Ant mutualists as a biotic interaction filter of flowering plant colonization on islands

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Abstract

Aim: Oceanic island floras are well-known for their disharmonic assemblages, with certain taxa and functional groups being over- or underrepresented compared to their source pools, due to effects of dispersal, environmental filtering, and biotic interactions. However, the role of biotic interactions in generating this disharmony remains poorly explored.

Location: Global islands.

Time Period: Present-day species distribution.

Major Taxa Studied: Flowering plants bearing extrafloral nectaries (EFNs) and domatia, and their ant parters.

Methods: We compiled plant distributions from the Global Inventory of Floras and Traits (GIFT) and ant distributions from the Global Ant Biodiversity Informatics database (GABI) for islands worldwide. We then assembled a dataset of ant genera known to interact mutualistically with plants bearing EFNs or domatia. Using this dataset, we quantified the representational disharmony of ant-associated plants and evaluated whether their ant partners act as a biotic interaction filter for the representation of ant-associated plants on islands.

Results: We found that domatium-bearing plants are generally underrepresented, whereas extrafloral nectary (EFN)-bearing plants are overrepresented, likely reflecting differences in their relationship with ant partners. Besides the effects of island characteristics, the representation of both domatium- and EFN-bearing plants shows a strong yet conditional relationship with the diversity of their interacting ant partners. Specifically, this biotic interaction filter is more pronounced on larger, less isolated islands.

Main Conclusions: Our findings underscore that mutualistic interactions are a key driver of island plant assembly and that their filtering effect depends on island characteristics. We conclude that explicitly integrating biotic interactions and their context is essential to advance our understanding of island biogeography.

Keywords

Domatia, extrafloral nectaries, source pool, island flora, island disharmony

Introduction

Understanding the mechanisms that govern the assembly of island biotas is a central topic in ecology and biogeography (Warren *et al.*, 2015; Whittaker *et al.*, 2023). Oceanic islands frequently exhibit island disharmony, where their species assemblages are distinct from mainland source pools due to the over- or underrepresentation of certain taxonomic or functional groups (Carlquist, 1974; Weigelt *et al.*, 2015; Taylor *et al.*, 2019; König *et al.*, 2020). These disharmonic patterns, often found in groups with specific traits, such as long-distance dispersal ability or specific reproductive strategies, reflect the combined consequence of processes including dispersal limitation (Gillespie *et al.*, 2012), environmental filtering (Carvajal-Endara *et al.*, 2017), and *in situ* speciation (Weigelt *et al.*, 2015; Burns, 2019).While biotic interactions have been recognized as a potential driver of island assembly (Pannell *et al.*, 2015; Taylor *et al.*, 2019), their specific role in shaping disharmonic assemblages remain poorly examined.

Biotic interactions, such as competition, predation, and mutualism, significantly affect species distributions and the composition of island plant assemblages (Connor *et al.*, 2013; Wisz *et al.*, 2013; Fowler *et al.*, 2023; Delavaux *et al.*, 2024). The influences of these interaction filters may vary depending on the type of interaction. In the case of mutualisms, interaction partners play an important role in plant dispersal, growth, and reproduction (Bronstein, 2015). Consequently, the absence of a required mutualist on islands can reduce plant fitness, leading to unsuccessful colonization or local extinction. This process contributes to the underrepresentation of plants that depend on those partners. For example, recent studies suggest that plants relying on pollinators for reproduction or mycorrhizal symbioses for nutrition acquisition may be underrepresented on islands due to the lack of appropriate partners (Delavaux *et al.*, 2019, 2024; Razanajatovo *et al.*, 2019). Furthermore, the distribution of interaction partner itself may be constrained by distance from source pools and distinct island environments, leading to a joint influence on island assemblages. For example, plants dispersed by animals (e.g. birds) likely gain an advantages in colonizing isolated islands, such as the Azores (Heleno & Vargas, 2015). Yet, the extent to which this interaction filter interplay with dispersal and environmental filters in affecting the distribution of associated species remain insufficiently understood.

Island characteristics, particularly area and isolation, are fundamental in shaping the composition of island floras as they directly influences processes like dispersal limitation and environmental filtering (Kreft *et al.*, 2007, 2010). Island isolation has long been recognized as a dispersal filter (Carlquist, 1966), which often leads to the overrepresentation of species with long-distance dispersal ability on remote islands (Heleno & Vargas, 2015). However, species lacking specialized dispersal syndromes can also constitute a substantial proportion of island floras (Vargas *et al.*, 2012). Meanwhile, island area primarily constrains species distribution by governing environmental heterogeneity. Larger islands tend to harbour higher habitat heterogeneity (Weigelt *et al.*, 2013) and therefore impose fewer constraints on species colonization, as demonstrated by the importance of climatic suitability for plant colonization on the Galápagos (Carvajal-

Endara *et al.*, 2017). Consequently, smaller islands may be associated with more distinctive composition of island assemblages. In contrast, the complex environments of larger islands also are suggested to promote *in situ* diversification, thereby increasing the disharmony of island floras (König *et al.*, 2020).

Ant-plant mutualisms are widespread and well-studied biotic interactions (Marazzi *et al.*, 2013; Weber & Keeler, 2013; Chomicki & Renner, 2015). Ant-adapted plants have evolved specialised morphological structures such as domatia and extrafloral nectaries (EFNs) that provide nesting sites or food rewards to ant mutualists, who in return protect their plant mutualists from herbivores and plant competitors (Bronstein *et al.*, 2006; Rico-Gray & Oliveira, 2007). By promoting the fitness of ant-associated plants on islands, ant mutualists may contribute to the colonization of these species and ultimately contribute to a higher representation compared to islands without ants. Therefore, ant-associated plants provide an ideal model for studying key processes affecting the colonization and persistence of species in insular systems.

Here, we test the role of a biotic interaction filter in insular ant-plant mutualisms by analysing whether the diversity of ant mutualists limits the representation of associated plants on islands. Given the strong spatial congruence between ants and ant-associated plants (Luo *et al.*, 2023), we expect that a higher diversity of ants interacting with plants promotes a greater diversity and representation of these plants on islands. To address the general lack of comprehensive biogeographic knowledge for both interaction partners, which is a key limitation in examining biotic interactions, we compiled a novel dataset by integrating recent knowledge from two comprehensive global databases of plants and ants (Guénard *et al.*, 2017; Weigelt *et al.*, 2020; Liu *et al.*, 2023). We first evaluate the representational disharmony of ant-associated plants by comparing the observed species richness to null communities drawn from mainland source pools (König *et al.*, 2020). Specifically, we ask these following questions: 1) Are domatium- and EFN-bearing plants over- or underrepresented on islands relative to their mainland source floras; 2) Is plant representation affected by the diversity of ant mutualists and island characteristics, and do these factors interact; 3) At the species level, does the colonization probability of ant-associated plants correlate with the diversity of ant mutualists and island characteristics?

Materials and Methods

Plant and ant distributions

We retrieved checklists of angiosperm species with domatia and extrafloral nectaries (EFNs) from previously assembled lists based on comprehensive literature reviews (Weber & Keeler, 2013; Chomicki & Renner, 2015). The original checklists were cleaned from duplicates and unspecified records, and then taxonomically standardized according to the World Checklist of Vascular Plants (WCVP, https://wcvp.science.kew.org; Govaerts et al., 2021). Unmatched species were rechecked via the

Taxonomic Name Resolution Service (TNRS, https://tnrs.biendata.org; Boyle et al., 2021). Overall, we retained 657 domatium-bearing and 3,179 EFN-bearing angiosperm species.

Plant distributions across islands and mainland regions were derived from checklists of native angiosperms from the Global Inventory of Floras and Traits (GIFT version 2.1), which contains the distribution of 352,232 native plant species across 3,088 regions worldwide (Weigelt *et al.*, 2020). As island geological history exerts a strong influence on the biogeographical processes acting on island floras (Whittaker & Fernández-Palacios, 2007), we focused on oceanic islands, defined as uplifted seafloor or volcanic islands (e.g. the Azores). A few islands that once were fully submerged below the ocean were also considered oceanic islands (e.g. New Caledonia). Therefore, we obtained 446 islands with plant information (288 oceanic islands, 158 continental islands).

We sourced native ant occurrences on islands from the Global Ant Biodiversity Informatics database (GABI), which is a comprehensive compilation of distributional data of 7,010 ant species across 2,678 islands (Guénard *et al.*, 2017; Liu *et al.*, 2023). Due to the lack of a comprehensive list of ant species that interact with domatia and EFNs, we first compiled a list of relevant ant genera based on a comprehensive literature review. We then extracted species richness of these specific ants from the GABI database, separately for domatium- and EFN-bearing plants. We refer to these two distinctive variables collectively as interacting ant richness in subsequent analyses. However, they were treated separately in analyses for their respective interaction types. As a result, we included 338 islands with both plant and ant distribution data available (Fig. S1).

Representational disharmony

To infer the effects of biotic interaction filters on island plant assemblages, we adapted the framework by König et al. (2020) to estimate mainland source pools for each island. Using this framework, we modelled species turnover of native angiosperms among mainland regions based on climate conditions and geographic distance. The fitted model was then utilized to predict species turnover among oceanic islands and their potential source regions. For potential source pools, we included non-overlapping adjacent mainland regions, which were primarily administrative units (e.g. countries, provinces, and states). When overlapping regions were present, we prioritized smaller regions with available checklists. Plant checklists for mainland regions were derived from the GIFT database. Additionally, we included 19 large continental islands as potential source pools, as oceanic island floras may colonize from both mainland areas and other large islands (Carlquist, 1967).

We quantified the representational disharmony of ant-associated plants by comparing the observed species richness of ant-associated plants on each island with 1000 null assemblages randomly sampled from their respective source pools, with sample sizes equal to the angiosperm species richness on the islands. The null distribution of ant-associated plant species richness was assumed to follow a Poisson distribution with a mean equal to the null expectation. We then calculated the probabilistic representational disharmony as the cumulative probability that the null expectation is less than or equal to the observed richness. To further evaluate the magnitude of disharmony, we transformed the probabilistic representational disharmony into the standardized effect size of representational disharmony (SES.RD) using a simulated Poisson distribution. A positive SES.RD value indicates an overrepresentation of ant-associated species on an island, while a negative value indicates an underrepresentation. Islands with an expectation of ant-associated plants less than 1 were excluded from further analyses, as it is statistically difficult to determine whether the absence of ant-associated species deviates from the null expectation when the null expectation approaches 0. In total, we measured the representational disharmony of domatium-bearing plants on 62 oceanic islands and 26 continental islands (n = 88), and EFN-bearing plants on 254 oceanic islands and 136 continental islands (n = 390). Different sets of number of islands in analyses are provided in Table S1. For detailed methods on the source pool estimation and representational disharmony of ant-associated plants on islands, see König et al. (2020) and Supplementary Methods.

Climatic variables and island characteristics

To evaluate climate conditions in delineating source pools, we chose four climatic variables hypothesized to affect plant distributions on islands (Kreft & Jetz, 2007; Calixto *et al.*, 2021; Cai *et al.*, 2023): mean annual temperature (°C), mean annual precipitation (mm/a), seasonality in temperature and precipitation (standard deviation of the monthly mean temperature or precipitation). All climatic variables were derived from the Climatologies at High Resolution for the Earth's Land Surface Areas (CHELSA; Karger et al., 2017) at a resolution of 30 arc-seconds and measured as mean values for each region. Further, we used three island biogeographic variables to examine the effects of island characteristics on the distribution of ant-associated plants, as island characteristics are known to influence particular ecological processes. Island area (km^2) was measured as the total landmass area of each island. As a measure of island isolation, we considered the proportion of surrounding landmass (SLMP), which takes stepping stones and coastlines into account. SLMP has been shown to be a strong determinant of plant diversity on islands and is inversely related to island isolation (Weigelt & Kreft, 2013). All island biogeographic characteristics were extracted from GIFT (see Weigelt et al., 2020 for a detailed description of all workflows).

Statistical analyses

To examine the effects of biotic interactions on the representational disharmony of ant-associated plants on islands, we applied linear regressions separately for domatium- and EFN-bearing plants. The standardized effect size of representational disharmony was modelled against island area, isolation, and the species richness of interacting ants. We performed a Pearson correlation analysis to avoid multicollinearity (All Pearson's $r < 0.7$; Table S2). To meet model assumptions and reduce the skewness, island area and interacting ant richness was natural log-transformed, and SLMP was logit-transformed. All variables were then standardized to zero mean and unit variance for comparable results. Because domatia and EFNs are most prevalent in the tropics (Fig. 1) (Weber & Keeler, 2013; Chomicki & Renner, 2015; Luo *et al.*, 2023), we only focused on tropical islands located within 23.4° latitude north and south. Given that biotas on oceanic islands are originally absent and represent an assembly processes from mainland source pools (Whittaker & Fernández-Palacios, 2007), this analysis was restricted to oceanic islands with evaluated representational disharmony and ant information, including 60 islands for domatia and 152 islands for EFNs.

Given that significant spatial autocorrelation was detected in the model residuals, we adopted simultaneous autoregressive error (SAR) models using the 'errorsarlm' function of the R package 'spatialreg' (Dormann *et al.*, 2007; Bivand & Wong, 2018). To define the optimal spatial structure, we constructed the neighbour by varying the upper distance bound from 100km up to the maximum island neighbour distance (i.e. 3,672 km) with 11 intervals. Pseudo R^2, Akaike's information criterion (AIC), and residual spatial autocorrelation were jointly considered to select the ideal distance band. We then applied the row standardization coding scheme to weight the neighbour list of each island. Spatial autocorrelation in model residuals was controlled in SAR models (Table S3). As interaction filters can interact with other processes simultaneously (Cadotte & Tucker, 2017), we included the interaction between island characteristics and interacting ant richness in all models. Both pseudo-R^2 and AIC significantly improved in models with the interaction term (Table S3).

To determine the factors influencing the colonization of individual ant-associated plants on islands, we performed presence-absence regressions for each plant species. To ensure sufficient sample sizes and to avoid class imbalance (Steen *et al.*, 2021), we only included species present on at least 30 oceanic islands. This criterion led to 21 EFN-bearing plants for further analyses. All domatium-bearing plants were excluded, as the most prevalent species (*Andira inermis*) occurred on only 15 study islands. We applied generalized linear models (GLMs) of the binomial family for the presence/absence of each of the 21 individual species, using interacting ant richness, island area, and the surrounding landmass proportion as explanatory variables. To account for potential spatial autocorrelation, we corrected these models by adding a spatial autocovariate. This autocovariate was created using the model residual of the non-spatial GLMs, weighted by the neighbour distance defined in the SARs, and implemented suing the R package 'spdep' (Bivand & Wong, 2018). To assess the overall effects of ants and island characteristics across all 21 EFN-bearing plants, we also performed a generalized linear mixed model (GLMM). This model incorporated a random slope for both species and islands. Details on model results and performance are provided in Table S4.

Results

Diversity of ant-associated plants on islands

Across the 446 islands in our dataset, we recorded a total of 251 domatium-bearing plants and 1,248 EFN-bearing plants (Fig. 1A, B). The diversity of ant-associated plants on islands showed a significant latitudinal gradient. Both species richness and the proportion of ant-associated plants relative to total angiosperms peaked in the tropics and decreased towards the poles. The Malay Archipelago harbours the greatest number of these species, including 99 domatium-bearing plant species in Borneo and 332 EFN-bearing plants in Singapore. The highest proportions were found on Little Cayman Island (2.7% domatium-bearing plants) and Cocos (Keeling) North Keeling Island (21.2% EFN-bearing plants).

The representational disharmony (SES.RD) of plants bearing domatia and EFNs varied significantly and showed pronounced geographical patterns on tropical oceanic islands (Fig. 1C, D). Domatium-bearing plants were generally underrepresented on oceanic islands relative to their source floras (mean SES.DR: -0.60 ± 0.17, n = 99). Specifically, 6 islands were significantly overrepresented (SES.RD > 1.96; e.g. Little Cayman Island), and 8 islands being significantly underrepresented (SES.RD < -1.96; e.g. New Caledonia) (Fig. 1C, E). The disharmony patterns of domatium-bearing plants do not significantly differ between oceanic and continental islands (Wilcoxon signed-rank test, p = 0.46). In contrast, we found that EFNs were generally overrepresented in island floras relative to source floras (mean SES.RD: 1.55 ± 0.14, n = 390). A large proportion of studied islands (170 out of 390) was significantly overrepresented, particularly those in Southeast Asia and the Caribbean region. Only 31 islands were significantly underrepresented (e.g. New Caledonia; Fig. 1D, F). The representation of EFN-bearing plants on oceanic islands was more disharmonic than on continental islands (Wilcoxon signed-rank test, p < 0.001).

Biotic interaction filter among islands

Among the simultaneous autoregressive error models tested, those including interaction terms performed best (Table S3). We found that interacting ant richness significantly shaped the representation patterns of both domatium- and EFN-bearing plants, but its effect depended on specific island characteristics (Fig. 2, Table S3). For domatium-bearing plants, higher interacting ant richness was associated with greater representation, particularly on larger and less-isolated islands (Fig. 3A, Fig. S2). EFN-bearing plants also showed a stronger relationship with interacting ants on islands closer to the mainland (Fig. 3D). On the other hand, the effect of island isolation was more pronounced on islands with higher interacting ant richness for both interaction types (Fig. 3C, F). In contrast, island area showed a non-significant negative relationship with EFN-bearing plants representation (Fig. 3E).

Of the 21 individual EFN-bearing plant species, 12 showed a significantly positive relationship with the richness of their interacting ant partners (Fig. 4A; Table S4). Consistent with this prevalence of positive effect, the model integrating all 21 species revealed an overall significant effect of interacting ant richness. In contrast, island characteristics showed a more variable effect. Only six species exhibited a positive relationship with island area (Fig. 4B), while results of island isolation was mixed, with eight species showing a negative relationship and eight a positive one (Fig. 4C). Accordingly, neither island area and isolation had a significant overall effect on colonization in the model including all 21 species.

Discussion

Our results confirm biotic interactions act as a key filter shaping island biota composition, demonstrating that the richness of ant partners significantly contributes to the biogeography of ant-associated plants on islands worldwide. Furthermore, we find the influence of biotic interactions is not uniform but conditional, being more pronounced on larger, less isolated islands. These results highlight that integrating the mediate influence of biotic interactions is essential to move beyond classical island characteristics and substantially advance our understanding of disharmony in island assemblages.

Diversity of ant-associated plants on islands

Domatium-bearing plants were generally underrepresented on islands compared to their source pool floras. Despite this overall pattern, myrmecophytes were notably overrepresented on some islands, e.g. Saibai Island off the coast of New Guinea where many epiphytic *Hydnophytum* species with domatia occur. Indeed, the genera *Hydnophytum*, *Myrmecodia*, and *Neonauclea* collectively account for the majority (58 out of 105 species) of all island endemic myrmecophytes and predominantly distributed across Indomalayan and Australasian islands. The high endemism in this region suggests that *in situ* diversification may be a key mechanism driving the disharmonic representation of myrmecophytes (Weigelt *et al.*, 2015). A notable exception to this regional trend is New Caledonia, which hosts low representation of domatium-bearing plants, despite its relatively close distance to source pools of high domatia diversity and its own diversity of Rubiaceae. This discrepancy may reflect the influence of complex evolutionary history of myrmecophytes (Chomicki & Renner, 2016).

Although EFN-bearing plants can be underrepresented on individual islands or archipelagos (e.g. the Hawaiian Islands; Keeler, 1985), they unexpectedly constitute a high overall representation in island floras at large spatial scales. This may be partly attributed to the broad distributions of dominant EFN-bearing families, such as Euphorbiaceae and Fabaceae, which account for over 30% of all insular EFN-bearing plants (Table S5). Furthermore, our data, though incomplete, indicate that insular EFN-bearing plants exhibit a higher proportion of herbaceous (34% compared to 25%) and hydrochorous (15% compared to 7%) species compared to their global distribution (Table S6). This is consistent with general observations that insular floras often favour non-woody species and those with long-distance dispersal ability (Heleno &

Vargas, 2015; König *et al.*, 2020), suggesting that the composition of EFN-bearing plants is a response of dispersal limitation and environment filter.

The distinct difference in the representational disharmony observed between domatium- and EFN-bearing plants may reflect fundamental differences in their interaction characteristics. Domatia are relatively resource cost and mostly obligate, while EFNs are less resource intensive and range from obligate to facultative interactions (Bronstein *et al.*, 2006; Marazzi *et al.*, 2013). While obligate interactions (e.g. ant-domatia) tend to limit plant distributions, facultative interactions (e.g. ant-EFNs) expand them (Stephan *et al.*, 2021). This is also supported by our findings that the diversity of ants that may interact with domatia is significantly lower than that for EFNs (Fig. S1). Thus, the disharmony of these two ant-associated plant groups appears to be shaped by a combined influence of dispersal, environments, and interaction filters.

Biotic interaction filter among islands

The importance of biotic interactions in shaping species diversity at large scales has been hitherto overlooked, despite a growing body of literature highlighting the role of mutualistic interactions (Delavaux *et al.*, 2019, 2024; Razanajatovo *et al.*, 2019; Taylor *et al.*, 2019). Using a new dataset containing the distribution of plants and ants on islands, we found strong empirical evidence that a higher representation of ant-associated plants on islands is consistently associated with higher diversity of interacting ants, a pattern observed at both the island and species levels. This finding aligns with studies showing that biotic interactions constrain species distributions in various habitats (Wisz *et al.*, 2013; Fowler *et al.*, 2023), including alpine regions (Cavieres *et al.*, 2014), and significantly adds to the macroecological understanding of island assembly (Taylor *et al.*, 2019; Schrader *et al.*, 2021). The absence of interacting ants can expose ant-associated plants to increased herbivory pressure, limiting their success of colonization. Conversely, ants can also benefit from plant-based resources to colonize and persist on islands. For example, extrafloral nectar is a key resource that facilitates the successful colonization of islands by invasive ants (Savage *et al.*, 2009; Sugiura, 2010).

We found that the effect of ants as interaction filters was more pronounced on less isolated islands. This suggests that isolation imposes a primary filter on the distribution of ants and their associated plants, which in turn governs the relatively importance of biotic interaction filters. On remote islands, long distance precludes the establishment of many potential interaction partners, thereby decreasing the signal of biotic interactions. In contrast, on islands closer the mainland sources, where more species could overcome dispersal barriers (Morrison, 2016), the presence of specific ant partners becomes a critical determinant of plant colonization. This interplay of abiotic and biotic filters consequently results in simplified interactions and networks on islands (Traveset *et al.*, 2016).

At the species level, we observed that island isolation had a non-significant overall effect on the colonization of EFN-bearing plants, yet it showed strong and contrasting effects among individual species. This paradox can be explained by the fact that the geographic isolation of a specific island does not necessarily correspond to its proximity to a particular species' distribution range. For example, *Erythrina variegata*, primarily distributed in Southeast Asia, faces a significant dispersal barrier to the Caribbean islands, despite the archipelago's relatively close distance to the American mainland (SLMP estimate = -1.12 ± 0.26; Table S4). However, explicitly delineate potential islands and source pools for each species remains a complex challenge (Carvajal-Endara *et al.*, 2017). Furthermore, our species-level analysis was restricted to widely distributed species (those present on ≥ 30 oceanic islands), which are often near-cosmopolitan (e.g. *Ipomoea pes-caprae*, *Thespesia populnea* etc). For these species, our results confirm that colonization probability is strongly affected by the diversity of interacting ants.

The effect of island area on the representational disharmony of domatium-bearing plants was dependent on ant diversity, while its effect on EFN-bearing plants was marginal. For domatium-bearing plants, larger islands provides greater habitat heterogeneity, which can support more diverse ants but also lead to higher herbivory pressure (e.g. from mammals; (Barreto *et al.*, 2021)). This can increase the selective advantage of ant defence. Furthermore, large islands can promote *in situ* diversification and thus amplify disharmony. This is reflected in the high proportion of domatium-bearing plants being endemic (16%; Table S7). In contrast, EFN-bearing plants show a low proportion of endemic species (5%), well below the global average for insular angiosperms (21%; (Schrader *et al.*, 2024)). This pattern aligns with EFNs loss in endemic lineages on islands where ant partners are absent, such as the Bonin Islands (Sugiura *et al.*, 2006). Given that EFN is an evolutionarily labile trait (Weber & Keeler, 2013), we hypothesize that in the absence of interacting ants partners, plants may fail to maintain EFN production, leading to its loss in endemic lineages. This may explain why EFN-bearing plants show a weak and negative relationship with island area.

Conclusion

Our study demonstrates that both biotic interactions (ant diversity) and abiotic factors (island area and isolation) are critical in shaping the diversity and representation of ant-associated plants on islands. We found that the effect of biotic interaction filter is more pronounced on larger and less-isolated islands. This key finding reveals that the relative importance of ecological processes can shift across environmental gradients. Moreover, our results show that the representation patterns and underlying drivers for domatium- and EFN-bearing plants are distinct, likely due to the differing characteristics of these two interaction types: domatia are costly and obligate, while EFNs are relatively inexpensive and facultative with ants. By providing a novel empirical example of how ant diversity shapes island plant assemblages, our study highlights the necessity of integrating biotic interactions into island plant biogeography. Furthermore, we suggest that the influence of biotic interactions is not uniform across mutualistic interactions, and we therefore advocate for explicitly incorporating interaction context (e.g. specific interaction characteristics, effect of enemy release, and resource availability) to advance our understanding of island assembly.

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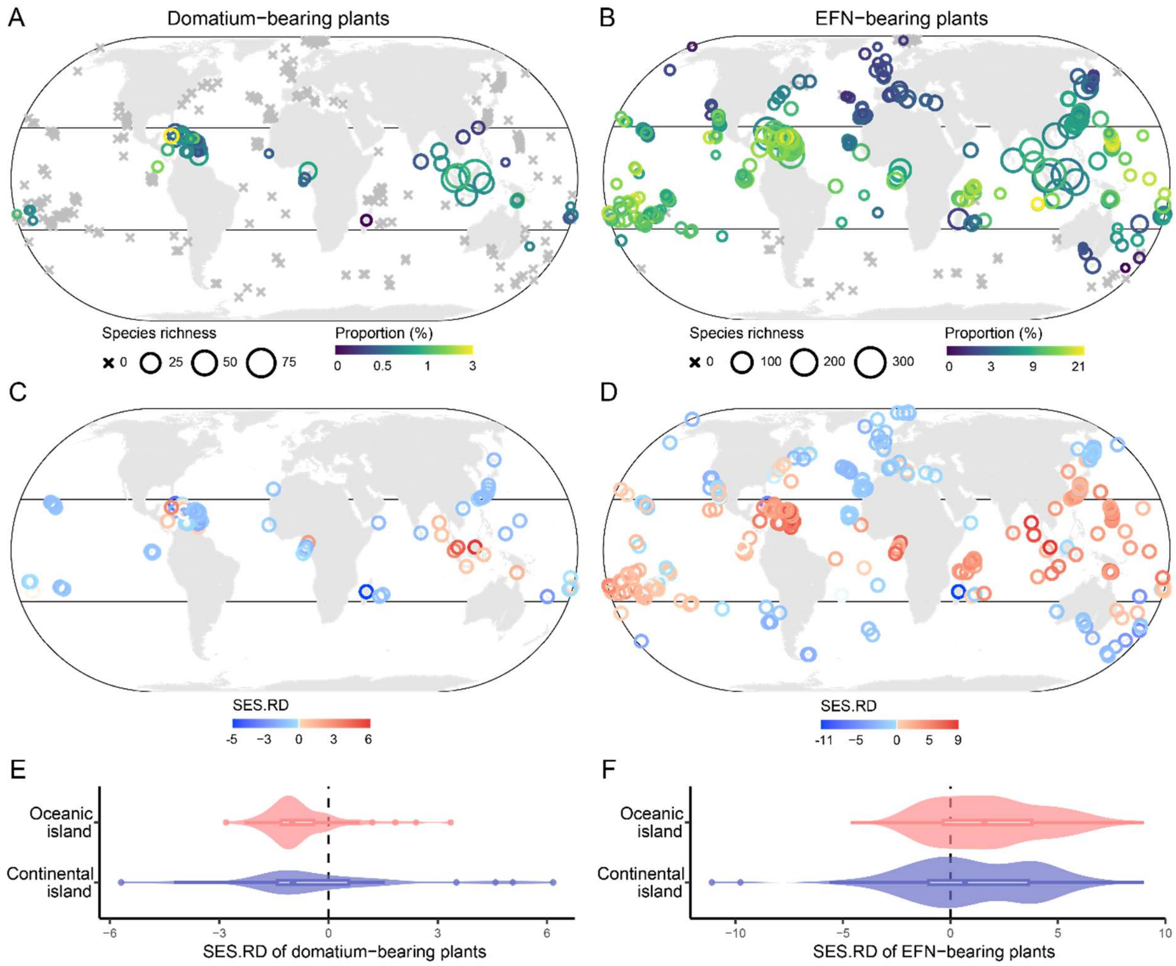

FIGURE 1 | (A, B) Species richness and proportion to all angiosperms for plants bearing domatia and extrafloral nectaries (EFNs) on 446 islands. (C, D) Disharmonic patterns of ant-associated plants on islands indicated by standardized effect size of representational disharmony (SES.RD; n = 99 for domatium-bearing plants, n = 390 for EFN-bearing plants). (E, F) Representational disharmony of ant-associated plants on continental islands and oceanic islands. Differences between continental and oceanic islands are examined by Wilcox rank test ($p = 0.46$ for domatium-bearing plants, $p < 0.001$ for EFN-bearing plants)

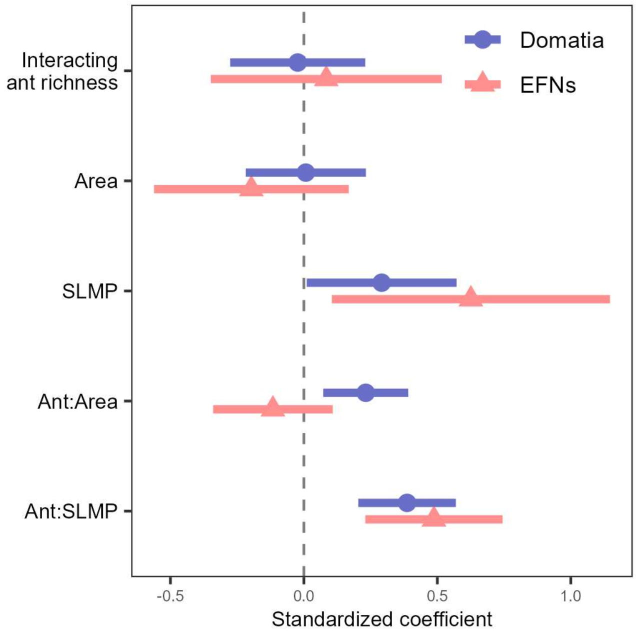

FIGURE 2 | Standardized coefficients of simultaneous autoregressive models for representational disharmony of domatium- (n = 60) and extrafloral nectary (EFN)-bearing plants (n = 152) on tropical oceanic islands. The figure shows the relative importance of species richness of interacting ants (Ant), island area, the proportion of surrounding landmass (SLMP), and the interaction between ants and both island area and SLMP. Horizontal bars indicate 95% confidence intervals.

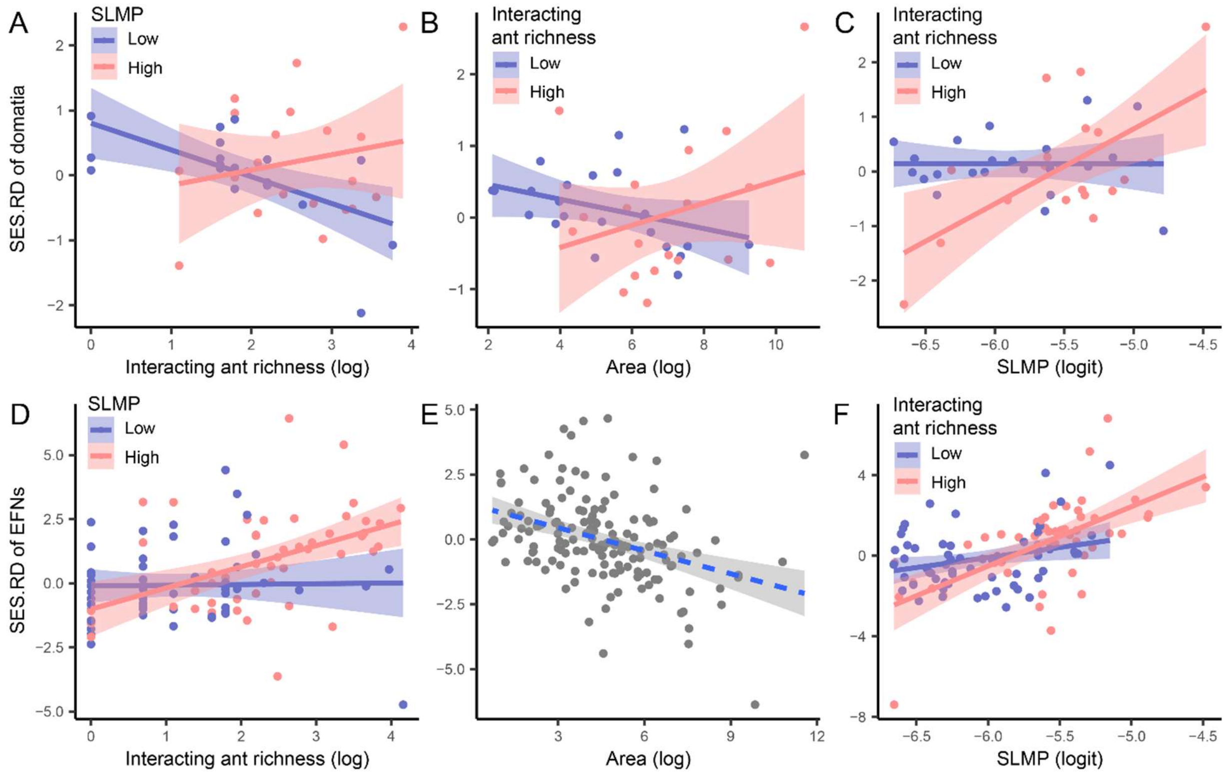

FIGURE 3 | Partial residuals of interacting ant richness (A, D), island area (B, E), the proportion of surrounding landmass (SLMP) (C, F), and their interactions on the taxonomic representation of domatium- (upper panels) and extrafloral nectary (EFN)-bearing plants (bottom panels) on oceanic islands. Interactions are showed for conditions of low (bottom 33%) and high (top 33%) interacting ant richness, small (bottom 33%) and large (top 33%) island area, and low (bottom 33%; high isolation) and high (top 33%; low isolation) SLMP, for domatium- and EFN-bearing plants, respectively. Coloured bands represent 95% confidence intervals. Results are illustrated by generalized linear models with spatial autocovariates. The interaction between interacting ant richness and island area for domatium-bearing plants is showed in Fig. S2 for simplification.

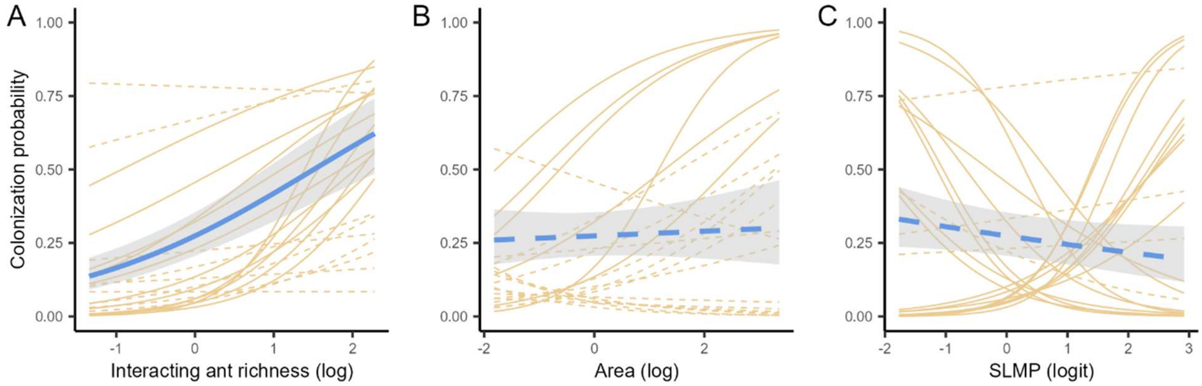

FIGURE 4 | Effects of interacting ant richness, island area and the proportion of surrounding landmass (SLMP) on the colonization probability of EFN-bearing plants. Separate generalized linear models of binomial family were applied to 21 EFN-bearing plants across 152 tropical oceanic islands. Yellow lines show the predicted colonization probability for each individual species, while blue lines show the overall predicted colonization probability across all 21 species. Solid lines indicate a statistically significant relationship ($p < 0.05$), and dashed lines indicate a non-significant relationship.