




## RESEARCH ARTICLE

# Scale-dependent shifts in functional and phylogenetic structure of Mediterranean island plant communities over two centuries

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## Abstract

1. Since the Industrial Revolution, the rapid global population and economic expansion have had tremendous impacts on biodiversity across spatial scales, especially for islands. While changes in species richness are easily inferred, the impact of human activity on the underlying community assembly processes has been difficult to ascertain because of lack of long-term community data.
2. Here, we document how the manifestations of plant community assembly have changed over time and space in a Mediterranean archipelago, using a long-term dataset of plant species composition on 16 Tuscan islands sampled across two centuries. The community structure of Mediterranean island plant communities was assessed by integrating species' trait and evolutionary distances.
3. We found that, with increasing island area, the functional and phylogenetic structure of plant communities shifted from clustered early (1830–1950) to overdispersed more recently (1951–2015). On large islands, extirpated species were generally more phylogenetically or functionally similar to remaining residents than expected by chance, while colonists were generally more distantly related to residents. The extinction of similar species and the colonization of dissimilar species drove plant communities towards overdispersion.
4. *Synthesis.* We provide evidence that plant community assembly on islands has dramatically changed following increased human impacts during the last two centuries, and that this change is shaped by the scale dependency of species extinctions and colonizations. Our results reveal accelerated species replacements of closely related residents by distant colonists on large islands over time, reflecting changes in community assembly and which could alter the functioning of island ecosystems in the future.

**KEYWORDS**

biogeography and macroecology, community assembly, island area, spatial scale, species turnover, temporal scale, Tuscan archipelago

## 1 | INTRODUCTION

The science of ecology is built upon the universal principle that species exist in some places and not in others, and there are a plethora of hypotheses explaining spatial patterns of species diversity. Generally, local communities are believed to be structured by a set of processes, including the influence of the abiotic environment on fitness (Weiher & Keddy, 1995; e.g. environmental filtering), biotic interactions, in particular interspecific competition (Leibold, 1998; MacArthur & Levins, 1967), and stochastic processes, including dispersal limitation, demographic stochasticity and ecological drift (Chase & Myers, 2011; Zhou & Zhang, 2008). These processes are scale dependent and tend to shift with spatial scales (Cavender-Bares et al., 2006, 2009). For example, interspecific interactions and density-dependent mechanisms should be strongest at the neighbourhood scale where individual organisms interact, and environmental filtering should be stronger than interspecific interactions at the habitat scale (Cavender-Bares et al., 2009), though these processes certainly interact to shape ecological communities across scales (Cadotte & Tucker, 2017).

Islands are natural laboratories for studying the generation and maintenance of species diversity, and therefore, island biogeography has been an inspiration for some of the most enduring theories in ecology and evolution (Whittaker & Fernández-Palacios, 2007). The most famous of them is the classic Theory of Island Biogeography (MacArthur & Wilson, 1967; hereafter, TIB). TIB proposed that island species diversity results from the balance between extinction and immigration rates, which vary with island size and isolation, respectively (MacArthur & Wilson, 1967; Si et al., 2014; Warren et al., 2015). TIB has provided fundamental insights into the formation of ecological communities on islands or island-like habitats and has generated a suite of testable hypotheses (Simberloff, 1969). Despite its success in predicting diversity patterns over the past half century, however, TIB has been limited in its ability to assess the role of non-neutral processes driving community assembly as well as the impacts of human activities (but see Si et al., 2017).

In recent years, with the rapid development of bioinformatic methods and data availability, functional and phylogenetic information has been used in studies of island biodiversity (Carvalho & Castro, 2017; Si et al., 2017; Weigelt et al., 2015), allowing researchers to understand how spatial processes influence community assembly and to predict how altered assembly mechanisms result in non-random species loss. It is generally understood that when traits are phylogenetically conserved and environmental filtering (or at least fitness differences are correlated with environmental differences) dominates community assembly, assemblages will be dominated by closely related species (functional and phylogenetic

clustering; Cadotte & Tucker, 2017; Webb et al., 2002). Conversely, competitive exclusion should limit the coexistence of closely related species at relatively small scales, resulting in the co-occurrence of more distantly related or dissimilar species (functional and phylogenetic overdispersion; Cavender-Bares et al., 2006, 2009; Webb et al., 2002). Non-random species loss and colonization could result in either community clustering or overdispersion (Li et al., 2015), while stochastic or multiple conflicting processes will generate random or near-random patterns of co-occurring species (Cadotte et al., 2017). Therefore, TIB could be extended to predict community patterns by moving beyond the assumptions of species equivalency in colonization and extinction rates when incorporating species' functional and phylogenetic information (Si et al., 2017).

The influence of human activities on diversity is an extremely well-studied topic (Vellend et al., 2017). However, how these activities modify the assembly mechanisms that generate biodiversity patterns over long time periods has seldom been addressed. Over the past centuries, human impacts on ecosystems have increased around the world and caused a large number of extinctions, extirpations, and invasions (Vellend et al., 2017; Winter et al., 2009). These impacts could also either homogenize island biota or accentuate differences if islands experience different human stressors (e.g. agriculture vs. urbanization). Minimally, it is hypothesized that human activities, especially movement, will alter functional and phylogenetic patterns on islands and homogenize them by breaking down dispersal barriers (Helmus et al., 2014; Sobral et al., 2016).

In this study, we explore the functional and phylogenetic structure of island plant communities, and how it has shifted over time and space, using a long-term, comprehensive dataset of plant species composition on the Tuscan Archipelago, Italy (Chiarucci et al., 2017). These data span two centuries and can be divided into an early era (1830–1950) and a modern era (1951–2015). With this dataset, Chiarucci et al. (2017) found changes in island species–area relationship for native flora, alien flora and different life forms (annual herbaceous, perennial herbaceous, woody species) across these two time periods. We expand on this original work by including functional and phylogenetic data to study the impacts of human activity on community assembly processes.

Spatial scale is one of the core components of Island Biogeography (MacArthur & Wilson, 1967). Random placement is expected to have a greater role in community assembly compared with habitat diversity on smaller island (Triantis et al., 2012). Empirically, phylogenetic clustering has been shown to increase with spatial scale in plant communities (Cavender-Bares et al., 2006, 2009; Swenson et al., 2006). Thus, we hypothesize that stochastic processes largely governed plant community structure on small islands, while deterministic assembly processes (e.g. environmental filtering) increased with island

area in the early period (Figure 1). Human activities (e.g. accelerating trade and transportation) are causing the homogenization of species composition across biogeographic barriers (or habitat barriers) by breaking down dispersal barriers, especially for island biota (Capinha et al., 2015; Fricke & Svenning, 2020; Helmus et al., 2014), and thus, they likely overshadow the role of environmental filtering to a certain extent on islands. Therefore, we also hypothesize that plant community structure on islands might be more random or overdispersed in the recent period compared with the early period (Figure 1). Additionally, shifts in community assembly patterns might depend on island size (Figure 1), since plant populations on smaller islands are more susceptible to the stochastic processes of species dispersal and extinction (Kadmon et al., 2007; Lomolino & Weiser, 2001; MacArthur & Wilson, 1967) which might overshadow human impacts at the community level.

## 2 | MATERIALS AND METHODS

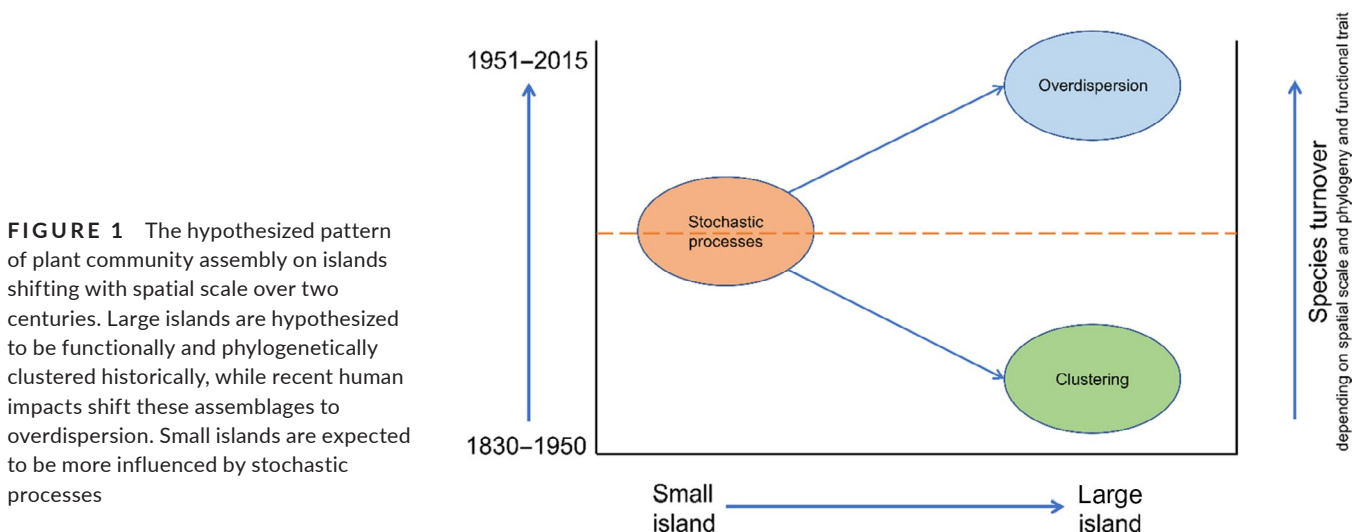
### 2.1 | Study area and community dataset

The Tuscan archipelago comprises eight large islands and several islets located between Corsica and Tuscany (Table S1). The climate of the Tuscan archipelago is typically Mediterranean characterized by mild winters and hot summers (average temperatures of 10 and 26°C, respectively) with rainfall concentrated (62% of annual rainfall) in autumn and winter (October–February; Carta et al., 2012).

The dataset for the extant species on each island was described in detail in Chiarucci et al. (2017) and is here briefly presented. The botanical team of the University of Florence (which was the most important botanical institution in Italy, hosting the largest Italian herbarium, the Italian Botanical Society and a library where most of the botanical literature about Italy is archived) searched and compiled all available published papers and some unpublished sources (masters' theses, doctoral dissertations and technical reports) dealing with the plants of the Tuscan archipelago (see list of sources used to assemble

the checklists of species in Chiarucci et al., 2017). These references were used to extract occurrence records for all species reported as spontaneous on the studied islands. The nomenclature was standardized to current taxonomy and subspecies were merged into species level (ThePlantList.org). The existing data on plant species occurrences on 16 islands (seven major islands, Monte Argentario fossil island and eight islets) were assembled in two main periods: from 1830 to 1950 and from 1951 to 2015. 1950–1951 was used as a pivotal shift date because of the major changes in the human presence and activities on the islands from the 1950s, when most of the archipelago's economy shifted from traditional agriculture to tourism (Chiarucci et al., 2017). After 1951, the regional economy and trade developed rapidly (Vera, 1993). Human interference including the expansion of tourism and tourism areas, frequent anthropogenic fires and large-scale invasion of alien species is more intense today than in the past. A total of 181 alien plants were found in the Tuscan archipelago from 1951 to 2015 (Chiarucci et al., 2017). Alien and native species were classified based on national and regional data (Celesti-Grapow et al., 2009, 2010a, 2010b; Lazzaro et al., 2016). Many alien plants (e.g. *Ampelodesmos mauritanicus*, a grass that came from Africa) in combination with anthropogenic fires arrest natural succession (Cyffka, 2005).

Many large islands experienced great changes in land-use patterns, and large areas of agricultural land (e.g. mountain pasture, plantations, field terraces) have been abandoned or transformed into tourism areas or urbanized land (Chiarucci et al., 2017). Urbanization, intensive farming, some industries and intense traffic are now found near the shore of some large islands (e.g. Elba; Cyffka, 2005; Davis & Richardson, 1995). The complete dataset assembled for the present study is reported in Chiarucci et al., 2017. In total, the dataset includes 10,892 occurrence data for 1,831 species from 16 islands across two study periods: 5,714 for the early period (1830–1950) and 5,178 for the recent period (1951–2015; Chiarucci et al., 2017). The total number of species recorded was 1,601 in the early period and 1,541 in the recent period. The two periods had 1,311 species in common, yielding a Jaccard similarity index of 0.72. Thus, 28% of the



species recorded in the dataset were found in only one of the two periods: 290 species disappeared, while 230 new species appeared in the archipelago in the recent period (Chiarucci et al., 2017).

## 2.2 | Community phylogeny and functional traits

The hypothesized phylogenetic tree for all species in our dataset was constructed using the R package V.PHYLOMAKER (Jin & Qian, 2019) with the largest dated mega-tree for vascular plants (Open Tree of Life) including 74,533 species and all families of extant vascular plants as the backbone, which provides high resolution relationships among families and most genera. The ferns were excluded from the phylogenetic reconstruction as there were few ferns (62 ferns) reported on the studied islands, which barely influence species richness but bias the distance-based measures of community diversity (Cadotte & Davies, 2016). Our further analyses were based on this subset including 1,769 species of seed plant.

To assess island functional community structure and assembly, we used three traits that reflect fundamental ecological strategies for plants (Leaf-Height-Seed scheme; Westoby, 1998): *specific leaf area* (SLA; area per unit dry mass), associated with leaf longevity, plant relative growth rate, mean residence time of nutrients and soil nutrient adaptations; *plant height*, a proxy for competitive vigour and tolerance or avoidance of environmental (climatic, nutritional) stresses; and *seed mass*, which influences dispersal and establishment ability. These trait data were obtained from the Botanical Information and Ecology Network database (Enquist et al., 2016) using the R package BIEN (Maitner et al., 2018), TRY DATABASE (Kattge et al., 2020) and BROTT 2.0 (Tavşanoğlu & Pausas, 2018). The SLA for 1,009 species, *plant height* for 1,358 species and *seed mass* for 1,249 species were identified at the species level, and the other trait data were obtained from congeneric relatives.

## 2.3 | Community structure measures

We used *traitgrams* to combine functional trait and phylogenetic distances (Cadotte et al., 2013) to estimate species' ecological differences. We calculated the functional distance (Gower distance; Gower, 1971) of the three traits using the function *gowdis* in R package FD (Faith, 1992) and the phylogenetic distance (patristic distance) using the function *cophenetic* in R package STATS. We then integrated functional and phylogenetic distances using the function *funct.phylo.dist* in R package PEZ (Pearse et al., 2015) to combine functional and phylogenetic distances into a single measure: the functional-phylogenetic distance matrix (Cadotte et al., 2013). The functional-phylogenetic distance includes a phylogenetic weighting parameter,  $a$ , which scales the relative contribution of functional and phylogenetic distances to the functional-phylogenetic distance matrix. For example, when  $a = 0$ , only functional distance contributes to the functional-phylogenetic distance matrix, and only phylogenetic distance when  $a = 1$ . Otherwise, at an intermediate value of  $a$ , both

functional and phylogenetic distances contribute to the resulting functional-phylogenetic distance matrix. In this study, we varied  $a$  from 0 to 1 (in intervals of 0.1), and the best  $a$  was determined by the highest adjusted  $R^2$  values of the regression model (described below). By integrating species traits and phylogenies, this combined method could overcome the shortcomings of approaches that are based exclusively on functional or phylogenetic distance (Cadotte et al., 2013, 2019; Mayfield & Levine, 2010; Si et al., 2017).

Mean functional-phylogenetic pairwise distance (MFPD) among species in each island was calculated to evaluate the functional-phylogenetic structure (Cadotte et al., 2013; Cadotte & Davies, 2016) in the two periods. MFPD was compared to null models to test whether the functional-phylogenetic structure differs from random expectations in plant community structure. Specifically, random communities were generated by maintaining the species richness of each island, but making the identities of those species random that were drawn from the whole species pool (i.e. all species on 16 studied islands in both sampling periods). The standardized effect size (SES) of MFPD was calculated as  $SES.MFPD = (\chi_{obs} - \chi_{null})/SD_{null}$ , where  $\chi_{obs}$  is the observed value of MFPD,  $\chi_{null}$  is the mean of the simulated values from 999 randomized communities, and  $SD_{null}$  is the standardized deviation of the simulated values. Positive standardized effect sizes indicate a higher observed value than expected by chance (e.g. zero value) and are referred to as overdispersed, and negative values indicate a lower observed value than expected, representing clustering (Cadotte & Davies, 2016). We calculated the SES.MFPD using the function *ses.mpd* in R package PICANTE (Kembel et al., 2010). We used three commonly employed null models in our analysis: null model 0: shuffle species labels across distance matrix; null model 1: randomize community matrix by drawing species from species pool; null model 2: randomize community matrix by drawing species from phylogeny and trait dendrogram pool (Cadotte & Davies, 2016). The null models returned qualitatively similar results, so we mainly report results based on null model 0.

To assess the processes that shape plant community structure, we calculated  $SES.\beta MFPD$  between extirpated and colonized species and these species to the species observed historically and to the species observed in both sampling periods on each island.  $\beta MFPD$  calculates the mean pairwise functional-phylogenetic distance between two assemblages (Cadotte & Davies, 2016; Li et al., 2015) using the function *comdist* in R package PICANTE (Kembel et al., 2010). The  $SES.\beta MFPD$  was calculated as  $SES.\beta MFPD = (X_{obs} - X_{null})/SD_{null}$ , where  $X_{obs}$  is the observed value of  $\beta MFPD$  between two assemblages,  $X_{null}$  is the mean of the simulated values from 999 randomized communities and  $SD_{null}$  is the standardized deviation of the simulated values of  $\beta MFPD$ . Positive values of  $SES.\beta MFPD$  indicate a greater difference between species compositions between the two assemblages than random, and negative values indicate a trend of more similar species compositions between the two assemblages than expected. For the colonizing species on one island, we used all species recorded but excluding species recorded on the selected island in the early period as species pool, then we created 999 randomized communities with the same number of colonizing species

on the selected island to calculate  $X_{\text{null}}$  and  $SD_{\text{null}}$ . For the extirpated species on one island, the species pool for null communities was the species occurred in the early period, then we used the same method to calculate  $X_{\text{null}}$  and  $SD_{\text{null}}$  for the extirpated species.

## 2.4 | Statistical analysis

We calculated the values of SES.MFPD across the range of  $\alpha$  values from 0 to 1 with an interval of 0.1. We then estimated the adjusted  $R^2$  values of the regressions between derived SES.MFPD and island area using linear regressions. The adjusted  $R^2$  value in our study reached its maximum (0.86) when  $\alpha = 0.3$  (Figure S1). In consideration of the contribution of both phylogenetic distance and functional distance to the functional-phylogenetic distance matrix, we calculated SES.MFPD and SES. $\beta$ MFPD at  $\alpha = 0.3$  respectively. We also calculated SES.MFPD and SES. $\beta$ MFPD at  $\alpha = 0$  (i.e. SES.MFD and SES. $\beta$ MFD) and  $\alpha = 1$  (i.e. SES.MPD and SES. $\beta$ MPD) respectively.

Changes in plant community structure (SES.MFPD) of each island across the two centuries were compared with a paired  $t$  test. We used a linear regression to explore the relationship between log-transformed island area/distance (to the mainland) and plant community structure for the two periods. Both variables were included in a single multivariate model to test for the correlation between plant community structure and these variables simultaneously. We also used a linear regression to explore the relationship between log-transformed island area and SES. $\beta$ MFPD of colonizing species to species occurred in the early period, species existed in both periods and extirpated species; SES. $\beta$ MFPD of extirpated species to species occurred in the early period, species existed in both periods and colonizing species.

Additionally, we tested the spatial autocorrelation of SES.MFPD, SES.MFD and SES.MPD using the global Moran's  $I$  (Legendre & Legendre, 2012) with the function *Moran.I* in R package *APE*. We found no evidence of significant spatial autocorrelation (i.e.  $p > 0.05$ ; Table S2), so we did not consider it in our analyses.

In order to test whether alien species increased or decreased functional and phylogenetic distance in island communities and thus influenced functional and phylogenetic construction, we calculated the observed  $\beta$ MFPD between alien species and native species. The number of alien species which appeared in the recent period was used in this analysis. To compare the observed  $\beta$ MFPD with sampled  $\beta$ MFPD, we generated null communities by randomly selecting species from the island species pool and maintaining species richness of alien species with 999 runs and sampled  $\beta$ MFPD was calculated based on null communities.  $\beta$ MFPD was considered as significantly lower when it was <2.5% of sampled  $\beta$ MFPD (i.e. Rank < 25), and significantly higher when it was more than 97.5% of sampled  $\beta$ MFPD (i.e. Rank > 975).

Because biotic processes such as competition can also produce clustering (Mayfield & Levine, 2010; Si et al., 2017), we additionally analysed observed variance in size ratios (VSR) as an attempt to detect potential drivers. To test whether community assembly is driven

by competition, we evaluated the evenness in the spacing between the log-transformed ranked trait values (i.e. VSR) for species within a community (Cadotte & Davies, 2016). If competition is the main driver of community assembly on the islands, traits will be evenly spaced (low VSR). To compare the observed VSR with sampled VSR, we generated null communities by randomly selecting species from the island species pool and maintaining species richness on each island with 999 runs. We can thus expect observed VSR of each island would be significantly lower than the 95% confident intervals of sampled VSR from null communities.

## 3 | RESULTS

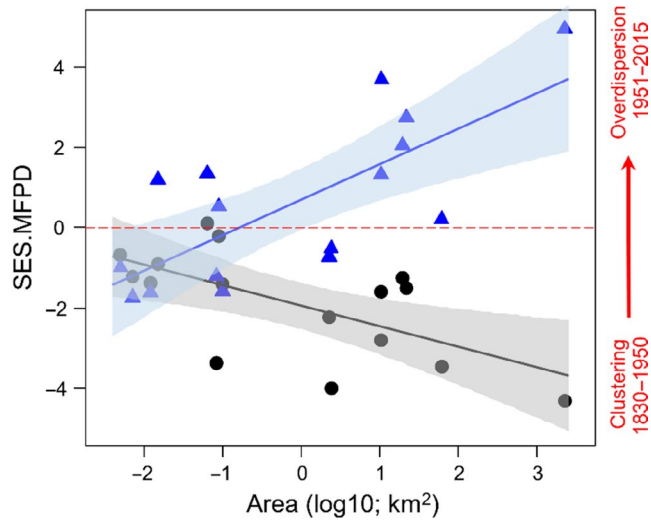
### 3.1 | The changes of plant community structure over two centuries

The average number of species per island was  $346 \pm 92$  (mean  $\pm$  SE, range 6 ~ 1,164) in the early period and  $313 \pm 79$  (2 ~ 978) in the recent period, exhibiting a marginally significant decline (Paired two-sample  $t$  test:  $t = 1.86$ ,  $p = 0.082$ ). The average numbers of extirpated and colonizing species per island between the two periods were  $98 \pm 26$  (0 ~ 352) and  $65 \pm 14$  (0 ~ 166) respectively.

SES.MFPD ranged from  $-4.31$  to  $0.11$  (mean:  $-1.89$ , SE: 0.33; 95%CI:  $-2.60$ ,  $-1.17$ ) in the early period, indicating that most plant communities were functionally and phylogenetically clustered (one-sample  $t$  test:  $t = -5.65$ ,  $p < 0.001$ ). SES.MFPD ranged from  $-1.73$  to  $4.96$  (mean:  $0.60$ , SE: 0.50; 95%CI:  $-0.46$ ,  $1.67$ ) in the recent period, indicating that plant communities were functionally and phylogenetically random or overdispersed (one-sample  $t$  test:  $t = 1.21$ ,  $p = 0.247$ ). Plant functional and phylogenetic community structure was significantly more overdispersed in the later period (paired two-sample  $t$  test:  $t = 3.76$ ,  $p = 0.002$ ).

### 3.2 | The influence of island area on plant community structure in both periods

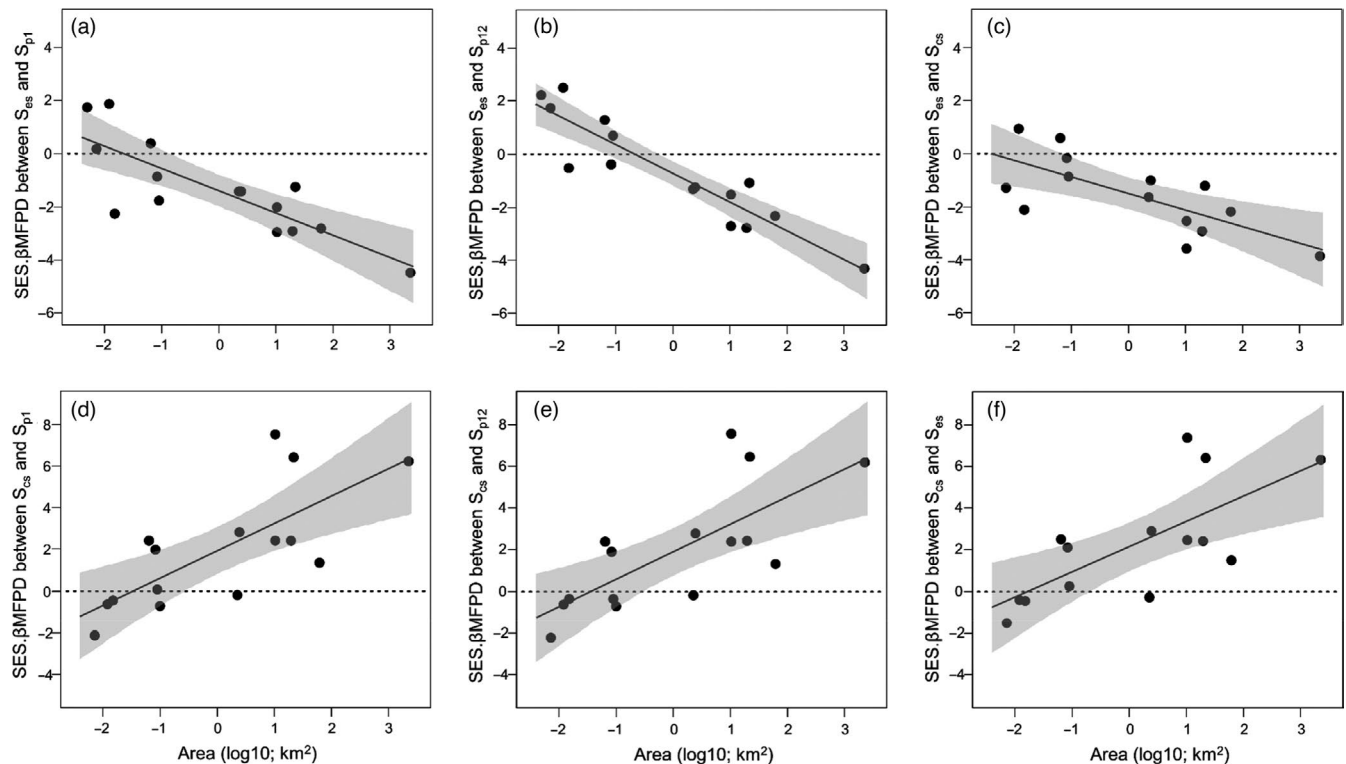
SES.MFPD was significantly influenced by island area in both periods (Figure 2), but in opposing directions. In the early period, SES.MFPD decreased with increasing island area ( $R^2_{\text{adj}} = 0.36$ ,  $p = 0.008$ ; Figure 2), while in the recent period, it increased with island area ( $R^2_{\text{adj}} = 0.50$ ,  $p = 0.001$ ; Figure 2). SES.MFD (Figure S2) and SES.MPD (Figure S3) show similar trends with SES.MFPD. However, the relationship between SES.MFD and island area was significant in the early period but not in the recent period, while the relationship between SES.MPD and island area was significant in the recent period but not in the early period. There was no relationship between distance and SES.MFPD, SES.MFD, and SES.MPD in both periods, separately (Table S3). Bivariate models reported similar results with univariate models (Table S4). Models testing relationships of distance with the residuals of island area on plant community structure also reported similar results (Table S5).



**FIGURE 2** The relationship between SES.MFPD and island area in the two time periods. Black filled circles indicate SES.MFPD in the earlier period (1830–1950) and blue triangles indicate SES.MFPD in the more recent period (1951–2015). The blue or black solid lines represent  $p < 0.05$ . Shaded regions indicate 95% confidence intervals

### 3.3 | The extinction of similar species and the colonization of dissimilar species

The averaged SES. $\beta$ MFPD between extirpated species and species occurring in the early period, species that existed in both periods and colonized species were  $-1.33 (\pm SE 0.46)$ ,  $-0.65 (\pm SE 0.52)$  and  $-1.55 (\pm SE 0.38)$ , respectively, and they all decreased with island area ( $R_{adj}^2 = 0.64$ ,  $p < 0.001$ ;  $R_{adj}^2 = 0.83$ ,  $p < 0.001$ ;  $R_{adj}^2 = 0.48$ ,  $p = 0.004$ , respectively; Figure 3a–c). This indicates that extirpated species were generally more phylogenetically or functionally similar to remaining residents than expected by chance on large islands. The averaged SES. $\beta$ MFPD between colonizing species and species that occurred in the early period, species that existed in both periods and extirpated species were  $1.96 (\pm SE 0.74)$ ,  $1.92 (\pm SE 0.75)$  and  $2.25 (\pm SE 0.74)$ , respectively, and they increased with island area ( $R_{adj}^2 = 0.50$ ,  $p = 0.002$ ;  $R_{adj}^2 = 0.50$ ,  $p = 0.002$ ;  $R_{adj}^2 = 0.48$ ,  $p = 0.003$  respectively; Figure 3e–f). This indicates that colonists were generally more distantly related to residents than expected by chance on large islands. SES. $\beta$ MFD (Figure S4) and SES. $\beta$ MPPD (Figure S5) showed qualitatively similar trends with SES. $\beta$ MFPD with island area.



**FIGURE 3** The relationships of beta diversity values against island area. All the relationships, SES. $\beta$ MFPD of extirpated species (a–c,  $S_{es}$  to  $S_{p1}$ ,  $S_{p12}$  and  $S_{cs}$ ) and SES. $\beta$ MFPD of colonizing species (d–f,  $S_{cs}$  to  $S_{p1}$ ,  $S_{p12}$  and  $S_{es}$ ) were significantly influenced by island area.  $S_{cs}$ , colonizing species;  $S_{es}$ , extirpated species;  $S_{p1}$ , species occurring in the early period;  $S_{p12}$ , species observed in both periods. (a)–(c) Random communities were generated by maintaining the species richness of  $S_{es}$  of each island, but making the identities of those species random that were drawn from the species pool (i.e. all species on each of 16 studied islands in the early period). (d)–(f) Random communities were generated by maintaining the species richness of  $S_{cs}$  of each island, but making the identities of those species random that were drawn from the species pool (i.e. all species on 16 studied islands in both periods with subtracting species on each island in the early period). Solid lines represent the fitted linear regressions and their slope  $> 0$  or slope  $< 0$  at  $p = 0.05$ . Shaded regions indicate 95% confidence intervals

### 3.4 | $\beta$ MFPD, $\beta$ MFD and $\beta$ MPD between alien species and native species

$\beta$ MFPD,  $\beta$ MFD and  $\beta$ MPD between alien species and native species were all significantly higher than null models (Table S6). This indicates that alien species increased functional and phylogenetic distance in island communities and thus induced functional and phylogenetic patterns to tend to be overdispersed in the recent period.

### 3.5 | The observed variance in size ratios of functional traits

In the early period, the observed VSR of seed mass on Pianosa, SLA on Gorgona and Montecristo and plant height on Giannutri, Gorgona, Isolotto Porto Ercole and Scola was significantly lower than sampled VSR from null communities (Table S7). In the recent period, the observed VSR of seed mass on Giannutri and Montecristo, SLA on Elba and plant height on Argentario, Formica Grande and Isolotto Porto Ercole was significantly lower than sampled VSR from null communities (Table S7). In the early period, the observed VSR of SLA on Argentario and plant height of Argentario, Capraia, Elba, Giglio, Montecristo and Pianosa in the early period was significantly higher than sampled VSR (Table S7). In the recent period, the observed VSR of seed mass on Giglio, SLA on Fobu, plant height of Argentarola, Capraia, Elba, Giglio and Montecristo in the early period was significantly higher than sampled VSR (Table S7). The analyses of VSR of traits showed that observed values were not significantly lower or higher than sampled values from null communities on other islands (Table S7).

## 4 | DISCUSSION

Human activities have greatly impacted biodiversity and community composition across spatial scales, especially since the Industrial Revolution (Helmus et al., 2014). Changes in species richness have been relatively well studied, although they remain controversial (Cardinale et al., 2018; Koh et al., 2004). In contrast, little is known about how human impacts have altered community assembly processes spanning more than a century because experimental manipulations at relevant geographical and temporal scales are impossible. Here, for the first time, our study provides evidence of a dramatic shift in plant community assembly patterns on islands as a result of human impacts across two centuries.

During the two centuries, average plant species richness per island decreased from 346 to 313 species, showing that the islands in the Tuscan archipelago lost, on average, c. 10% of their plant species. Prior to the recent massive human impacts, plant communities on these islands tended to be functionally and phylogenetically clustered, especially on larger islands, supporting the overriding importance of environmental filtering and perhaps dispersal limitation in

shaping plant community assembly. This result is consistent with a recent study on island bird communities in the Thousand Island Lake region of China, which also revealed that islands tended to have clustered assemblages (Si et al., 2017).

A fundamental shift in community structure has occurred as island plant communities became functionally and phylogenetically random or overdispersed in the recent period (1951–2015) compared to the early period (1830–1950). Functional–phylogenetic distances between species increased significantly between the two periods. These results indicate that the processes structuring island plant communities shifted from ones like environmental filtering that select for similar species, to processes such as invasion that results in the establishment and spread of dissimilar species (Figure 3), and further that increases in competitive exclusion, through reduced and homogenized habitat that supports the coexistence of dissimilar species.

One important finding in our study is that island plant community assembly patterns were strongly influenced by island size (Figure 2). We found that clustering increased with increasing island area in the early observations (1830–1950). A recent avian study by Si et al. (2017) found the opposite, that is, the SES.MFPD of island bird communities increased with island area. Much of their mechanistic interpretation relied on the active dispersal and habitat selection of birds. Sessile organisms such as plants that are subject to strong negative biotic interactions in their immediate neighbourhoods might respond very differently to island size. It is well known that plant populations on small islands are more susceptible to the stochasticity of species dispersal and extinction than are actively dispersing organisms (Kadmon et al., 2007; Lomolino & Weiser, 2001). Our results show that random species turnover (i.e. species loss and invasion) is indeed more prevalent on small islands (Figure 3), and it might be that in the absence of these stochastic processes, small islands would be as clustered as larger islands. Therefore, stochastic processes might drive plant community structure on small islands, while deterministic assembly processes such as environmental filtering tend to predominate on large islands.

In contrast to the historical patterns observed, we found that overdispersion increased with island area more recently (Figure 2). Not only does this show a reversal of the historical assembly patterns but it also suggests that the processes governing species composition on islands have been fundamentally altered (see also Helmus et al., 2014). Human impacts have resulted in a dramatic non-random shift in plant community assembly over two centuries, driven by three likely mechanisms. Firstly, human-facilitated movement is causing the homogenization of species composition across habitat barriers by breaking down dispersal barriers for island biota (Capinha et al., 2015; Fricke & Svenning, 2020; Helmus et al., 2014), and it likely overshadows the strength of environmental filtering or fitness differences for groups of closely related species on larger islands. After 1951, many large islands experienced substantial changes in land-use patterns due to a shift from the traditional economy based on pastoralism, forestry, agriculture to a new economy based on tourism (Chiarucci et al., 2017). With the development of

regional economies (especially tourism), trade and transportation have accelerated compared with the traditional agricultural era.

Secondly, we found that colonists were generally more distantly related to residents than by chance on larger islands (Figure 3). One possible reason for this finding is that dissimilar species might be more likely to successfully invade intact communities (Li et al., 2015), or priority effects could inhibit the colonization of closed related species (Fukami, 2015; Si et al., 2017), or that with the breakdown of biogeographic dispersal barriers, colonists are now drawn from a much larger, more evolutionarily diverse species pool. The movement of tourists, especially to large islands, has likely broken down dispersal barriers and accelerated the colonization of alien species and those from the mainland or other Mediterranean islands. Therefore, the increasingly dissimilar colonists also probably included species that came from outside the archipelago and that either benefited from human-facilitated movement or were purposefully introduced on islands. These invasions of alien species significantly increased functional and phylogenetic distance in island communities (Table S6).

Thirdly, we found that extirpated species were generally more closely related or functionally similar to residents than by chance on larger islands (Figure 3). This could be attributed to the similar and closely related species that share similar niche requirements (Wiens & Graham, 2005) experienced the greatest competition and were more likely to be competitively excluded because of limited resources (Gómez et al., 2010; Si et al., 2014; Sobral et al., 2016) imposed by a decline in primary habitat for these species. Thorn et al. (2016) show that, in a managed forest, the decline in available habitat and resource increases community functional and phylogenetic diversity even while species richness decreases. The extension of tourism and tourism areas has greatly compressed the suitable habitat since 1951 on some larger islands (e.g. Elba; Chiarucci et al., 2017; Cipriani et al., 2011). In addition, land abandonment in agriculture has caused large area reduction of artificial or semi-natural habitats (e.g. mountain pasture, plantations, field terraces) which some species are historically more suited for Cyffka (2005).

The classic Theory of Island Biogeography has proposed that island size and isolation drive differences in species diversity on islands. But our study did not find relationships between island isolation and functional-phylogenetic structure of Mediterranean island plant communities. The possible reason is that the range of distance (from 4.25 to 61.2 km; Table S1) is relatively small compared to the dispersal abilities of species. In addition, human activities undermine natural geographic isolation among different regions, especially in modern times (e.g. Helmus et al., 2014).

Recent studies suggested that the use of phylogenetic structure to infer community assembly mechanisms sometimes could be misleading (Davies, 2021; Kraft et al., 2015; Mayfield & Levine, 2010). Alternative hypotheses are possible and have to be excluded before definitive conclusions about community assembly mechanisms can be made (Kraft et al., 2015; Mayfield & Levine, 2010). In our study, island plant community structure was assessed by integrating species' trait and evolutionary distances. This combined method could overcome the shortcomings of approaches that are based exclusively

on functional or phylogenetic distance. VSR analyses are also used to infer community assembly mechanisms. Low VSR (i.e. traits are evenly spaced) indicates that competition is likely to be driving community assembly. From these results, we inferred that competition is important for island plant communities on Giannutri and Montecristo in the early period, and coupled with environmental filtering, results in significantly clustered communities. However, different traits exhibit different VSR patterns. For example, the observed VSR of seed mass was significantly lower than null VSR values, while the observed VSR of plant height was significantly higher than the null expectations for communities on Montecristo in the recent period. Given the complexity in relating different traits to competition, the interpretation of VSR analyses is complex. Furthermore, opposing trait VSR patterns could reflect the fact that species compete across some axes, but are subject to environment-fitness covariance across others (Cadotte & Tucker, 2017).

Evolutionary processes also influence island diversity and community assembly patterns (Gillespie, 2004; Wiens, 2012). For example, rapid diversification on islands would produce phylogenetically clustered communities (Cardillo, 2011). This should be most obvious on large islands that are more likely to support speciation which results in community clustering (e.g. the early period in our study), versus small islands, where community composition would be governed primarily by colonization and extinction and demographic stochasticity. While we do observe greater clustering on islands in the early period, we cannot distinguish between evolutionary and ecological processes on island community structure with our current dataset. Future analyses will need to assess the global range of the species observed on these islands to determine whether they are the product of local speciation or whether they exist elsewhere, especially on the mainland, and other factors limit their presence on islands. However, given the scale and distance separating islands, endemic speciation driving clustering is not likely to be an important driver.

There are two limitations of our study include the role of intra-specific trait variation and potential biases in the source of species data. Recent studies showed that intraspecific trait variation could be quite important for assessing community assembly mechanisms (Albert et al., 2012; Luo et al., 2016). In our study, although plant traits are likely to have changed across both temporal (over two centuries) and geographic scales, we are unable to assess this with available data. Our study, like other long-term temporal studies that rely on historic records (e.g. Li et al., 2015; Zhang et al., 2015) are often limited to using interspecific trait data. The extent to which accounting for intraspecific variation would alter our results is unclear, though, we suspect that given the spatial and taxonomic scale of our comparison, our general conclusions would be similar. Future analyses should strive to find ways to infer intraspecific variation effects on community assembly in historical communities. An additional concern is biases in the literature from which the collection of plant species lists, such as failing to record rare species. This is a methodological problem faced by a study using historic records to assess large-scale changes in diversity (Daru et al., 2018). In our study, we took considerable pains to cross-reference multiple sources of data



(manuscripts, theses, herbaria records etc.) when building our dataset (see Section 2). Indeed, the detailed vetting of our species list is one of the things that makes this dataset so unique.

## 5 | CONCLUSIONS

Our study reveals that the functional and phylogenetic structure of plant communities varied from random to clustered with increasing island area prior to massive human influence on these islands (1830–1950; Figure 1). In contrast to this historical pattern, community structure varied from random to overdispersed with increasing island area in the recent era (1951–2015; Figure 1). Consequently, we provide the first evidence that the effect of island size on plant community assembly patterns dramatically shifted over two centuries in response to human pressure. This dramatic shift resulted from functionally and phylogenetically biased species local extinctions and colonizations, with stronger effects on larger islands. Our results suggest that assessing biodiversity changes on islands requires analyses that move beyond equilibrium species richness assumptions and consider community assembly. They reveal that increasing human activities and impacts can profoundly influence plant community assembly, to the point of fundamentally altering diversity–island area relationships. Our results also reveal accelerated species replacements of closely related residents by distant colonists on large islands over time, a process that could alter the functioning of island ecosystems in the future.

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## CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

## AUTHORS' CONTRIBUTIONS

C.Z. and L.L. conceived the study; A.C. and M.V.C. collected the data; C.Z. and L.L. developed the analyses with input from M.W.C., M.L., X.S. and C.G.W., C.Z. and L.L. wrote the manuscript and all authors contributed to revisions. All authors approved this final manuscript.

## DATA AVAILABILITY STATEMENT

The trait data used in this paper are accessible through the Dryad Digital Repository <https://doi.org/10.5061/dryad.prr4xgxmh> (Zhang et al., 2021).

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## SUPPORTING INFORMATION

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

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