

Biogeography of orchids and their pollination syndromes in small Mediterranean islands

M. Lussu^{1,2,3}  | P. Zannini^{1,2,3} | R. Testolin^{1,2,3} | D. Dolci² | M. Conti^{3,4} | S. Martellos^{2,3,4} | A. Chiarucci^{1,2,3}

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

²Centro Interuniversitario per le Biodiversità Vegetale Big Data - PLANT DATA, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum University of Bologna, Bologna, Italy

³LifeWatch Italy, Lecce, Italy

⁴Department of Life Sciences, University of Trieste, Trieste, Italy

Correspondence

Michele Lussu, BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum University of Bologna, Via Irnerio 42, 40126 Bologna (BO), Italy. Email: michelelussu86@gmail.com

Funding information

National Recovery and Resilience Plan (NRRP); LifeWatch Italy through the project "LifeWatchPLUS (CIR-517 01_00028)

Abstract

Aims: Despite the research on orchid in insular conditions, few studies are focused on the spatial distribution of their reproductive syndromes across complex insular systems. By using island species–area relationships (ISAR), we explore orchid biogeography in the Central Western-Mediterranean islands. In this study, we aim to investigate variation in ISARs using orchid pollination mechanisms as proxies to establish permanent populations explaining how the *c* and *z* parameters of ISARs vary among island types and pollination strategies and defining the most influential factors in shaping orchids' distribution.

Location: Mediterranean Basin.

Taxon: Orchidaceae.

Methods: Checklist of native orchids was obtained for 112 islands of Central-Western Mediterranean Basin. The Arrhenius power function ($S = c \cdot A^z$) was used to fit ISARs for the total number of orchids as well as for functional groups defined by the pollination strategies, across different island types. We used GLM to investigate the relation between pollination syndromes with area and isolation as well as elevation, island origin, taxa richness of the source area and habitat diversity.

Results: We found that ISARs differ between continental and volcanic islands depending on isolation. The *z*-value was found to be higher for more specialized strategies while the *c*-value increases from autogamy to allogamy, supporting the role of these two parameters in understanding distributional dynamics. Distance from the mainland is a negative predictor for all the strategies except when deception is decoupled; island area is a positive predictor only for allogamic, deceptive and food deceptive strategies, while habitat diversity is a positive predictor for allogamic, rewarding and deceptive strategies.

Main Conclusions: Pollination syndromes contribute in explaining the distribution of orchids in insular conditions. Furthermore, we identified differences in ISARs across pollination syndromes in which the intercept increases when the pollination shifts from a generalist to a more specialized one.

KEYWORDS

biodiversity, functional traits, island biogeography, Mediterranean, Orchidaceae, pollination, species richness, species–area relationships

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Journal of Biogeography* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

Since islands harbour relatively simplified ecosystems and biotas, they are widely used to understand global ecological and evolutionary dynamics (Whittaker et al., 2017). The species–area relationship is a powerful tool to explain biological richness on insular systems (Lomolino & Weiser, 2001; Triantis et al., 2012). Although it was originally used to describe how species richness depends on island size and its current applications range from biogeography to macroecology, community ecology and conservation biology (Whittaker et al., 2017), the use of pollination syndromes in SARs can significantly contribute to clarifying the distribution patterns of insular biodiversity.

While the debate around which is the best model to explain the ISARs is still vigorous, (Chiarucci et al., 2011, 2021; Lomolino & Weiser, 2001; Triantis et al., 2012; Yu et al., 2020), the Arrhenius equation ($S = c \cdot A^z$) has been proven to depict the biological meaning of insular conditions than the other equations (Matthews et al., 2016; Triantis et al., 2012), as well as quantify temporal changes in island diversity (Chiarucci et al., 2017). In this model, the two fitted parameters show the relation between area (A) and the number of species (S) by giving the number of species per unit area (c) and how species richness responds to the area increase (z). Although it has been demonstrated that c and z- values are complementary parameters, it has also been shown that they are taxon related (Gould, 1979; Fattorini et al., 2017). Greater z-values on volcanic islands are linked with higher rates of speciation, whereas populations on continental islands are less separated from those on the mainland, leading to lower z-values. While z- value has a positive correlation with area and isolation (Williamson, 1988; Rosenzweig, 1995), individual distribution (Tjørve & Turner, 2009) but it is also negatively related to dispersal capacity (Williamson, 1988), common species abundance and human impact (Ficetola & Padoa-Schioppa, 2009; Tjørve et al., 2008; Walentowitz et al., 2022). Thus, the value of parameter c generally decreases from continental to volcanic islands. In comparison with other taxa, the higher c-value found in plants is related to their small spatial needs as well as to their capacity to endure adverse environments for extended periods of time (e.g. to dormancy) (Triantis et al., 2012).

Despite this versatility, SAR has rarely been applied outside the species concept. Pollination is one of the essential plant traits that promotes the colonization of new areas because it is the primary process enabling sexual reproduction and the establishment of stable populations (Ollerton et al., 2019; Štípková et al., 2020). Geophytes are plants with underground storage organs, such as bulbs, corms or tubers, that allow them to survive adverse environmental conditions. According to Thomson et al. (2010), these plants generally have more diversified ecological adaptations and are better dispersers than other growth forms, implying that they can establish bigger population sizes on small islands (Panitsa et al., 2006). Furthermore, due to their small size and shorter life cycle, geophytes can establish greater populations on small islands and may have lesser extinction risks than larger species (Höner & Greuter, 1988). Animal-mediated

pollination occurs in most flowering plants, having evolved as an efficient way to maximize the likelihood of fertilization. To maximize pollination success (i.e. reducing pollen loss), several species have evolved specialized syndromes that minimize the number of pollinating species (Ollerton et al., 2011). Although this advantage, zoophilic pollination can lead to ecological and evolutionary difficulties, since plants must co-occur with pollinators and flowering time must be synchronized with animal activity. A third of the more than 28,000 species of orchids known are geophytes which is the most dominant growth form in temperate climates (Chase et al., 2015). Orchids have a cosmopolitan distribution and are featured by its dust-like seeds, produced in thousands per fruit, making orchids a group with great dispersal capacities (Givnish et al., 2016). The complexity of orchids' flowers reflects their interactions with pollinators, mainly insects, but also mammals and birds (Schiestl & Schlüter, 2009). Animals involved in orchids' pollination can receive a reward or be tricked (Cozzolino & Widmer, 2005). Among Mediterranean orchids, rewarding species usually produce carbohydrate-rich nectar that can be rapidly assimilated while, in contrast, the most common deception strategies promise food or sex. Within these deceptive strategies, food deception involves several pollinators and acts promising nectar by emphasizing traits that indicate its presence and changing colour patterns, flower colour, scent, size, shape, nectar guides, pollen-like papillae and inflorescence shape to avoid being discovered. In contrast, sexual deception is specialized towards only one or a very few species of pollinators mimicking the hormonal component produced by females (Cozzolino et al., 2021; Jersáková et al., 2006). Despite such intricate relationships with pollinators, in some widespread species, such as *Neottia nidus-avis* and *Ophrys apifera*, self-pollination is the dominant mode (Claessens & Kleynen, 2011). Few studies deal with the geographic distribution of reproductive strategies. Both in tropical and temperate biomes, a greater diversity of species was found at intermediate altitudes, but deception is more often found on low mid-altitudes, rewarding strategies on mid-high altitudes and self-pollinated on high elevation (Djordjević et al., 2022; Jacquemyn et al., 2005; Pellissier et al., 2010; Štípková et al., 2020). The area–species relationship in orchids has been positively tested (Ackerman et al., 2007; Schödelbauerová et al., 2009; Taylor et al., 2021) although attention to the Mediterranean region has only recently been addressed (Lussu et al., 2020; Tsiftsis, 2020). On a broader scale, however, continental islands such as Borneo are particularly rich in orchids which are generally underrepresented on volcanic islands (Taylor et al., 2021). The large continental islands are particularly rich in orchids both because their biota is a part of the continental biota from which they originated (partially overcoming the filtering action given by colonization processes) and because of the large area is a proxy of the available ecological niches (Givnish et al., 2016; Taylor et al., 2021). In contrast, studies conducted at smaller scales show that area alone or associated with altitude promotes the presence of orchids (Ackerman et al., 2007; Lussu et al., 2020) but they also identify distance from closer mainland and habitat diversity as strong predictors of orchids richness (Keppel et al., 2016; Tsiftsis, 2020).

Here, we aim at investigating pollination syndromes as a proxy to establish permanent populations, by testing the following hypotheses: (i) differences in ISARs between continental and volcanic islands as a result of species radiation and species turnover, assuming that continental islands show higher z values due to their proximity to biological source; (ii) we hypothesize the variation of c and z values across pollination syndromes (allogamic vs. autogamic, rewarding vs. deceptive, food vs. sexual deception) assuming that specialized groups have higher z values and lower c values than less specialized ones because of their poor dispersal capacity; and (iii) identify which are the most influential factors in defining orchid distribution hypothesizing that distance from the biological source (mainland or closer big island) negatively influences species richness, while elevation is a positive driver of orchids' occurrence in the Central-Western Mediterranean Islands.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area encompasses islands and islets of the Central-Western Mediterranean Basin, distinguished by the presence of massive continental masses from Eurasia and Africa, exceptional habitat fragmentation and millennium anthropic pressure from a population of 466 million people (Kühn et al., 2019). We selected 113 islands and islets, divided into 17 archipelagos (Figure 1). The largest Central-Western Mediterranean Islands (Corsica, Sardinia, Sicily and Mallorca) were treated as biological sources for the closer archipelagos. A detailed geographic and land use characterization of the 2212 Mediterranean islands larger than 0.01 km² was recently published by Zannini et al. (in press). On the basis of their origin, islands and archipelagos were divided into two groups: 'volcanic' islands, with volcanic origin, which were never connected to each other and/or to the mainland, and

continental islands, originating from continental fragmentation processes. Thirteen insular groups have been classified as continental and four as volcanic (see Appendix S1 in Supporting Information).

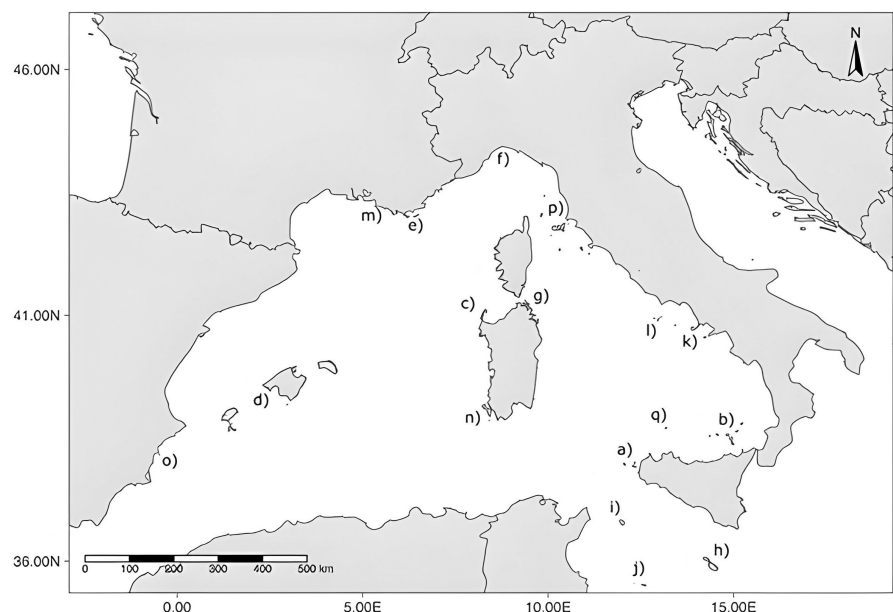
2.2 | Characterizing orchid occurrence and pollination strategies

For each geographic unit (island or archipelago), a list of native orchids was compiled by using local floras and other published studies (see Appendix S2). Due to the intricate complexity of the species concept in Orchidaceae (Chase et al., 2015), we only used the taxonomic ranks of species and subspecies, excluding the lower ones (varieties and forms). Nomenclature was harmonized according to the *Plants of the World Online* (<https://powo.science.kew.org/>). Taxa were classified according to their fertilization (allogamic and autogamic) and pollination (rewarding and deceptive) strategies (Claessens & Kleynen, 2011). Deceptive strategy was then decoupled into food and sexual deception (Claessens & Kleynen, 2011; Kühn et al., 2019). For each island, we calculated orchid richness for all taxa as well as for each of the functional groups (allogamic, autogamic, rewarding, deceptive, food and sexual deceptive).

2.3 | Analytical methods

The first hypothesis was tested by fitting ISARs with the Arrhenius power function (Arrhenius, 1921) using the 'sar_power' function of the 'sars' R package (Matthews et al., 2019). ISARs were modelled separately for the complete data set and separately for continental ($n=75$) and volcanic islands ($n=39$). To test the second hypothesis, ISARs were fitted to the orchid richness of the different functional groups according to fertilization and pollination strategies. The results were compared using a Z-test to identify significant differences in c and z values among pollination groups.

FIGURE 1 Map of the archipelagos and islands of the Central-Western Mediterranean basin: (a) Aegadian Islands, (b) Aeolian Islands, (c) Asinara Archipelago, (d) Balearic Islands, (e) French Islands, (f) Spezzino Archipelago, (g) Maddalena Archipelago, (h) Maltese Islands, (i) Pantelleria, (j) Pelagian Islands, (k) Phlegraean Islands, (l) Pontine Islands, (m) Riou Archipelago, (n) Sulcis Archipelago, (o) Tabarca, (p) Tuscan Archipelago, (q) Ustica [single column].



We tested the third hypothesis characterizing each island according to the percentage of habitat types (artificial surfaces, forests, shrub and/or herbaceous vegetation associations, open spaces with little or no vegetation and wetlands). Habitat diversity was assessed using the Shannon Diversity Index on land use data from the Corine Land Cover (CLC 2018) data set, specifically using the third hierarchical level of classification. Shannon Diversity Index was computed using the 'diversity' function in the package *R* 'vegan' (Dixon, 2003). Maximum elevation was estimated from the Copernicus EU-DEM digital surface model (<https://land.copernicus.eu/imagery-in-situ/eu-dem/eu-dem-v1.1>). Distance from the closer mainland, expressed as the shortest distance between an island's coastline and the coastline of the nearest mainland, was obtained with QGIS 3.16 software (QGIS Development Team, 2023). Due to their size, Corsica, Sardinia, Sicily and Mallorca, the bigger islands in the Central-Western Mediterranean were considered the biological sources of the nearby archipelagos. Generalized linear models (GLMs) with Poisson distribution were used to define the most important factors associated with orchid richness and developed using the islands with at least one species. Models were fitted by using the 'glm' function in the *R* packages 'stats', and ranked with 'model.sel' using the Akaike information criterion (AIC).

3 | RESULTS

The aggregated data set of Orchidaceae occurring in the Central-Western Mediterranean Islands includes 78 taxa classified in 15 genera. The most species-rich genera are *Ophrys* (34 taxa), *Anacamptis* (8) and *Orchis* (7). The most common taxa across islands are *Serapias lingua* and

Serapias parviflora, recorded in 30 and 29 islands, respectively. Almost two-thirds of the recorded taxa (23) are quite rare, having been recorded only on one island. Seven taxa were classified as autogamic, 70 allogamic, 17 as rewarding taxa and 53 as deceptive. Within deceptive taxa, 21 were identified as food deceptive and 32 as sexual deceptive. The majority of islands (66) did not host any orchid taxa, while the remaining 47 islands host at least one orchid taxa. The most species-rich island is Isola d'Elba, with 32 infrageneric taxa, followed by Malta (27), Sant'Antioco (25), Capri (23), Ischia and San Pietro (20 each).

3.1 | ISARs and island types

The Arrhenius function fits well with the orchid species richness per island, both considering all the islands and the separate sets of continental and volcanic islands (Figure 2). In contrast to our first hypothesis, we found that continental islands have a lower *c*-value and a higher *z*-value (2.98 and 0.4, respectively) than volcanic islands (5.0 and 0.25, respectively) (Figure 2).

3.2 | ISARs and pollination syndromes

We found comparable *c* and *z* values between allogamic and autogamic taxa (*c*=3.19, 0.35 and *z*=0.36, 0.34 for allogamic and autogamic taxa, respectively) when ISARs are applied to pollination syndromes (Table 1) (for graphical representations, see Appendix S3 as Figure S3.3). Differences were found between rewarding and

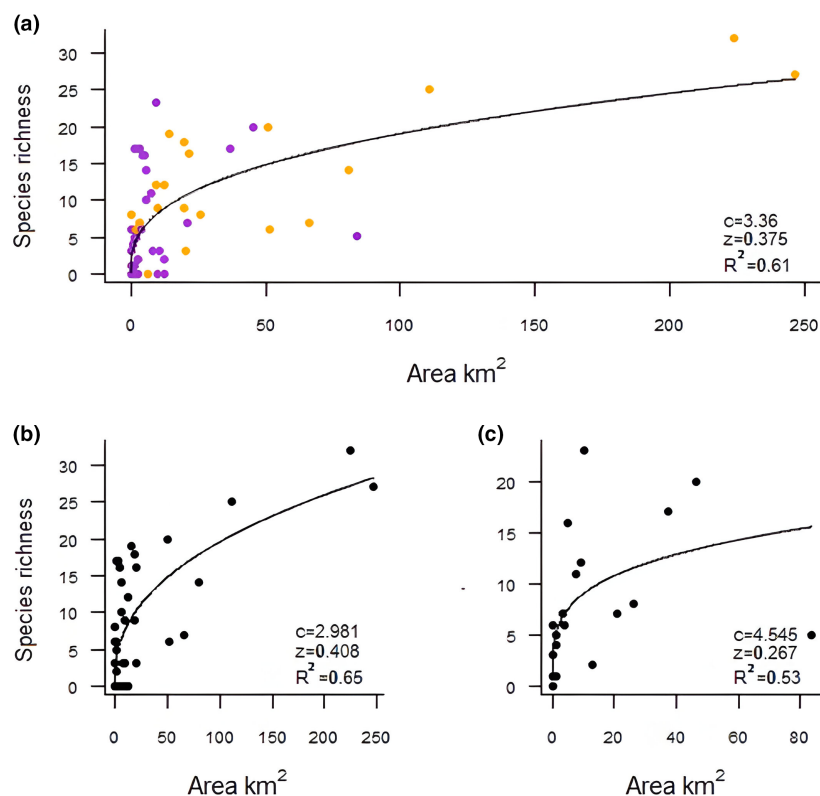


FIGURE 2 Insular species-area relationships (ISARs) of total orchid species richness in Central-Western Mediterranean Islands, fitted by the Arrhenius power function for the whole set of islands (a) continental islands are shown in orange while volcanic in orange. Lower panels show ISARs for continental (b) and volcanic islands (c) separately [single column].

TABLE 1 ISARs for each pollination strategy and their occurrence on island types investigated in the study.

	<i>c</i>	<i>z</i>	Adjusted R^2	R^2
Allogamy	3.194	0.368	0.61	0.62
Continental	2.779	0.408	0.65	0.66
Volcanic	4.406	0.248	0.53	0.56
Autogamy	0.350	0.347	0.42	0.43
Continental	0.177	0.448	0.38	0.4
Volcanic	0.570	0.366	0.69	0.7
Rewarding syndrome	0.993	0.235	0.12	0.13
Continental	0.894	0.089	0.07	0.09
Volcanic	1.00	0.354	0.23	0.27
Deceptive syndromes	2.039	0.428	0.54	0.55
Continental	1.781	0.477	0.64	0.65
Volcanic	3.188	0.220	0.3	0.34
Food deception	1.608	0.364	0.46	0.47
Continental	1.145	0.451	0.58	0.57
Volcanic	2.708	0.193	0.29	0.33
Sexual deception	0.753	0.461	0.44	0.45
Continental	0.973	0.436	0.56	0.57
Volcanic	0.875	0.174	0.13	0.08

deceptive strategies, with higher values observed for both parameters in deceptive species ($c=0.99$, 2.03 and $z=0.23$, 0.42 for rewarding and deceptive taxa, respectively). When deception strategy is decoupled, food deceptive strategy on volcanic islands has higher c -value (2.7 and 1.44, respectively) while in sexual deceptive species, we found higher c -value on continental islands (0.97 and 0.87, respectively). In all the syndromes investigated, z -values were higher in continental islands than in volcanic ones, except for rewarding syndromes (0.08 and 0.35 for continental and volcanic islands, respectively, [Table 1](#)).

3.3 | Factors affecting orchids occurrence

At the taxa level, habitat diversity and area are strong positive predictors of orchid species richness, while the number of species on the closer mainland is a weak predictor ([Table 2](#)). As expected, distance from the closest source has a negative and strong influence. When species are decoupled in pollination strategies, distance is still a negative predictor for all the functional groups, except for sexual deceptive species. Area strongly supports orchid species richness for allogamic, deceptive, food-deceptive groups. Elevation slightly predicts the species richness of autogamic taxa. The number of species in the source area does not affect any of the functional groups tested. Habitat diversity is a good predictor for the species richness all functional groups except for autogamic taxa, while it is a weaker predictor for allogamic taxa. Volcanic origin positively affects the species richness of sexual deceptive species ([Tables 2 and 3](#)).

4 | DISCUSSION

4.1 | ISARs differences between continental and volcanic islands

As suggested by Gould (1979) and reaffirmed by Fattorini et al. (2017), comparative analyses of SARs are richer in biological meaning when the same taxon is studied under various insular conditions. Our research demonstrates how the intercept c and slope z vary across a highly diversified taxon in different insular scenarios and how a functional approach based on traits relevant for colonization processes can provide new insights into plant distribution on islands.

The relationship between orchid species richness and island area varies throughout continental and volcanic islands, as well as along isolation gradients, as expected by theoretical and empirical models. However, the signal we got for volcanic and continental islands did not support the hypothesis that continental islands show lower c and higher z values. This pattern can be found when ISARs analyses are performed on the entire data set as well as when our data set is decoupled into continental and volcanic island subsets. In contrast to previous studies, suggesting an increase of z and a decrease of c -values, from continental to volcanic islands (Triantis et al., 2012), we found a higher z -value and a lower c -value for continental than volcanic islands. A possible explanation might be that, in our data set, the most taxa-rich islands are those of continental origin. Indeed, despite the fact that we found no significant differences in distance from the closer mainland in our data set (mean 29.4 km for continental islands and 36.2 km for volcanic islands), the most remote islands are continental Lampedusa and Lampedusa (218 and 207 km away from the mainland, respectively), while the three most isolated volcanic islands are Pantelleria, Strombolicchio and Stromboli (100, 60 and 55 km away from the mainland, respectively). Thus, these results may support the hypothesis that ISARs may be complementary to other tests in perceiving mathematical variations in complex insular archipelagos or groups of islands where other tests may fail.

4.2 | ISARs variation across pollination syndromes

When investigating ISARs of groups with different pollination strategies, z values were found to vary from 0.34 in autogamic to 0.36 in allogamic taxa, respectively. This result confirms our hypothesis as well as previous studies showing that the z -value is linked to dispersal ability (Williamson, 1988; Wright, 1981). In fact, autogamic species such as *Limodorum abortivum* represent primitive lineages that appeared before the Mediterranean reached its current structure, and their wide distribution is due to passive movement following plate tectonics (Chase et al., 2015). In contrast, allogamic taxa appeared more recently, during the Quaternary, when habitat fragmentation and bee speciation may have promoted orchid radiation (Breitkopf et al., 2015; Cardinal & Danforth, 2013).

TABLE 2 Summary statistics of the generalized linear models (GLM), which were used to test which predictor explains orchid's occurrence in allogamy, autogamy, rewarding and deceptive taxa.

Predictors	Allogamy			Autogamy			Rewarding			Deceptive		
	Incidence rate ratios	CI	p	Incidence rate ratios	CI	p	Incidence rate ratios	CI	p	Incidence rate ratios	CI	p
(Intercept)	6.92	5.44–8.72	<0.001	0.67	0.38–1.12	0.146	0.91	0.47–1.64	0.767	6.06	4.67–7.78	<0.001
Distance	0.98	0.98–0.99	<0.001	0.98	0.95–1.00	0.038	0.97	0.95–0.99	0.004	0.98	0.98–0.99	<0.001
Area	1.01	1.00–1.01	0.008	1.01	0.99–1.02	0.327	1.00	0.99–1.02	0.490	1.01	1.00–1.01	0.009
Elevation	1.00	1.00–1.00	0.876	1.02	1.00–1.03	0.006	1.00	0.99–1.01	0.944	1.00	0.99–1.00	0.877
Taxa closer mainland	1.00	0.99–1.00	0.136				0.99	0.98–1.00	0.222	1.00	0.99–1.00	0.290
Habitat diversity	1.01	1.01–1.02	<0.001				1.02	1.01–1.03	0.001	1.01	1.01–1.02	<0.001
Origin [volcanic]	0.81	0.60–1.09	0.161				1.43	0.69–2.99	0.335	0.71	0.51–0.98	0.040
R ² Nagelkerke	0.960			0.460			0.619			0.935		

Our findings show that the intercept values rise from autogamy to deception. It has been observed that *c* tends to decrease as taxa transition from generalistic to specialized (Öckinger et al., 2010). Our findings are consistent with this conclusion because more specialized strategies, such as sexual deception, have narrower niches due to their intimate relationships with pollinators. This result is also evident when deception strategy is decoupled where the less specialized one (food deception) shows a higher *c*-value (1.60) than the more selective one, sexual deception (0.75).

Although pollination syndrome is a very informative functional trait in Mediterranean orchids, it represents a constraint for broader investigations. Indeed, since reproductive strategy is a crucial trait in temperate ecosystems such as the Mediterranean Basin, comparative studies that integrate species richness and functional diversity are recommended to better understand orchid distribution and to design conservation programs and land management.

4.3 | Factors affecting orchids distribution in Central-Western Mediterranean Basin

The Mediterranean Basin reached its actual spatial arrangement during the Pleistocene, when the main evolutionary lineages of European orchids had already differentiated (Inda et al., 2012). Later on, in the Quaternary, the continental platforms were already fragmented and new archipelagos such as the Aeolian Islands were formed through volcanism. During these periods, large islands (Sicily, Sardinia, Corsica and Majorca) took the role of 'sources' from which small islands underwent immigration processes. Adopting orchids to investigate the role of island origin, we found that ISARs vary widely between continental and volcanic islands, with the *c*-value being higher on volcanic islands. Several studies report the dependence of *c*-values on the degree of isolation (Patiño et al., 2014; Triantis et al., 2012), while our results are the opposite (*c*-values decrease from continental to volcanic islands). This finding might be explained by the fact that the most remote islands in our sample have a common continental origin. According to previous literature on orchids in insular systems, area is a good predictor of orchids' richness in the Central-Western Mediterranean Basin. This hypothesis is consistent with that of Lussu et al. (2020) which indicates a strong relationship between species and area throughout the Mediterranean. Area, however, has no effect on the occurrence of sexual deception syndromes, as represented by the genus *Ophrys*, which is adapted to sunny, hot and dry calcareous substrates found on the vast majority of Mediterranean islands where it has its diversification centre (Breitkopf et al., 2015). Our results confirm the role of distance from the mainland in defining ISARs. As a result of the reduction in species richness with increasing distance from the mainland (Rosenzweig, 1995), remote islands are less likely to be reached during colonization processes (Whittaker et al., 2017). Distance works as a filter for many orchids in the Central-Western

TABLE 3 Summary statistics of the generalized linear models (GLM), which were used to test which predictor explains orchid's occurrence for all the species richness, and when deceptive taxa are decouple into food and sexual deceptive.

Predictors	Species richness			Food deceptive			Sexual deceptive		
	Incidence rate ratios	CI	p	Incidence rate ratios	CI	p	Incidence rate ratios	CI	p
(Intercept)	2.77	5.30–9.61	<0.001	2.77	1.94–3.87	<0.001	1.72	1.08–2.65	0.018
Distance	0.98	0.98–0.99	<0.001	0.99	0.98–1.00	0.009	1.00	0.99–1.00	0.252
Area	1.01	1.00–1.01	0.001	1.01	1.00–1.01	0.045	1.01	1.00–1.01	0.106
Elevation	1.00	1.00–1.01	0.597	1.00	1.00–1.01	0.630	1.00	0.99–1.01	0.982
Taxa closer mainland	1.00	0.99–1.00	0.106	0.99	0.99–1.00	0.078	1.00	0.99–1.01	0.273
Habitat diversity	1.01	1.01–1.02	<0.001	1.01	1.01–1.02	<0.001	1.02	1.01–1.02	<0.001
Origin [volcanic]							0.28	0.15–0.50	<0.001
R ² Nagelkerke	0.742			0.760			0.829		

Mediterranean islands, as remote islands are rarely colonized. Although their small seeds make them good dispersers, these islands may not provide the environmental conditions required for these species to stabilize permanently. Our findings are consistent with previous research indicating that elevation is a recognized predictor of orchid richness (Ackerman et al., 2007; Djordjević et al., 2022). This relation is particularly strong for both autogamous and rewarding groups indicating an altitudinal gradient on Mediterranean islands as well as supporting what has been found in both insular and continental contexts (Djordjević et al., 2022; Jacquemyn et al., 2005). This pattern can be explained by the fact that these syndromes are very often associated with meadows and forests dominated by *Quercus ilex* which occur on the most elevated islands very often as remnant of an intense human impact at lower elevations.

5 | CONCLUSIONS

We explored the complementary roles of *c* and *z* values in describing the ISARs of orchids with a functional-based perspective. Our findings show that area and elevation are pivotal variables in increasing orchid species richness and that island isolation acts as a filter for colonization. Investigations on functional traits as pollination syndromes are essential to understanding the processes of distribution, colonization and persistence of plants on islands. The abundance of data available on orchids and their ecological networks makes them an excellent model for exploring colonization processes and how a single highly diversified taxon may respond to environmental changes. As a result, comparative studies in different biomes at larger scales are recommended and could make great contributions to understand orchid biogeography.

ACKNOWLEDGEMENTS

No permit was necessary. M. L., P. Z. and D. D. have been supported by LifeWatch Italy through the project 'LifeWatchPLUS

(CIR- 517 01_00028)'. This project funded by the European Union – NextGenerationEU.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data are available at <https://doi.org/10.5281/zenodo.10392832>.

ORCID

Michele Lussu  <https://orcid.org/0000-0002-1313-4732>

REFERENCES

- Ackerman, J. D., Trejo-Torres, J. C., & Crespo-Chuy, Y. (2007). Orchids of the West Indies: Predictability of diversity and endemism. *Journal of Biogeography*, 34(5), 779–786. <https://doi.org/10.1111/j.1365-2699.2006.01676.x>
- Arrhenius, O. (1921). Species and area. *The Journal of Ecology*, 9(1), 95. <https://doi.org/10.2307/2255763>
- Breitkopf, H., Onstein, R. E., Cafasso, D., Schlüter, P. M., & Cozzolino, S. (2015). Multiple shifts to different pollinators fuelled rapid diversification in sexually deceptive *Ophrys* orchids. *New Phytologist*, 207(2), 377–389. <https://doi.org/10.1111/nph.13219>
- Cardinal, S., & Danforth, B. N. (2013). Bees diversified in the age of eudicots. *Proceedings of the Royal Society B: Biological Sciences*, 280(1755), 20122686. <https://doi.org/10.1098/rspb.2012.2686>
- Chase, M. W., Cameron, K. M., Freudenstein, J. V., Pridgeon, A. M., Salazar, G., Van Den Berg, C., & Schuiteman, A. (2015). An updated classification of Orchidaceae: Updated classification of Orchidaceae. *Botanical Journal of the Linnean Society*, 177(2), 151–174. <https://doi.org/10.1111/boj.12234>
- Chiarucci, A., Bacaro, G., Triantis, K. A., & Fernández-Palacios, J. M. (2011). Biogeographical determinants of pteridophytes and spermatophytes on oceanic archipelagos. *Systematics and Biodiversity*, 9(3), 191–201. <https://doi.org/10.1080/14772000.2011.603381>
- Chiarucci, A., Fattorini, S., Foggi, B., Landi, S., Lazzaro, L., Podani, J., & Simberloff, D. (2017). Plant recording across two centuries reveals dramatic changes in species diversity of a Mediterranean archipelago. *Scientific Reports*, 7(1), 5415. <https://doi.org/10.1038/s41598-017-05114-5>

- Chiarucci, A., Guarino, R., Pasta, S., Rosa, A. L., Cascio, P. L., Médail, F., Pavon, D., Fernández-Palacios, J. M., & Zannini, P. (2021). Species-area relationship and small-island effect of vascular plant diversity in a young volcanic archipelago. *Journal of Biogeography*, 48(11), 2919–2931. <https://doi.org/10.1111/jbi.14253>
- Claessens, J., & Kleyne, J. (2011). *The flower of the European orchid: Form and function*. J. Kleyne.
- Cozzolino, S., Scopece, G., Lussu, M., Cortis, P., & Schiestl, F. P. (2021). Do floral and ecogeographic isolation allow the co-occurrence of two ecotypes of *Anacamptis papilionacea* (Orchidaceae)? *Ecology and Evolution*, 11(15), 9917–9931. <https://doi.org/10.1002/ece3.7432>
- Cozzolino, S., & Widmer, A. (2005). Orchid diversity: An evolutionary consequence of deception? *Trends in Ecology & Evolution*, 20(9), 487–494. <https://doi.org/10.1016/j.tree.2005.06.004>
- Dixon, P. (2003). VEGAN, a Package of r Functions for Community Ecology. *Journal of Vegetation Science*, 14(6), 927–930.
- Djordjević, V., Tsiftsis, S., Kindlmann, P., & Stevanović, V. (2022). Orchid diversity along an altitudinal gradient in the Central Balkans. *Frontiers in Ecology and Evolution*, 10, 929266. <https://doi.org/10.3389/fevo.2022.929266>
- Fattorini, S., Borges, P. A. V., Dapporto, L., & Strona, G. (2017). What can the parameters of the species-area relationship (SAR) tell us? Insights from Mediterranean islands. *Journal of Biogeography*, 44(5), 1018–1028. <https://doi.org/10.1111/jbi.12874>
- Ficetola, G. F., & Padoa-Schioppa, E. (2009). Human activities alter biogeographical patterns of reptiles on Mediterranean islands. *Global Ecology and Biogeography*, 18(2), 214–222. <https://doi.org/10.1111/j.1466-8238.2008.00433.x>
- Givnish, T. J., Spalink, D., Ames, M., Lyon, S. P., Hunter, S. J., Zuluaga, A., Doucette, A., Caro, G. G., McDaniel, J., Clements, M. A., Arroyo, M. T. K., Endara, L., Kriebel, R., Williams, N. H., & Cameron, K. M. (2016). Orchid historical biogeography, diversification, Antarctica and the paradox of orchid dispersal. *Journal of Biogeography*, 43(10), 1905–1916. <https://doi.org/10.1111/jbi.12854>
- Gould, S. J. (1979). An allometric interpretation of species-area curves: the meaning of the coefficient. *The American Naturalist*, 114, 335–343.
- Höner, D., & Greuter, W. (1988). Plant population dynamics and species turnover on small islands near Karpathos (South Aegean, Greece). *Vegetatio*, 77, 129–137.
- Inda, L. A., Pimentel, M., & Chase, M. W. (2012). Phylogenetics of tribe Orchideae (Orchidaceae: Orchidoideae) based on combined DNA matrices: Inferences regarding timing of diversification and evolution of pollination syndromes. *Annals of Botany*, 110(1), 71–90. <https://doi.org/10.1093/aob/mcs083>
- Jacquemyn, H., Micheneau, C., Roberts, D. L., & Pailler, T. (2005). Elevational gradients of species diversity, breeding system and floral traits of orchid species on Réunion Island. *Journal of Biogeography*, 32(10), 1751–1761. <https://doi.org/10.1111/j.1365-2699.2005.01307.x>
- Jersáková, J., Johnson, S. D., & Kindlmann, P. (2006). Mechanisms and evolution of deceptive pollination in orchids. *Biological Reviews*, 81(2), 219–235. <https://doi.org/10.1017/S1464793105006986>
- Keppel, G., Gillespie, T. W., Ormerod, P., & Fricker, G. A. (2016). Habitat diversity predicts orchid diversity in the tropical south-West Pacific. *Journal of Biogeography*, 43(12), 2332–2342. <https://doi.org/10.1111/jbi.12805>
- Kühn, R., Cribb, P., & Aerenlund Pedersen, H. (2019). *Field guide to the orchids of Europe and the Mediterranean*. Kew Publishing.
- Lomolino & Weiser. (2001). Towards a more general species-area relationship: Diversity on all islands, great and small. *Journal of Biogeography*, 28(4), 431–445. <https://doi.org/10.1046/j.1365-2699.2001.00550.x>
- Lussu, M., Marignani, M., Lai, R., Loi, M. C., Cogoni, A., & Cortis, P. (2020). A synopsis of Sardinian studies: Why is it important to work on Island orchids? *Plants*, 9(7), 853. <https://doi.org/10.3390/plant9070853>
- Matthews, T. J., Guilhaumon, F., Triantis, K. A., Borregaard, M. K., & Whittaker, R. J. (2016). On the form of species-area relationships in habitat islands and true islands. *Global Ecology and Biogeography*, 25(7), 847–858. <https://doi.org/10.1111/geb.12269>
- Matthews, T. J., Triantis, K. A., Whittaker, R. J., & Guilhaumon, F. (2019). Sars: An R package for fitting, evaluating and comparing species-area relationship models. *Ecography*, 42(8), 1446–1455. <https://doi.org/10.1111/ecog.04271>
- Öckinger, E., Schweiger, O., Crist, T. O., Debinski, D. M., Krauss, J., Kuussaari, M., Petersen, J. D., Pöyry, J., Settele, J., Summerville, K. S., & Bommarco, R. (2010). Life-history traits predict species responses to habitat area and isolation: A cross-continental synthesis. *Ecology Letters*, 13(8), 969–979. <https://doi.org/10.1111/j.1461-0248.2010.01487.x>
- Ollerton, J., Liede-Schumann, S., Endress, M. E., Meve, U., Rech, A. R., Shuttleworth, A., Keller, H. A., Fishbein, M., Alvarado-Cárdenas, L. O., Amorim, F. W., Bernhardt, P., Celep, F., Chirango, Y., Chiriboga-Arroyo, F., Civeyrel, L., Cocucci, A., Cranmer, L., Da Silva-Batista, I. C., De Jager, L., ... Quirino, Z. (2019). The diversity and evolution of pollination systems in large plant clades: Apocynaceae as a case study. *Annals of Botany*, 123(2), 311–325. <https://doi.org/10.1093/aob/mcy127>
- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120(3), 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Panitsa, M., Tzanoudakis, D., Triantis, K. A., & Sfenthourakis, S. (2006). Patterns of species richness on very small islands: The plants of the Aegean archipelago. *Journal of Biogeography*, 33(7), 1223–1234. <https://doi.org/10.1111/j.1365-2699.2006.01481.x>
- Patiño, J., Weigelt, P., Guilhaumon, F., Kreft, H., Triantis, K. A., Naranjo-Cigala, A., Sólymos, P., & Vanderpoorten, A. (2014). Differences in species-area relationships among the major lineages of land plants: A macroecological perspective. *Global Ecology and Biogeography*, 23(11), 1275–1283. <https://doi.org/10.1111/geb.12230>
- Pellissier, L., Vittoz, P., Internicola, A. I., & Gigord, L. D. B. (2010). Generalized food-deceptive orchid species flower earlier and occur at lower altitudes than rewarding ones. *Journal of Plant Ecology*, 3(4), 243–250. <https://doi.org/10.1093/jpe/rtq012>
- QGIS Development Team. (2023). QGIS Geographic Information System. Open Source Geospatial Foundation Project <http://qgis.osgeo.org>
- Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge University Press.
- Schiestl, F. P., & Schlüter, P. M. (2009). Floral isolation, specialized pollination, and pollinator behavior in orchids. *Annual Review of Entomology*, 54(1), 425–446. <https://doi.org/10.1146/annurev.ento.54.110807.090603>
- Schödelbauerová, I., Roberts, D. L., & Kindlmann, P. (2009). Size of protected areas is the main determinant of species diversity in orchids. *Biological Conservation*, 142(10), 2329–2334. <https://doi.org/10.1016/j.biocon.2009.05.015>
- Štípková, Z., Tsiftsis, S., & Kindlmann, P. (2020). Pollination mechanisms are driving orchid distribution in space. *Scientific Reports*, 10(1), 850. <https://doi.org/10.1038/s41598-020-57871-5>
- Taylor, A., Keppel, G., Weigelt, P., Zotz, G., & Kreft, H. (2021). Functional traits are key to understanding orchid diversity on islands. *Ecography*, 44(5), 703–714. <https://doi.org/10.1111/ecog.05410>
- Thomson, F. J., Moles, A. T., Auld, T. D., Ramp, D., Ren, S., & Kingsford, R. T. (2010). Chasing the unknown: Predicting seed dispersal mechanisms from plant traits. *Journal of Ecology*, 98(6), 1310–1318. <https://doi.org/10.1111/j.1365-2745.2010.01724.x>

- Tjørve, E., Kunin, W. E., Polce, C., & Calf Tjørve, K. M. (2008). Species-area relationship: Separating the effects of species abundance and spatial distribution. *Journal of Ecology*, *96*(6), 1141–1151. <https://doi.org/10.1111/j.1365-2745.2008.01433.x>
- Tjørve, E., & Turner, W. R. (2009). The importance of samples and isolates for species-area relationships. *Ecography*, *32*(3), 391–400. <https://doi.org/10.1111/j.1600-0587.2008.05515.x>
- Triantis, K. A., Guilhaumon, F., & Whittaker, R. J. (2012). The Island species-area relationship: Biology and statistics: The Island species-area relationship. *Journal of Biogeography*, *39*(2), 215–231. <https://doi.org/10.1111/j.1365-2699.2011.02652.x>
- Tsiftsis, S. (2020). The complex effect of heterogeneity and isolation in determining alpha and beta orchid diversity on islands in the Aegean archipelago. *Systematics and Biodiversity*, *18*(3), 281–294. <https://doi.org/10.1080/14772000.2020.1738584>
- Walentowitz, A., Troiano, C., Christiansen, J. B., Steinbauer, M. J., & Barfod, A. S. (2022). Plant dispersal characteristics shape the relationship of diversity with area and isolation. *Journal of Biogeography*, *49*(9), 1599–1608. <https://doi.org/10.1111/jbi.14454>
- Whittaker, R. J., Fernández-Palacios, J. M., Matthews, T. J., Borregaard, M. K., & Triantis, K. A. (2017). Island biogeography: Taking the long view of nature's laboratories. *Science*, *357*(6354), eaam8326. <https://doi.org/10.1126/science.aam8326>
- Williamson, M. (1988). Relationship of species number to area, distance and other variables. In A. A. Myers & P. S. Giller (Eds.), *Analytical Biogeography* (pp. 91–115). Springer. https://doi.org/10.1007/978-94-009-1199-4_5
- Wright, S. J. (1981). Intra-archipelago vertebrate distributions: the slope of the species-area relation. *Journal of Biogeography*, *8*(4), 365–375.
- Yu, J., Li, D., Zhang, Z., & Guo, S. (2020). Species-area relationship and small-island effect of bryophytes on the Zhoushan Archipelago, China. *Journal of Biogeography*, *47*(4), 978–992. <https://doi.org/10.1111/jbi.13790>

BIOSKETCH

Michele Lussu is interested in orchids ecology and evolution with a special focus on dynamics that shape their occurrence.

Author contributions: M.L. ideated the project, organized the research group and developed the first theoretical framework and carried out the statistical analyses; A.C. contributed to setting the theoretical framework; M.C. D.D. and S.M. contributed to setting the general framework and to write down a first draft of the discussions; P.Z. and R.T. reviewed the plant occurrence data, assembled and supported the statistical analyses. The manuscript was drafted by M.L. and subsequently developed by all the authors.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Lussu, M., Zannini, P., Testolin, R., Dolci, D., Conti, M., Martellos, S., & Chiarucci, A. (2024). Biogeography of orchids and their pollination syndromes in small Mediterranean islands. *Journal of Biogeography*, *51*, 869–877. <https://doi.org/10.1111/jbi.14792>