aggregation of the data with each 1 km cell increased the total variance explained to 42%. When a random intercept for each EUNIS habitat was included, the variance explained by the fixed effects increased to 13%, while the overall explained variance including both fixed and random effects reached 56%. However, in both the above-mentioned models, significant spatial autocorrelation of residuals was detected (Moran's $I = 0.02$, $P < 0.01$). An additional random intercept for islands removed the spatial autocorrelation (Moran's $I = 0.01$, $P > 0.05$). In the latter model, plot size and island richness explained 17% of the variance ($P < 0.001$), while the other predictors were not significant ($P > 0.05$). The overall variance explained by both fixed and random effects (1 km cell, EUNIS habitat and islands) increased to 61% (Table 3; Fig. S5).

drivers of species richness at both scales. Within our data set, 12 islands were classified as cross-scale hotspots, encompassing around 70% of species and habitat richness, as well as almost 50% of the rarest species while occupying less than 40% of the total island surface. Gamma richness was mainly explained by island area, with minor and opposite contributions of mean annual temperature, which showed a positive relationship, and annual precipitation, which showed a negative relationship. As for alpha richness, after accounting for the idiosyncratic effect of habitats and islands, plot size and gamma richness remained the only significant predictors, positively related to the number of species found in local plant communities.

As for gamma and alpha richness coldspots, 10 of them were represented by islands smaller than 0.3 km². Some of these islands corresponded to whole archipelagos like those of the Cyclopes (Faraglione di Mezzo, Faraglione Grande, Isola Lachea) and Li Galli (Gallo Lungo, La Castelluccia); others represent the smallest members of different island groups (Basiluzzo and Scoglio Faraglione for the Aeolian archipelago, Gavi for the Pontine islands, and Il Cretaccio for Tremiti islands) or single islets that are not part of any island network (Isola di Cirella). Negative or random deviations of species richness at very small island sizes are a well-known pattern in islands biogeography, strongly connected to the so-called small island effect (Lomolino, 2000b). Indeed, when available area becomes very small, species richness patterns are largely dominated by stochastic processes (Morrison, 2011; Chiarucci et al., 2021), possibly leading to depauperated species pools that can even translate into very low richness of local plant communities. As for larger coldspot islands, the smaller than expected number of
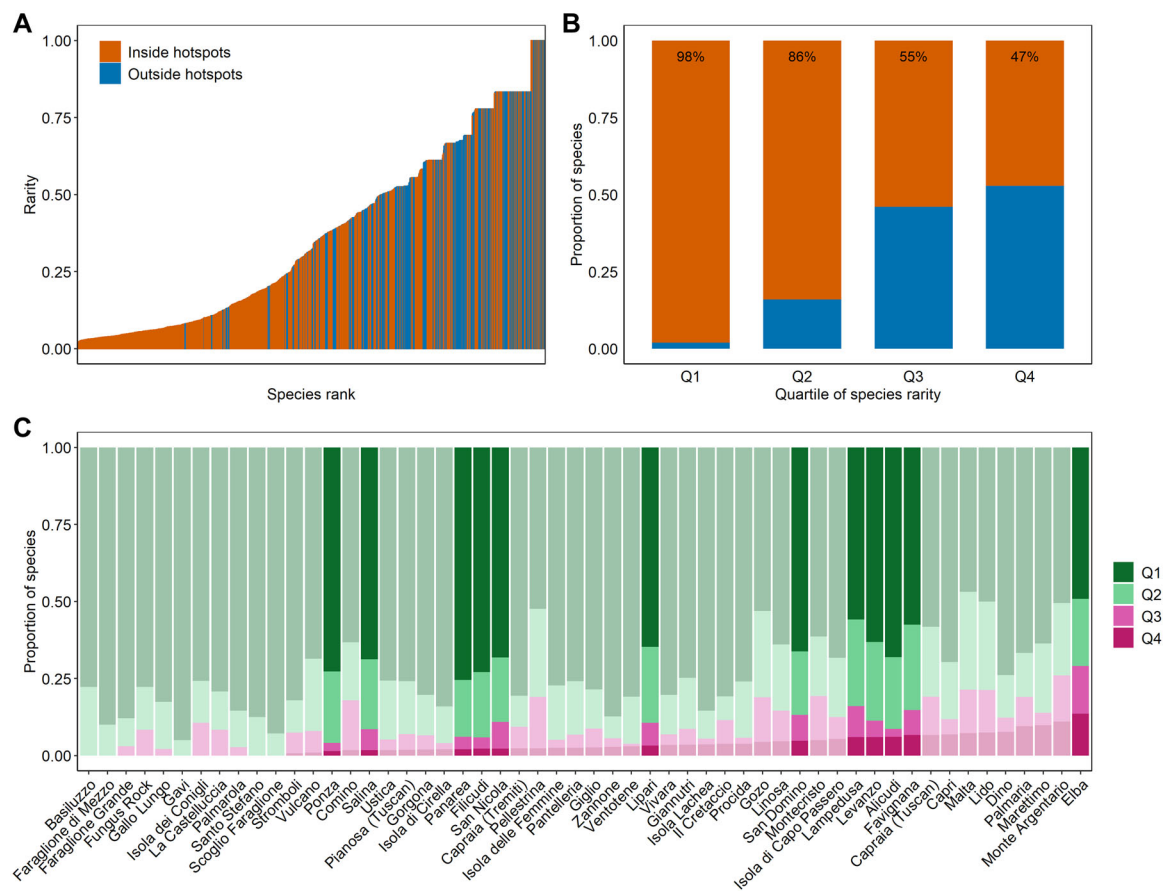
Fig. 4. Species rarity and its representativeness in the selected hotspot islands. **A,** Species ranked in increasing order of rarity. Each bar represents a species and is colored according to its presence inside or outside the selected hotspot islands. **B,** Quartiles of species rarity (Q1, very common species; Q2, common species; Q3, uncommon species; Q4, rare species). The colors represent the proportion of species inside and outside the selected hotspots' island. The percentage of species inside the hotspots is reported on top of each bar. **C,** Proportion of species belonging to each quartile of rarity in each island. Darker bars represent the selected hotspot islands. Islands are plotted in increasing order of proportion of the rarest species (Q4).

Table 2 Significant generalised linear mixed-effects models of island species richness

Predictor	Coef ± SE	z	P	mR²	AICc
Area (log)	0.71 ± 0.07	10.32	***	0.68	626
Area (log)	0.77 ± 0.07	11.02	***	0.71	623
Mean annual temperature (mean)	0.17 ± 0.07	2.47	*		
Area (log)	0.70 ± 0.07	10.42	***	0.71	624
Annual precipitation (mean)	−0.14 ± 0.07	−2.08	*		

For each model, the scaled coefficients, z-values, and P-values of the fixed effects are reported; AICc, Akaike information criterion for small sample sizes; mR², marginal R^2; significance codes: <0.001 (***); <0.05(*).

species could be due to different factors, being idiosyncratic to each island or archipelago. Among these, the widespread presence of invasive plants might have played a role, like in the case of the Tuscan islands (Capraia, Gorgona, Giannutri, Giglio, Montecristo), which have undergone a marked decrease in species richness over the last decades (Chiarucci et al., 2017). Furthermore, urbanization and landscape homogenization might also have had an impact on gamma richness through habitat reduction on some islands. This could be the case of the sandy Venetian islands Lido and Pellestrina, which showed lower species richness compared to the other islands of similar size and underwent a strong and continuous urbanization process during the last century.

Among the identified 12 cross-scale hotspots—all included in the Natura 2000 network, either partially or completely—eight were represented by Sicilian islands: Favignana and Levanzo (Aegadian islands), Alicudi, Filicudi, Lipari, Panarea, and Salina (Aeolian islands), and Lampedusa (Pelagian islands). This is consistent with the fact that Sicily, being located at the interface between the African and European continents and being the main source of plant species for these islands (Mazzola et al., 2001; Troia, 2012), is one of the most species-rich and botanically interesting regions of the Mediterranean basin (Médail & Quézel, 1997, 1999). Further north, Ponza (Pontine islands) and Elba (Tuscan islands) have also been classified as plant richness hotspots. As for the

Table 3 Generalised linear mixed-effects models of plant community species richness

Fixed effects	OLRE (Plot) + 1 km (cell)			OLRE (Plot) + 1 km (cell) + Habitat			OLRE (Plot) + 1 km (cell) + Habitat + Island		
	Coef ± SE	z	P	Coef ± SE	z	P	Coef ± SE	z	P
Mean annual temperature	−0.06 ± 0.04	−2.92	**	−0.04 ± 0.03	−2.64	**	−0.02 ± 0.04	−0.77	ns
Annual precipitation	−0.06 ± 0.05	−2.56	*	−0.04 ± 0.04	−2.08	*	0.02 ± 0.05	0.83	ns
Potential evapotranspiration	0.11 ± 0.04	5.31	***	0.08 ± 0.03	4.99	***	0.02 ± 0.05	1.02	ns
Island richness (Chao2)	0.15 ± 0.03	9.97	***	0.13 ± 0.02	10.43	***	0.19 ± 0.08	4.62	***
Geological origin (volcanic)	0.24 ± 0.07	6.74	***	0.12 ± 0.06	4.03	***	0.04 ± 0.14	0.54	ns
Plot size (log)	0.09 ± 0.02	11.46	***	0.15 ± 0.02	17.23	***	0.14 ± 0.02	16.53	***
AICc	29 797; *null model*: 30 019			28 667; *null model*: 29 042			28 419; *null model*: 28 690		
mR^2	0.11			0.13			0.17		
cR^2	0.42			0.56			0.61		

The scaled coefficients, z-values, and P-values of the fixed effects, as well as AICc, mR^2, and cR^2 are reported; the AICc of the corresponding null model with the same random effects structure is also reported; random effects: OLRE (observation level random effect = Plot. Accounts for overdispersion); Habitat (level 3 EUNIS habitat class); Island (groups plots belonging to the same island). Significance codes: <0.001 (***); <0.01 (**); <0.05(*).
AICc, Akaike information criterion for small sample sizes; cR^2, conditional R^2; mR^2, marginal R^2.

first, it is indeed considered of great phytogeographic importance for representing the northernmost distribution limit of several plant species associated with southern Tyrrhenian volcanic islands (Stanisci et al., 2005). As for Elba, the island has the second largest surface area in our data set after Malta, while hosting half the proportion of alien species relative to the size of the flora (9% for Elba, Carta et al., 2018; 18% for Malta, Deidun, 2010). Elba is also characterized by considerable geological and bioclimatic variability, which in turn induces higher habitat and niche diversity (Carta et al., 2018; Chiarucci et al., 2021). These factors are likely responsible for the great species richness observed for Elba, especially if compared to the other islands of the Tuscan archipelago. On the eastern side of the Italian Peninsula, San Domino and San Nicola (Tremiti) were also included in the final selection of richness hotspots. These islands are located north of the Gargano promontory, which is recognized as a regional biodiversity hotspot (Perrino et al., 2013). Interestingly, considering species richness at two spatial scales (alpha and gamma) led to the inclusion of additional hotspots that would have remained undetected if the analyses had been carried out at the gamma scale only (i.e., Alicudi, Favignana, Panarea, and Salina). This stresses the importance of analyzing species richness at multiple scales, especially when implications for conservation are to be drawn from such studies (Sfenthourakis & Panitsa, 2012; Sabatini et al., 2022).

As for the drivers of species richness, island area was the main predictor of gamma richness in our data set, explaining alone almost 70% of the variation in the data. This is consistent with the predictions of the theory of island biogeography (MacArthur & Wilson, 1967), according to which larger islands can sustain larger populations that are less exposed to demographic stochasticity, thus showing lower extinction rates. Furthermore, we found a strong correlation between island area and other proxies of environmental heterogeneity, like maximum elevation and climatic variability. This is coherent with a secondary effect of area on species richness: larger islands are usually characterized by greater environmental heterogeneity and habitat diversity (Lomolino, 2000a), hence a greater number of species. However, the inclusion of such factors, once the effect of area was accounted for, did not improve our models of gamma richness, preventing the disentanglement of specific contributions. Similarly, other factors related to island shape (i.e., eccentricity), isolation (measured as the distance from the nearest source landmass), or origin (continental vs. volcanic) did not significantly improve the prediction of gamma richness when coupled with island area. We found, however, a marginal influence of climate, with a negative effect of precipitation and a positive effect of mean annual temperature. These results are consistent with the identification of most richness hotspots among southern Italian islands, characterized by warmer temperatures and lower annual precipitation compared to other regions in our data set. However, we cannot exclude that the higher richness of those regions is related to intrinsic factors rather than climate per se, that is, to their biogeographic signature (Médail, 2022).

As for alpha richness, the apparent positive effect of potential evapotranspiration and the negative effect of annual precipitation are again consistent with the identification of alpha hotspots in southern Italian islands (i.e., Alicudi, Favignana, Levanzo, Panarea, and Salina). On the other hand, the positive effect of volcanic origin and the negative effect on annual mean temperature seem to contradict previous findings (Kreft et al., 2008; Kougioumoutzis & Tiniakou, 2015; Chiarucci et al., 2021). Yet, the presence of spatial autocorrelation prevented a meaningful interpretation of model coefficients. When spatial autocorrelation was removed by accounting for habitat and island effects, climate and geological origin became non-significant.

The only factor remaining significant, apart from plot size, was the estimated gamma richness, which showed a positive relationship with alpha richness. This result reflects the prominent role of the regional species pool—hence regional large-scale factors—in determining the diversity of local communities (Ricklefs, 1987; Zobel, 2016). However, plot size and gamma richness only explained 17% of the variance in alpha richness, while the inclusion of habitat and island as random effects increased the overall explained variance to 61%. The influence of island and habitat identity on the variability in local species composition has been previously demonstrated for the Tuscan archipelago (Chiarucci et al., 2021), further supporting the importance of factors idiosyncratic to each habitat and island in explaining local plant species richness patterns. In the case of small Mediterranean islands, these intrinsic effects can be ascribed to local environmental specificities like fine-scale topography which in turn determines microclimatic niches—and the nature of the substrate (Médail, 2022), which we did not explicitly account for in this work. Therefore, further data on fine-scale soil composition and microclimate, as well as on anthropogenic impacts, are required to elucidate the relationship between community richness and local environmental factors in these regions.

Despite being solely based on the species–area relationship, thus not accounting for species rarity or compositional irreplaceability, our selection of 12 cross-scale hotspot islands included over 70% of the species and habitats in the data set, which comprised nearly half of the rarest species. Nevertheless, the other half was not included in our selection, meaning that coldspots can also be worth protecting—especially if characterized by high ecological irreplaceability and vulnerability (Margules & Pressey, 2000)—and should not be neglected a priori by conservation managers (Kareiva & Marvier, 2003). The incomplete inclusion of rare species in the hotspot islands was to be expected, given that the selection had been based on the species–area relationship rather than accounting for species rarity, which was defined empirically instead of relying on a priori information. Thus, the rarest species in our data set are, by definition, located only in one or a few islands or habitats and would always be excluded when some kind of selection is carried out. This represents one limitation of the study, as opportunistically collected data sets do not allow consideration of objective endemicity or rarity or the actual presence of species of priority conservation interest (e.g., those listed in the 92/43 EU "Habitats" Directive). Indeed, our data set consists of a collection of vegetation plots sampled during the past decades, mostly for vegetation classification purposes and according to different methods and rules (Guarino et al., 2018). As an example, therophytes were commonly omitted from the relevés of Mediterranean garrigues and perennial dry grasslands, despite the fact that these vegetation types host many annual plants growing in the gaps of the plant communities dominated by chamaephytes and hemicryptophytes (Brullo, 1985). Although this practice may not have much bearing on the classification of vegetation and habitats, its negative effect on the estimation of gamma richness cannot be ignored (Guarino et al., 2022). Indeed, the heterogeneity of sampling criteria and targeted vegetation may still have led to an underestimation of the actual number of species per island, with possible discrepancies in inter-island comparisons. Therefore, although our analyses did not show a clear influence of sampling intensity on the estimation of gamma richness, results regarding islands that just (e.g., ±20 species) met (i.e., Elba, Lampedusa, Lipari, and Vivara) or missed (i.e., Alicudi and Favignana) the criteria for the inclusion among gamma hotspots should be interpreted with caution. Nevertheless, previous studies showed that large collections of vegetation plot data, including the main plant assemblages in different islands, can be used to detect fundamental biogeographic patterns (Chiarucci et al., 2021). When complete species lists are missing, as it is often the case for small islands (Borges et al., 2016), vegetation plot data represent a useful source of information and allow analyses at different spatial scales. By using the most extensive collection of vegetation plots in the area available to date, this work provides information on the distribution of the overall vascular plant species richness, indicating an optimized subset that contains most of this diversity. However, we considered just one dimension among many used to identify diversity hotspots (e.g., endemism, evolutionary distinctiveness, functional diversity, phylogenetic diversity, and threat; Fattorini, 2021). Given the well-known lack of congruence among different types of hotspots (Orme et al., 2005; Zhao et al., 2016; Niskanen et al., 2017), further data and studies are required to assess other facets of plant diversity in the region. In addition, hotspot identification represents only one among many criteria forming the basis of systematic conservation planning, which should prioritize protected area designs based on complementarity, comprehensiveness, representativeness, and irreplaceability, to maximize effectiveness while minimizing costs (Kukkala & Moilanen, 2013). Therefore, while identifying those areas that host most species richness provides useful information for biodiversity protection, other aspects—including consideration of different taxonomic groups, societal costs, and reserve connectivity—should be considered to formulate appropriate conservation strategies.

5 Conclusions

By building upon classic biogeographic theory, we used a comprehensive data set of vegetation plots located in 54 small Central Mediterranean islands to explore species richness patterns at the regional and local scales. We identified several richness hotspots that encompass a large proportion of the overall plant diversity in our data set. We also assessed the effect of different environmental, geographical, and topographical factors on gamma and alpha richness, identifying the prominent role of area and other idiosyncratic factors in determining the observed richness patterns at both spatial scales. This work represents a first effort to aid plant conservation priorities in small islands of the Central Mediterranean Basin in the context of systematic conservation planning. Further studies encompassing different aspects of plant species diversity (e.g., endemism rate, functionality, irreplaceability, and threat) are required to formulate more comprehensive protection strategies. Likewise, the collection of further vegetation data in undersampled islands as well as fine-scale environmental information is needed to further elucidate

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the distribution on plant species richness in the area and its response to island and habitat peculiarities.

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Conflict of Interest

The authors declare no conflict of interest.

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Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.13034/suppinfo:

Fig. S1. Diagram describing several steps employed for data pre-processing, variable extraction/calculation, and analysis.

Fig. S2. Sensitivity analysis of the estimations of island vascular plant species richness to plot size. Estimates of island richness using the Chao2 asymptotic estimator for regions where at least 25 plots of different size classes were available are reported. The dots represent the regional richness estimates. The error bars represent the 95% confidence intervals.

Fig. S3. Relationships between the log-transformed values of island area, number (**A**) and density (**B**) of plots per island, as well as between density of plots, gamma richness estimates (**C**) and the percent increase of estimated gamma richness compared with that observed (**D**). The values of the Pearson correlation coefficients (*r*) are reported.

Fig. S4. Correlations among predictors of island vascular plant species richness. The values represent the Pearson *r* correlation coefficient. Nonsignificant correlations are left blank. AP, annual precipitation; MAT, mean annual temperature; PET, potential annual evapotranspiration; SD, standard deviation.

Fig. S5. Standardised fixed-effect coefficients from Poisson generalised linear mixed-effects models (GLMMs) of plot species richness. Random effects (from left to right): OLRE (observation-level random effect. Accounts for overdispersion); 1 km (groups of plots located within the same 1 km cell. Accounts for the spatial aggregation of the data); Habitat (groups plots belonging to the same level 3 EUNIS habitat); Island (groups plots belonging to the same island). Dots and bars represent the mean and the 95% confidence interval of the coefficients. Significant coefficients are drawn in black. Marginal R^2 (mR^2) and conditional R^2 (cR^2) are provided.

Table S1. Area, number and density of plots, list of EUNIS level 3 habitats and data sources for each island in the final dataset. A key to the habitat codes and a reference list are provided at the bottom of the table.

Table S2. Observed and estimated number of vascular plant species for each island, as well as gamma, alpha, and overall richness status (hotspot or coldspot), according to the 70% threshold (see Section 2). An indication of the value of mean alpha and gamma richness residuals for islands that were neither hotspots or coldspots is reported in brackets (+ for positive, − for negative).