Island biogeography of the megadiverse plant family Asteraceae

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Abstract

The hyperdiverse plant family Asteraceae, with over 32,000 species globally, forms an iconic component of island floras, including many spectacular radiations, but a global picture of their insular diversity is lacking. Here, we uncover the global biogeographical and evolutionary patterns of Asteraceae on islands to reveal the magnitude and potential causes of their evolutionary success. We compile a global checklist of Asteraceae species native and endemic to islands and combine it with macroecological analyses and a phylogenetic review of island radiations. Asteraceae have a global distribution on islands, comprising approximately 6,000 native island species, with 58% endemics. Yet, diversity of the family on islands is lower than expected given its overall diversity. However, Asteraceae are the most diverse family on oceanic islands, suggesting an exceptional ability to thrive in isolation. In agreement with island biogeography predictions, native Asteraceae diversity increases with area and decreases with isolation, and endemism increases with both island area and isolation. The hotspots for insular diversity and endemism are Madagascar and the Caribbean, both being regions we identify as most lacking phylogenetic studies. We identify 39 confirmed island radiations, and 69 putative radiations that remain to be phylogenetically investigated, exceeding numbers for other iconic insular groups, such as birds. Our results reveal Asteraceae offer immense potential for research in ecology and evolution, due to their close tracking of island biogeography expectations, large sample sizes (species and radiations), cosmopolitan distribution, and high number of potentially undiscovered radiations.

Introduction

The top ten most diverse plant families make up 43% of Angiosperm species (Govaerts et al., 2021). Understanding the distribution and drivers of diversity of these large families is thus a crucial step towards explaining the success of flowering plants in general. Key biogeographical settings for exploring the patterns and processes that shape angiosperm diversity are islands. Due to their distinct boundaries, global distribution, and replication, island systems have played a crucial role in the development of key evolutionary and ecological theories (MacArthur and Wilson, 1967; Carlquist, 1974; Losos and Ricklefs, 2010; Whittaker et al., 2008; Warren et al., 2015; Whittaker et al., 2017; Gillespie et al., 2020). The geographic isolation and unique habitats found on islands have given rise to remarkable angiosperm biodiversity that is often characterized by high levels of endemism (Kier et al., 2009: Cai et al., 2023), adaptive radiations (Kim et al., 2008; Givnish et al., 2008), paleoendemism (Fernández-Palacios et al., 2011; Veron et al., 2019), and repeated evolution of convergent traits (Carlquist, 1965; Burns, 2019).

While islands are valuable natural laboratories for studying plant diversity, global-scale data on the distribution of major plant families on islands are only starting to emerge. Recent global studies have explored biodiversity patterns for a few major families and lineages on islands (Taylor et al., 2021; Veron et al., 2021), factors impacting the assembly of island floras (Kreft et al., 2008; Weigelt et al., 2015; Carvajal-Endara et al., 2017; König et al., 2021), and traits associated with insular diversity (Grossenbacher et al., 2017; Nürk et al., 2019; Zizka et al., 2022; Barajas-Barbosa et al., 2023). These studies reveal how links between island features (e.g. area, isolation, age), functional traits (e.g. insular woodiness), and biogeographical rates (e.g. colonization, speciation, extinction) are important determinants of the number of native and endemic species of flowering plants on islands, whilst suggesting that evolutionary success on islands may not necessarily mirror that found on continents (Fernández-Palacios et al., 2021).

Out of all plant families, arguably the one most often associated with evolutionary success on islands is the most diverse family of all - Asteraceae. Asteraceae (Compositae), commonly known as the daisy or sunflower family, boast the greatest species number of any plant family in the world, with an estimated 32,000 - 34,000 species (“The Plant List (Version 1.1)”, 2013; Gostel and Bonifacino, 2020; Govaerts et al., 2021). Species of this family occur natively on every continent except Antarctica and are found in a wide range of habitats, but are most abundant in dry and semi-arid habitats and in Mediterranean-type ecosystems, deserts, grasslands, and mountains (Funk et al., 2009). Members of the family exhibit great variation in growth habit: from small annual herbs to woody perennial shrubs, lianas, and trees; cushion forms and succulents; and even rarely epiphytic and aquatic plants.

On islands, Asteraceae are thought to be remarkably diverse, and often form an iconic component of insular floras of both continental and oceanic origin. For instance, it is the most species-rich family on the remote Juan Fernández Archipelago (Bernardello et al., 2006) with 30 native species and four genera endemic to the islands, and is among the top five most diverse families on the large continental island of Madagascar (Antonelli et al., 2022). Additionally, the family has high levels of endemism on oceanic islands: a study by Lenzner et al., 2017 compiled diversity data on major plant families across 14 oceanic archipelagos and found that Asteraceae had the highest number of single-island endemics for the oceanic islands considered in the study. Their success in dispersal, establishment, and diversification on islands has been suggested to result from a combination of intrinsic factors (Carlquist, 1974; Crawford et al., 2009; Jeffrey, 2009): Asteraceae possess unique fruit morphology that aids in long-distance dispersal (Carlquist, 1966; Heleno and Vargas, 2015); the head-like inflorescence (capitulum) often attracts generalist pollinators; and are capable of several breeding systems that favor establishment on islands. Many species are self-compatible (Grossenbacher et al., 2017) and species in several island lineages are functionally self-incompatible with the capacity to self-seed and a genetic system (i.e. sporophytic self-incompatibility) which aids in both the establishment of small populations from a single or few colonizing individuals and retention of genetic diversity after arrival (Crawford et al., 2024).

In addition to a high native and endemic species richness on islands, Asteraceae are known for their presumed propensity to radiate (that is, to undergo cladogenesis in-situ on islands at relatively fast rates). Two recent studies, one reviewing adaptive radiations across flowering plants (Schenk, 2021) and another focused on adaptive radiations on oceanic islands across all taxonomic groups (Cerca et al., 2023), both found Asteraceae to be overrepresented in terms of adaptive radiations compared to other clades. Indeed, the family provides numerous examples of spectacular island radiations: *Scalesia* on the Galápagos Islands (Fernández-Mazuecos et al., 2020), the woody *Sonchus* alliance on the Canary Islands (Kim et al., 1996), *Dendroseris* on the Juan Fernandez Islands (Sang et al., 1994; Cho et al., 2020). One of the textbook examples of adaptive radiation on islands is the Asteraceae silversword alliance of Hawaiʻi, a clade of 33 species in three endemic genera (*Argyroxiphium*, *Dubautia*, *Wilkesia*), which evolved from a common ancestor that colonized Hawaiʻi by a long-distance dispersal event from North America around 5 million years ago (Mya), and which exhibit high diversity in morphology and ecological adaptation (Baldwin and Sanderson, 1998; Carlquist et al., 2003; Landis et al., 2018). Another notable example is the Hawaiian *Bidens*. The monophyletic 20 species of *Bidens* endemic to Hawaiʻi originated from a single colonization event c. 1.8 Mya, having thereafter radiated across the archipelago, occupying a wide variety of different habitats including sand dunes, lava fields, rainforests, and wetland bogs, and have the highest rates of speciation per unit area documented for any island plant radiation to date (Knope et al., 2012; Knope et al., 2020a).

An increasing number of phylogenetic studies focusing on selected island clades of Asteraceae from specific islands or archipelagos (Strijk et al., 2012; Vitales et al., 2014; Landis et al., 2018; White et al., 2020; Fernández-Mazuecos et al., 2020) are providing insight into the potential drivers of diversification in those Asteraceae groups. One hypothesis is that the high diversity of Asteraceae on islands results from a combination of high continental diversity, high rates of long-distance dispersal, and overall high rates of in-situ speciation that well exceed extinction rates (consistent with the high net diversification rates observed in continental Asteraceae) (Katinas et al., 2013; Mandel et al., 2019; Magallón and Castillo, 2009, Panero and Crozier, 2016).

While it is assumed from the above examples that Asteraceae are highly diverse on islands and have a propensity to radiate, in fact, a complete global picture of the diversity and distribution of the family is yet to be assembled. Furthermore, an assessment of Asteraceae's potential to radiate across islands globally is still lacking, because previous studies focused solely on adaptive radiations and/or on oceanic islands, and thus the magnitude of island radiations within the family is unknown.

To address these issues, we compiled a global checklist of island Asteraceae and used this to answer four key questions: 1) How does the island species richness of Asteraceae compare with that of other families? 2) How is island Asteraceae diversity distributed across space and major clades of the family? 3) What are the environmental and biogeographical drivers of native and endemic insular diversity on islands? 4) How many island radiations have occurred within Asteraceae and are there commonalities between radiations?

Methods

Data collection

Island Asteraceae checklist

We compiled a global checklist of Asteraceae native and endemic to islands. The foundation of the island Asteraceae checklist was the Global Inventory of Floras and Traits (GIFT) database (version 3.0; Weigelt et al., 2020; Denelle et al., 2023). GIFT collates and leverages plant checklists and floras with regional-level data on distribution, environment, and functional traits and has a particular strength in island floras. We started by extracting all Asteraceae checklists from GIFT where there was at least one species native to an island. Species non-native or introduced to islands were excluded. We did not consider islands with zero Asteraceae in the database because many of these may be false negatives, since GIFT relies on published floras disentangling the true absence of Asteraceae on an island from a data gap is challenging. To facilitate comparison across regions and sources, the GIFT database records the original species names and endemicity status from the primary floras and checklists and standardizes the taxonomy against the World Checklist of Vascular Plants (WCVP, Govaerts et al., 2021). For the island Asteraceae checklists we carried out additional curation. Because Asteraceae are a taxonomically complex family, we matched WCVP standardized names against the Global Compositae Database (GCD, https://www.compositae.org/gcd, Gostel and Bonifacino, 2020) and retrieved the name status (accepted, uncertain, unaccepted) and the tribe and subfamily classification. We further updated the GCD taxonomy to the latest classification outlined in Susanna et al., 2020 based on the family-level phylogeny in Mandel et al., 2019.

The final dataset is a global checklist of Asteraceae native to islands and is composed of 915 island checklists (SD1) and supported by 240 primary sources (SD2). The global checklist of insular Asteraceae is structured by island geographic units. For each island in the data set, we have a checklist of Asteraceae species, name standardization (original name, WCVP name, and GCD name status), reference to the primary source, intrafamily taxonomic classification, the floristic status of the species (native, endemic, non-endemic) to that geographic unit, distribution, and conservation status.

Island features and environmental variables

For each island in the global checklist, we gathered abiotic data on island features and climatic variables known to be important predictors of global diversity on islands (MacArthur and Wilson, 1967; Whittaker et al., 2008; Kreft et al., 2008). Environmental data were available from GIFT, which includes information on abiotic variables for each island in the data set. We extracted the following variables: latitude and longitude, area (km^2), distance to nearest mainland (distance, km), surrounding landmass proportion (SLMP, sum of the proportions of landmass within 100, 1,000, and 10,000 km buffer distances (Weigelt and Kreft, 2013)), Last Glacial Maximum mainland connection (GMMC), Last Glacial Maximum area (LGM area), island age (Mya), mean and maximum elevation (m), terrain ruggedness index (TRI, m), botanical continent (level 1, standardized biogeographic scheme for recording plant distributions defined by the Biodiversity Information Standards (TDWG)), and biome (Ecoregions, Dinerstein et al., 2017)). We classified islands into two physical types based on past connectivity to the mainland: "continental" islands, those located on the continental shelf or continental fragments and previously connected to the mainland, and "oceanic" islands, built mainly by volcanic activity or sea-floor uplift or atolls and never connected to another landmass. This classification was initially based on the geology category in GIFT, but we manually adapted and assessed it for each island/archipelago. We also included a "mixed" category, for archipelagos composed of a mixture of continental and oceanic islands. We aggregated islands into "archipelago grouping", a refined and cleaned archipelago assessment based on the GIFT archipelago levels (arch_lvl_1, arch_lvl_2, arch_lvl_3) to capture shared biogeographic and geologic history. For example, all the islands in the Caribbean are grouped together in GIFT under the archipelago classification of the West Indies (GIFT arch_lvl_1), and for this study, we refined the West Indies archipelagos classification to include the Greater Antilles, Lesser Antilles, and the Bahamas as separate archipelagos. All cases in which the archipelago grouping differs from the one in GIFT are highlighted in the data. Additionally, we collected data on four climatic variables (CHELSA 2.1 (Karger et al., 2017)) for each island: annual mean temperature (°C), mean annual precipitation ($\mathrm{kg\,m^{-2}}$), temperature seasonality (°C/100), and precipitation seasonality ($\mathrm{kg\,m^{-2}}$). As a result, our global island Asteraceae checklist includes Asteraceae diversity data and associated island spatial and environmental data (SD1).

Comparison of island diversity among flowering plant families

To contextualize the insular diversity of Asteraceae, we compared it with other flowering plant families by gathering island diversity data for all angiosperm families that natively occur on islands following a similar procedure. From GIFT, we extracted every island checklist with at least one native angiosperm species. Then for each family, we calculated the total number of species native to islands and the total number of species endemic to islands. We calculated insular diversity for each family across both (a) all island types (continental, oceanic, and mixed) and (b) only oceanic islands. This provided us with a global assessment of island diversity across flowering plant families, illustrating which families have the greatest diversity of native and endemic species on islands.

To determine whether island diversity was higher or lower than expected given the overall number of species within each family, we ran binomial tests and simulated island communities. For each angiosperm family, we performed a binomial test to compare the proportion of island species to the proportion of total species of that family to angiosperms globally. The binomial test was conducted using the binom.test() function in R, where “x” represents the number of native island species (i.e. number of successes), “n” represents the total number of angiosperm species native to islands (i.e. number of trials), and “p” represents the proportion of the family to angiosperms globally (i.e. probability of success). The number of species within each family and the total number of angiosperm species globally (333,799) were calculated with the World Checklist of Vascular Plants (WCVP, Govaerts et al., 2021), and the number of island-native angiosperm species (99,659) and oceanic-island native species (23,853) were calculated with GIFT. With the binomial test, the null hypothesis is that the observed proportion of a family on islands is equal to its frequency globally (p), and the alternative hypothesis is that the observed proportion on islands is not equal to this global frequency.

Additionally, for visualization purposes, we ran simulations to estimate the null expectation of island diversity and compare it to the observed diversity for the ten most diverse families on both all island types and oceanic islands. For the top ten families, we created a global pool that represents the total number of species in each family overall. We randomly sampled from the global pool to create island communities with the same total number of species as the actual number of native island species overall (10,000 iterations). This gives a null distribution of the island diversity for each family given the overall diversity of the family. We then compared the observed island diversity to the null distribution.

Modeling the biogeographical drivers of island diversity

We used generalized linear mixed models (GLMMs) to understand which island features and environmental variables are linked to Asteraceae (1) native species richness (NSR) and (2) proportion of single-island endemics (pSIE) across islands. Prior to modeling, we carried out a thorough exploration of the data following a protocol described in Zuur et al., 2010. This included inspection and checks for potential outliers, distribution of response variables, zero inflation, collinearity among response variables, pair-wise relationships between response and predictor, and non-independence of the response variable. Several predictor variables showed high collinearity, in particular, variables found to be correlated to isolation (distance, SLMP, GMMC, LGM area, latitude) and topography (mean elevation, maximum elevation, TRI). Hence, we dropped correlated variables to retain one predictor for isolation (SLMP) and one for topography (maximum elevation). Because several predictor variables were skewed, we log-transformed area, SLMP, maximum elevation, mean annual precipitation, temperature seasonality, and precipitation seasonality. All continuous predictor variables were centered and scaled. Additionally, we multiplied SLMP (surrounding landmass proportion) by -1 to convert this variable to a more intuitive proxy for isolation; with this inverse transformation of SLMP, a higher -SLMP refers to a more isolated island. We removed islands smaller than 1 km^2 because diversity on these islets is influenced by different processes (i.e. the small-island effect (Whitehead and Jones, 1969 Schrader et al., 2020)). The final data set included 510 islands, 272 oceanic and 238 continental islands (SD3).

We employed AIC model selection independently for the (1) NSR and (2) pSIE models, choosing the best global model for each from a range of candidate models (19 for NSR and 15 for pSIE) (see Table S1). The models (NSR and pSIE) are independent, with potentially different environmental variables correlating best with the two measurements of diversity. In line with the current literature recommendations, we fit the NSR models with a negative binomial and pSIE models with a beta-binomial error distribution (Stoklosa et al., 2022).

In our global model for NSR, we fit a negative-binomial GLMM to predict total native species with area, isolation (-SLMP), island type (categorical with two levels: oceanic and continental), max elevation, and temperature seasonality, with archipelago included as a random effect. In our global model for pSIE, we fit a GLMM using a beta-binomial and native species richness used as weights to predict the pSIE with area, isolation (-SLMP), island type (categorical with two levels: oceanic and continental), max elevation, and mean annual temperature, with archipelago included as a random effect. All models were fit using the glmmTMB package in R (Brooks et al., 2017).

Island age is an important variable in island biogeography, correlated to species richness (Whittaker et al., 2008); however, island age is challenging to accurately estimate (Rijsdijk et al., 2020; Price and Clague, 2002), and we do not have full coverage of age estimates for all islands in our dataset. Therefore, we ran a model for both NSR and the pSIE that includes island age as an additional fixed effect for the subset of oceanic islands where an age estimate was available (221 islands). We followed the General Dynamic Model of island biogeography (Whittaker et al., 2008) and included island age as $\text{Age}+\text{Age}^2$.

To validate the fitted models, we assessed for collinearity in predictors via variance inflation factor scores (VIF, with a threshold of less than five) and checked the residuals with the DHARMA package (Hartig, 2022), which simulates the standardized residuals from the fitted model and also checks for overdispersion and zero inflation. DHARMa reports statistical evidence of non-uniformity in the QQ plot. The plots themselves indicated that the effect size of these deviations from the expected distribution is small, and the significance of the deviation may be caused by the large number of data points (see Figure S2).

Island radiations within Asteraceae

We conducted a literature review of island radiations within Asteraceae to (1) synthesize our understanding of island radiations in Asteraceae, how many radiations there are and where they occur, (2) identify common characteristics shared between radiations, and (3) highlight understudied clades and regions that are promising for future research. Radiations are generally defined as rapid increases in the diversity of a lineage (Linder, 2008). In the context of island biogeography, a radiation is typically considered to be the differentiation of a significant number of species in a short period of time through in-situ cladogenetic speciation (via lineage splitting) occurring within an island region, from a single common ancestor that colonized an island or (meta-)archipelago. Radiations are often categorized as adaptive or non-adaptive based on a series of criteria (e.g. Schluter, 2000). In this study, we were interested in both types of radiations, as together they represent the diversity of cladogenetic mechanisms in the family, and we, therefore, include both types and record radiation type strictly as assessed by the primary publication.

In our literature search, we considered an island radiation to include three or more endemic species that are geographically restricted to an island or archipelago(s), and which result from a single colonization event and thus share a common ancestor. While our primary goal was to synthesize knowledge on the diversity of phylogenetically confirmed insular radiations within the family, we also wanted to highlight potential understudied radiations that are promising groups for future research. To this end, our review included both confirmed and putative radiations. Confirmed radiations were backed up by a well-sampled published phylogeny of the island taxa and mainland relatives, which has confirmed the island endemics to form a clade resulting from a single colonization event, that is, they are not the product of multiple colonisations from the mainland (Igea et al., 2015; Papadopulos et al., 2011). Putative radiations were defined as having at least three endemic species from a genus occurring on an island or archipelago but have not yet been fully sampled in a phylogeny; this designation is based on taxonomy alone and indicates the need for future phylogenetic research. By focusing on genera in our definition of radiation, we run the risk of missing insular radiations that are composed of multiple genera (e.g., as is the case for the confirmed Hawaiian silversword alliance radiation) when they originated by a single colonization (i.e. single ancestry). For both confirmed and putative cases, radiating clades distributed across multiple archipelagos were considered as one insular radiation. For example, the Polynesian *Bidens*, which are distributed across the Hawaiian, Marquesas, Society, and Austral Islands all result from a single colonization of the Pacific islands and were considered a single insular radiation (Knope et al., 2020b). While delimiting radiations to their widest island range could conceal the subsequent inter-regional radiations (e.g. the 20 monophyletic *Bidens* on Hawai'i), we included the archipelago and island distribution in our review to retain this information. For summary and visibility purposes, we grouped radiations into wider regions composed of groups of islands and archipelagos, which are defined in Table SD4.

To identify insular radiations, we took a two-fold approach. First, we carried out a literature search in Google Scholar using the keywords (Asteraceae OR Compositae) AND Island AND Radiation. Second, we searched through the Island Asteraceae Checklist and filtered out genera with at least three endemic species on an island or archipelago. The checklist has a major advantage in helping to identify unknown or understudied potential radiations that would otherwise not be captured in the traditional literature search. With the list of candidate radiations, we manually assessed each potential case. If the radiation met our above criteria for "confirmed" radiation, we collected data on the geographic distribution, island type, taxonomy, number of species, type of radiation (i.e. adaptive or non-adaptive; as assessed by the original publication), traits often hypothesized to be associated with island radiations (breeding system, dispersal syndrome, ploidy level, hybridization), crown age, phylogenetic work done on the clade, and references. Characteristics and traits were collected at the radiation level. If species in a radiation had different traits, the radiation was marked as multi-state; for example, the *Lipochaeta-Melanthera* radiation on Hawai'i is made up of both diploids and polyploids, and so we listed the ploidy level of this radiation as mixed. When we could not confirm the radiation through a well-sampled phylogeny, but taxonomic evidence indicated the group of endemic species might be a radiation, we marked the group as 'putative radiation' and collected data on the geographic distribution, island type, taxonomy, potential number of species, and references.

Results and Discussion

Asteraceae are one of the most diverse families on islands

Asteraceae are the largest plant family in the world, with 33,994 currently accepted species globally (Govaerts et al., 2021). Our comprehensive checklist of insular Asteraceae shows that this family is also remarkably diverse on islands: we found 6,135 species of Asteraceae are native to islands, of which 3,535 (58%) are endemic to islands globally. On oceanic islands specifically, we found 1,833 native Asteraceae species and 955 (52%) endemic species.

As Asteraceae species are generally perceived to be good dispersers and excellent island colonizers (Carlquist, 1966; Carlquist, 1974), the proportion of island native and endemic species of the total Asteraceae species pool would be expected to be higher in Asteraceae than in other large families, and higher than expected by chance. Surprisingly, our comparison between the diversity of angiosperm families on islands showed that Asteraceae are not the most species-rich family across all islands (Figure 1; Table S2) and that they are underrepresented in terms of island species given its overall diversity (Figure 1; Table S3). These results align with a recent study focused on island disharmony in plants (König et al., 2021), which found that while Asteraceae are generally under-represented on islands given their species richness in mainland source pools, the family is nonetheless pervasive on islands. Orchidaceae and Rubiaceae have the highest number of native island species with 11,118 and 6,188 species respectively. The high insular diversity of Orchidaceae and Rubiaceae is found disproportionately on large, tropical continental islands and archipelagos (including New Guinea, Borneo, and the Philippines), which are not particularly rich in Asteraceae species. On oceanic islands, Asteraceae are the most diverse family for both the number of native and endemic species. Yet, despite high species richness compared to other families, Asteraceae diversity on oceanic islands is lower than expected given their diversity globally (Figure 1B).

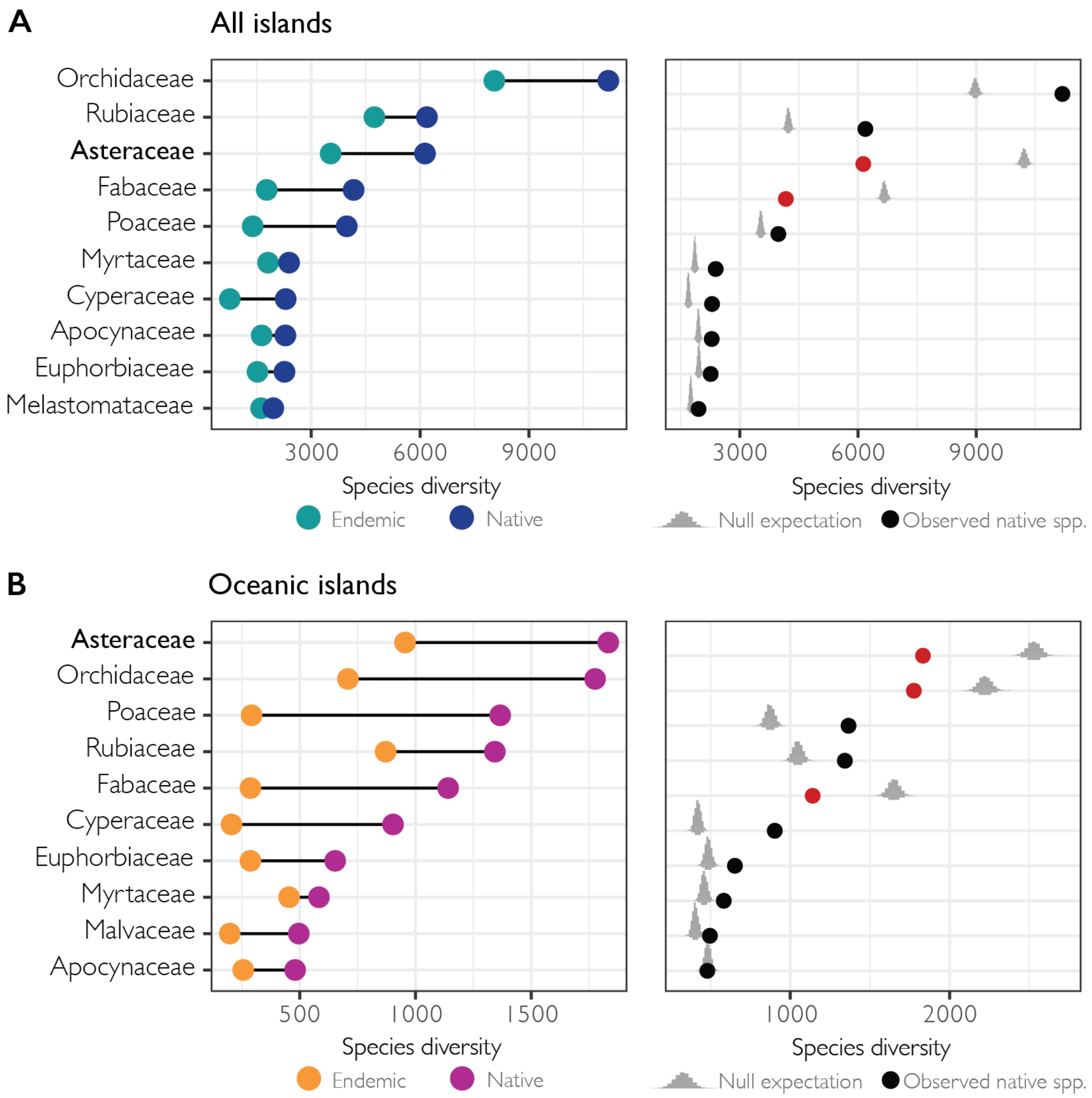

Figure 1: **The ten most diverse angiosperm families on (A) all islands and (B) oceanic islands, with the island diversity compared to the null expectation.** The left panel ranks the ten most diverse angiosperm families on all islands for native and endemic species. Families are ranked in descending order by the number of native species. The right panel compares the observed number of native island species per family (points) to the null expectation of island diversity (histogram). Families for which the observed number of species is lower than the null expectation are highlighted with a red point, and those above the null expectation in black. The global diversity of each family is listed in Table S2.

Island species account for 18% of the total species diversity of Asteraceae (Table S2). The results of the binomial test indicate that the observed number of Asteraceae species native to islands is significantly different than expected based on the proportion of Asteraceae to angiosperms globally (10%) and that the island proportion (6%) is significantly lower than expected under the null model (Table S3, Figure 1). Additionally, a comparison of the observed number of island Asteraceae species to the island community simulations confirms that the observed number of island species is lower than the null expectation across all islands and oceanic islands (Figure 1).

While this result suggests Asteraceae may be poorer colonizers or have higher rates of extinction on islands relative to the mainland than previously expected, this can only be confirmed by estimating rates of colonization and diversification using species-level molecular phylogenies (Valente et al., 2020), but given the enormous size of the family, this is yet to be realized. On the other hand, family age could be a factor contributing to the under-representation of Asteraceae on islands. We found that most plant families are much older than the islands in our dataset (Figure S1) and, given that the key biogeographic determinants of diversity on islands are colonization and diversification rates since island origin, this would suggest that family age is not an important determinant. However, the diversity of the mainland species pool is a consequence of family age and global diversification rates. Notably, among the ten most diverse families on islands, Asteraceae are the youngest family (Table S2), which could potentially account for their under-representation on islands, as older families may have been more diverse with larger mainland pools at the time of emergence of the islands in our dataset thus giving them a colonization "advantage" earlier on. Future research comparing mainland pools to island diversity through time is needed to test the impact of family age and diversification rate on insular diversity.

Asteraceae have a global distribution across islands

Native species of Asteraceae have a truly global distribution across the world's islands (Figure 2). In our global checklists, Asteraceae occur natively on 791 islands including 308 oceanic islands, and across 146 archipelagos. Their distribution reaches north to the Svalbard Islands and Greenland (80°N and 75°N) and south to Macquarie Island and Heard Island (55°S and 53°S). Insular diversity ranged from one (minimum inclusion criterion) to 550 native species, with 29 islands (4%) harboring more than 100 native species and 155 islands (20%) harboring only one native species (our dataset only includes islands with at least one native Asteraceae species). Across all island types, 128 islands (16%) have at least one endemic species.

While its distribution is global, the diversity of the family is not evenly distributed geographically, and several island regions are notable hotspots of diversity. Madagascar is the most diverse island overall for both native (550) and endemic (487) species. The Caribbean, in particular the Greater Antilles with 671 native and 430 endemic species, is another major center of island Asteraceae diversity. At the island level, the three large islands (Cuba, Hispaniola, Jamaica) are all in the top ten most diverse islands globally for number of endemic species (196, 145, 58). This pattern of the Caribbean as an important area of endemism for the family further supports a review by Francisco-Ortega et al., 2008, who found that the region has the highest number of endemic genera in Asteraceae globally. Across oceanic islands, Macaronesia, the Hawaiian Islands, and the Mascarenes are hotspots of island diversity. The Canary Islands is the most diverse oceanic archipelago with 299 native species, and seven of the ten most diverse oceanic islands for native species are islands in the Canaries, with Tenerife being the most species-rich (159 species). The Hawaiian Islands are the second most diverse oceanic archipelago with 102 native and 95 endemic species, and have a remarkably high proportion of endemism (93%), followed by the Mascarenes with 79 native and 64 endemic species.

In comparing hotspot regions, the British Isles (850 native species, 368 endemic species) and Iceland (334 native species, 261 endemic species) stand out as diversity anomalies. While these two regions appear as hotspots of island diversity, the majority of species in these two island regions are apomictic (Richards, 2003). Apomixis, a mode of asexual reproduction via seeds, is a poorly understood trait in Asteraceae (Noyes, 2007) and one that challenges taxonomic species concepts and delimitation (Haveman, 2013). To investigate the impact of apomictic species on our results, we performed a sensitivity analysis with apomictic genera removed (see Figure S5), which revealed minor changes to the ranking of top island hotspots, but no effect on our findings otherwise (including the models).

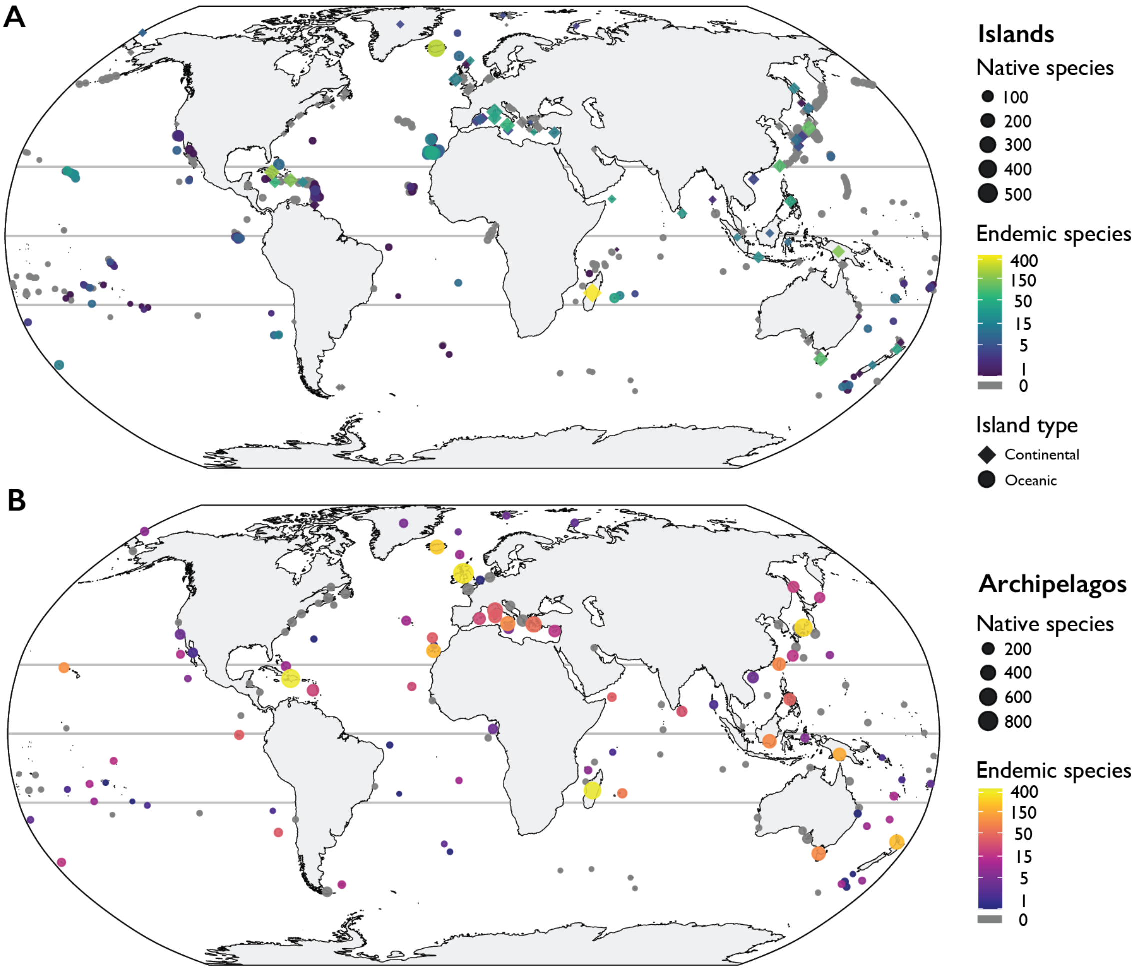

Figure 2: **Geographical diversity patterns of island Asteraceae.** (A) Global distribution of Asteraceae across all island types. The shape of the marker represents the island type (i.e. continental or oceanic), the size represents the number of species, and the color indicates the number of endemics, with grey meaning no island endemics. (B) Global distribution of Asteraceae on archipelagos.

The diversity of island species is also unevenly distributed across the major clades and taxonomic tribes of the family (Figure 3). The tribe with the highest number of native island species is Cichorieae (1660 spp.); while this tribe is an important component of island floras (e.g. *Tolpis* and the woody *Sonchus* alliance in Macaronesia, *Dendroseris* in the Juan Fernández Islands), its overall diversity is inflated due to the high number of apomictic species, well-known in this tribe (e.g. *Hieracium* on Iceland, *Taraxacum* on the British Isles). Aside from Cichorieae, the three most diverse tribes for both native and endemic island species are Astereae (793 native island species, 465 endemic species), Senecioneae (653, 447), and Gnaphalieae (589, 339). Together, these four widespread tribes make up nearly 60% of all native insular Asteraceae species (Table S4, Figure S3). While these tribes are also some of the largest tribes in the family, when we compare observed island diversity to expected diversity given the overall size of the tribe (Table S5), we find that island species are over-represented in Cichorieae, Astereae, and Gnaphalieae and within the expected range for Senecioneae. The two tribes with the highest proportion of native island species compared to the total diversity are Feddeeae (100%) and Distephaneae (86%). Feddeeae is a monotypic tribe with a single species, *Feddea cubensis* endemic to Cuba (Figure S3). The *Distephanus* clade is a group distributed across Africa, Madagascar, and the Mascarenes and has a notable overrepresentation of island species relative to overall diversity (36 island species, 43 total species) (Table S5).

The intra-family diversity patterns are influenced by both the global distribution of a tribe and the presence of islands within that range. Asteraceae clades that have an overrepresentation of island species despite limited islands available within their overall range likely have intrinsic traits potentially well-adapted to islands. Additionally, several tribes with high island species richness are well-known for having widespread weedy species (e.g. Gnaphalieae, Senecioneae). Future research on these widespread native species could provide insight into traits that facilitate successful colonization and establishment in novel habitats on islands.

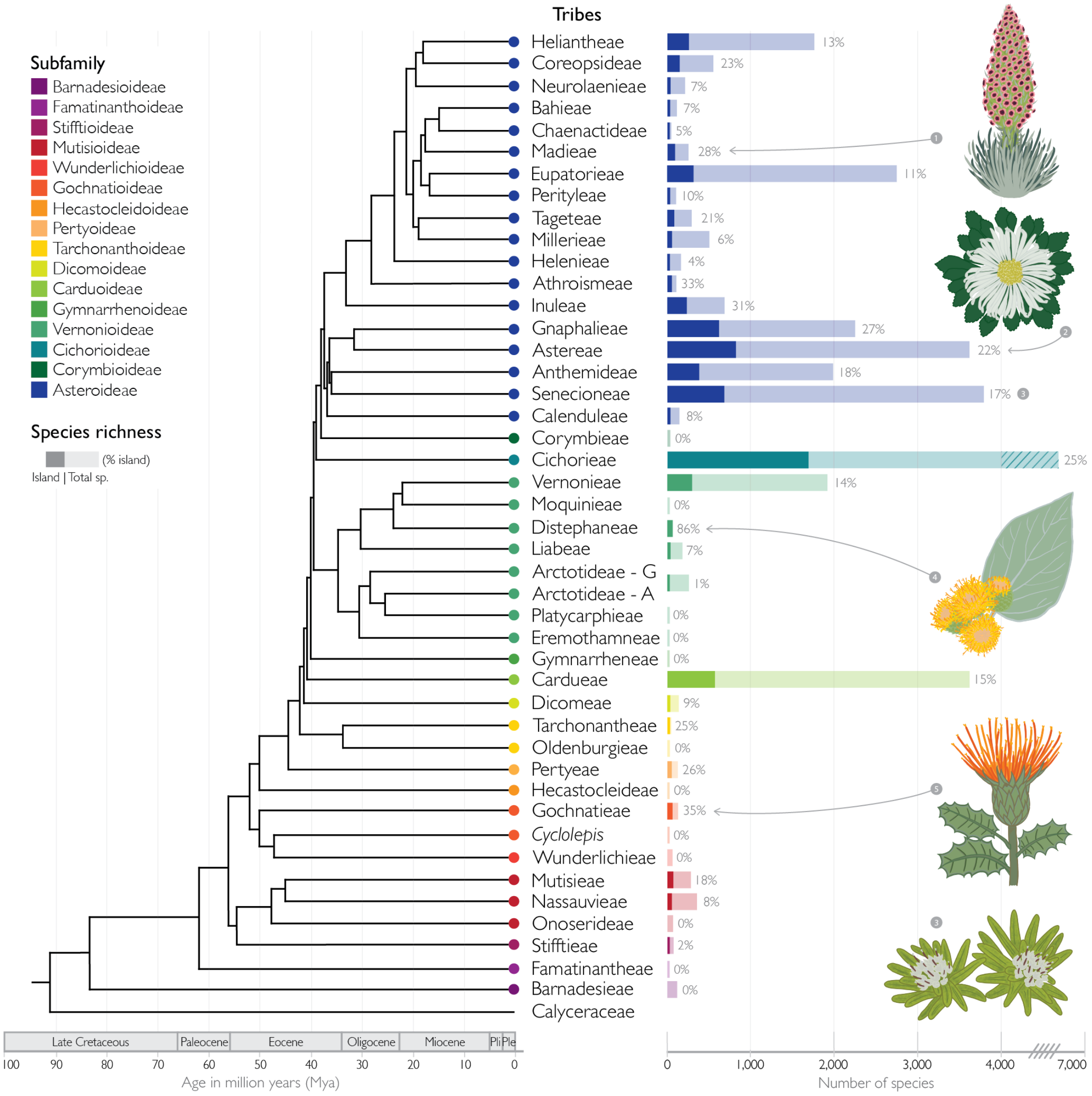

Figure 3: **Island diversity within the subfamilies and tribes of Asteraceae.** (A) Time-calibrated molecular phylogeny of the tribes and major clades within Asteraceae from Mandel et al., 2019. Tribes are colored by subfamily classification. (B) The number of species native to islands (dark bar) compared to the overall number of species globally (light bar) in each tribe. The percentage of native island species to total species globally is specified next to each tribe. Illustrations highlight clades with high island diversity: (1) *Argyroxiphium sandwicense* endemic to Hawaiʻi, Madieae; (2) *Commidendrum rugosum* endemic to Saint Helena, Astereae; (3) *Abrotanella inconspicua* endemic to New Zealand, Senecioneae; (4) *Distephanus populifolius* endemic to Mauritius, Distephaneae; (5) *Anastraphia ilicifolia* endemic to Cuba, Gochnatiaeae. Illustrations by Lizzie Roeble.

Drivers of island species richness and proportion endemism

Species richness in Asteraceae follows classic island biogeography theory, with area and isolation (-SLMP) being the strongest predictors of both NSR and pSIE (Figure 4). Area has a positive association with NSR ($\beta = 0.64$, CI 0.56-0.72) and the pSIE ($\beta = 1.55$, CI 1.17-1.94) (Table S6). This pattern of an increasing number of species with area conforms with both the species-area relationship (Matthews et al., 2021) and the *Theory of Island Biogeography* (MacArthur and Wilson, 1967) and is well-supported across various island systems in other taxonomic groups (Kisel and Barraclough, 2010; Triantis et al., 2012; Valente et al., 2020; Ohyama et al., 2021). While isolation is a strong predictor of both NSR and pSIE, it has an inverse relationship on the two measures of diversity, having a negative effect on NSR (β = -0.32, CI -0.45 - -0.19) but a positive effect on pSIE (β = 0.48, CI 0.09-0.88), with more isolated islands having a higher proportion of endemism. The increase in endemism with isolation is also a prediction of island biogeography, as MacArthur and Wilson proposed the existence of a zone of radiation, where diversification should outpace the dispersal-mediated build-up of species on near islands, and islands change from a dispersal- to an evolution-driven system as isolation increases (MacArthur and Wilson, 1967; Losos and Schluter, 2000; Heaney, 2000; Valente et al., 2020).

Island type (oceanic vs continental), represents the geological origin of islands and is a proxy for connectivity over time, affects both NSR and pSIE. Oceanic islands have fewer native species (β = -0.38, CI -0.57- -0.19), and a higher proportion of single-island endemics (β = 1.36, CI 0.48-2.23). Maximum elevation has a positive effect on NSR (β = 0.13, CI 0.05-0.22), with higher islands having more native species. Temperature seasonality is the best climatic predictor for NSR (positive effect), whereas mean annual temperature is the best climatic predictor for pSIE (positive effect). In the subset model that was filtered to oceanic islands and included Age+Age^2 as an additional predictor, we did not observe an additional effect of island age on NSR nor pSIE (Table S7 and Figure S4).

Both the NSR and pSIE models have substantial predictive power in explaining island Asteraceae diversity (see methods and Figure S2 for model diagnostics). The overall variance (conditional R^2) explained in the NSR model is 90% and the variance explained by the fixed effects alone (marginal R^2) is 56% (Table S6) (Nakagawa R^2 (Nakagawa et al., 2017)). In a separate model, with data aggregated for each archipelago, without random effects, the marginal R^2 was 75.1%, with model coefficients all pointing in the same direction as our original model (Table S8), indicating the robustness of our qualitative results to geographical scale. In the pSIE model, the overall variance (conditional R^2) explained by the model is 69% and the variance explained by the fixed effects alone (marginal R^2) is 40%. Comparing the marginal and conditional R^2, we find that the inclusion of archipelago as a random factor contributes to a large proportion of the variance explained in both the NSR and pSIE models. This is likely due to the nature of the island dataset and the common biogeographic history of the islands belonging to an archipelago that contribute to the conditional variance. There are 49 archipelagos in the dataset that are represented by a single island - often due to limited floristic data available, and in these archipelagos, the models have high predictive power. Additionally, the main model patterns and relationships with the predictors are unaffected when apomictic species are removed (see sensitivity analysis in Figure S5).

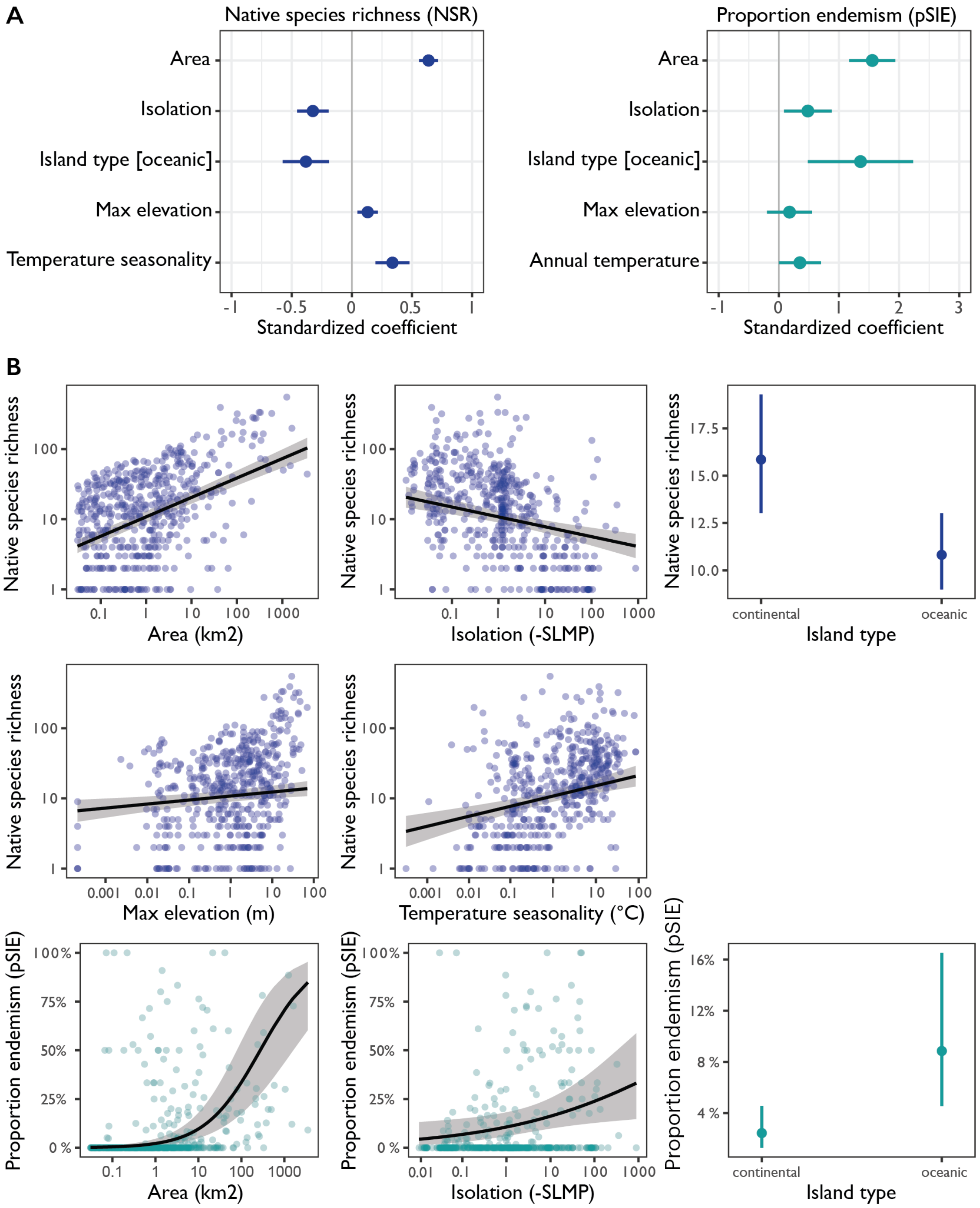

Figure 4: **The relative importance of island features and climatic variables on native species richness (NSR) and proportion of single-island endemics (pSIE).** (A) Coefficient estimates for the global models of native species richness (blue, top left) and the proportion of single-island endemics (green, top right). The bars around the coefficient estimates represent the standard error. The gray vertical line at 0 indicates no effect, and island variables with a positive coefficient estimate indicate an increase in NSR or pSIE, whereas a negative coefficient estimate indicates a decrease in the response variables. (B) Marginal effects for the significant island and environmental variables. Only significant effects ($p<0.05$) are visualized. The black line represents the predicted response under the model and the gray band is the 95% confidence interval. The following predictor variables were log-transformed: area, isolation (-SLMP), maximum elevation, and temperature seasonality.

Island Asteraceae radiations have occurred nearly everywhere

Apart from passerine birds of the Galápagos and Hawaiʻi, the *Anolis* lizards of the Caribbean, or the lemurs of Madagascar, few groups of organisms evoke evolutionary diversification on islands as much as Asteraceae, with its several "flagship" radiations - most famously the Hawaiian silverswords. However, to date, the geographical extent and number of insular radiations in the family have only been studied for a subset of cases (exclusively adaptive radiations from a subset of oceanic islands). We identified 39 phylogenetically-confirmed insular radiations and 69 putative radiations across continental and oceanic islands, totaling 108 island radiations within the family worldwide. The 39 confirmed radiations range in size from three (the minimum threshold) to 160 species, with an average of 18 species per radiation (median = 11) (Figure 5, Table SD4). New Zealand and surrounding islands are home to the two largest radiations: the *Celmisia* group with c. 160 species and the *Raoulia* alliance with 42 species. On oceanic islands, the largest radiations are the Polynesian *Bidens*, with 42 species distributed across Hawaiʻi, Marquesas, Society, and Austral Islands, followed by the Hawaiian Silversword alliance with 33 species and the woody *Sonchus* alliance with c. 31 species radiating on Macaronesia. The mean crown age of the radiations ranges from 0.4 to 24.18 million years (Myr), but the majority of radiations for which a crown age is available are younger than 5 Myr, confirming that they represent mostly recent diversification events.

Asteraceae have radiated across a wide geographic range of islands, with radiations found on large continental islands (e.g. *Apodocephala-Lowryanthus* on Madagascar) to oceanic archipelagos (e.g. *Scalesia* on the Galápagos) to archipelagos with mixed geologic origin (e.g. *Anastraphia* on the Caribbean), and from tropical islands (e.g. *Hesperomannia* on Hawaiʻi) to sub-Antarctic islands (e.g. *Pleurophyllum* across the Auckland, Campbell, and Antipodes Islands, which is nested in the larger *Celmisia* group radiation). The majority of confirmed radiations have occurred on oceanic islands (26/39 radiations, Figure 5), and while our mixed effects models support the strong, positive association of isolation on endemism, this could also be a reflection of previous island research focusing on oceanic systems. While radiations have occurred worldwide, several regions are notably rich in confirmed radiations. At least seven radiations with a total of 302 species have occurred on New Zealand and outlying Subantarctic islands. Macaronesia and the Hawaiian Islands also disproportionately support a high number of Asteraceae radiations, with at least ten radiations of 120 species total on Macaronesia, and six radiations comprising 90 species on Hawaiʻi. If we also consider putative radiations, the number of radiation in these two regions increases to 15 and 8 respectively.

Despite the high number of confirmed radiations, it is only when surveying the putative radiations that we begin to see the remarkable degree to which this family has, potentially, speciated across islands. In our review, we identified 69 putative radiations, which range in size from three to 67 species (Table SD4). In general, many of the putative radiations are found within geologically-complex regions or fall within large, taxonomically-complex clades. More specifically, several regions have a high number of putative radiations. The Caribbean is a known hotspot of Asteraceae diversity (Francisco-Ortega et al., 2008). We identified four confirmed radiations that were represented in a well-sampled phylogeny and 26 putative radiations with an overall total of c. 351 species. Madagascar is a hyper-diverse island with high endemism and Asteraceae are one of the five most species-rich plant families composing the island's flora (Antonelli et al., 2022); we found two confirmed radiations on Madagascar and identified 16 putative radiations that require future phylogenetic work to investigate and delineate. Additionally, while several genera on Madagascar (i.e. *Helichrysum*, c. 110 endemic species; *Senecio*, c. 50 endemic species; *Vernonia*, c. 70 endemic species) meet our criteria of a putative radiation, they were not included in the putative radiation list because these genera are known to be taxonomically complex (paraphyletic and polyphyletic) and distinguishing the potential radiation from multiple colonization events, even tentatively, is too challenging without a well-sampled phylogeny (Galbany-Casals et al., 2014; Pelser et al., 2010; Keeley et al., 2007; Siniscalchi et al., 2019).

Basing the assessment of putative radiations on taxonomy alone has the potential to under- and over-estimate the number of island radiations. On the one hand, an under-estimate of the number of radiations can occur when numerous island endemics within a single large genus arise from multiple independent colonization events and subsequent radiations. For example, phylogenetic work on *Psiadia* on the Indian Ocean islands supports two independent radiations on the Mascarenes (Strijk et al., 2012). On the other hand, an over-estimation can occur when numerous small island-endemic genera are actually part of one larger island radiation. This can lead to two assessment errors: the small island endemic genera inflate the putative number of radiations if they meet the threshold criteria of three endemic species or the size of the actual radiation is obscured when the small endemic genera are segregated out based on the taxonomy. For example, the woody *Sonchus* alliance on Macaronesia comprises six genera, but from a well-resolved phylogeny (Kim et al., 1996) we know these genera all arose from a single colonization event and radiated across Macaronesia. Notwithstanding these considerations, our assessment of putative radiations not only shows the potential magnitude of radiations within the family but also provides direction for future phylogenetic research on island diversification.

The combination of confirmed and putative radiations totals to 108 island radiations within the family, indicating that Asteraceae have the remarkable capacity to radiate across a wide diversity of islands, including oceanic islands and continental islands, islands and archipelagos with varying degrees of area and isolation, and across a wide spectrum of island ecosystems and habitat types. How the overall number of island radiations within Asteraceae compares to other flowering plant families still remains unknown because a comparable analysis of island radiations has not been conducted. However, recent reviews of radiations with different scopes or on wider taxonomic groups shed light on the magnitude of Asteraceae radiations on islands revealed here. In a review (Cerca et al., 2023) that was restricted to adaptive radiations on oceanic islands, Asteraceae stood out as the family with the highest number of adaptive radiations (finding 19 radiations) compared to all taxonomic groups (arthropods, birds, mollusks, plants, amphibians, and reptiles). Additionally, a comprehensive review of island radiations in birds (Illera et al., 2024), using the same criteria as used here, found 39 island radiations compared to Asteraceae's 108 radiations (confirmed and putative). Together, these studies indicate Asteraceae may be exceptionally rich in island radiations compared not only to other flowering plant families but also to other broader taxonomic groups. However, some of those groups are much less diverse than Asteraceae (e.g. birds 11,000 species compared to the 33,000 Asteraceae), so whether the propensity to radiate is also exceptionally higher in Asteraceae remains to be investigated.

Ultimately, future research should aim to move from identifying radiations to understanding the processes underlying plant diversification. To this end, for confirmed radiations, we examined several different characteristics and traits that are often associated with plant diversification on islands (Figure 5C, Table SD4). Out of all traits reviewed, the one trait that reveals a strong link with radiations is woodiness. The majority of confirmed radiations have at least one woody species,

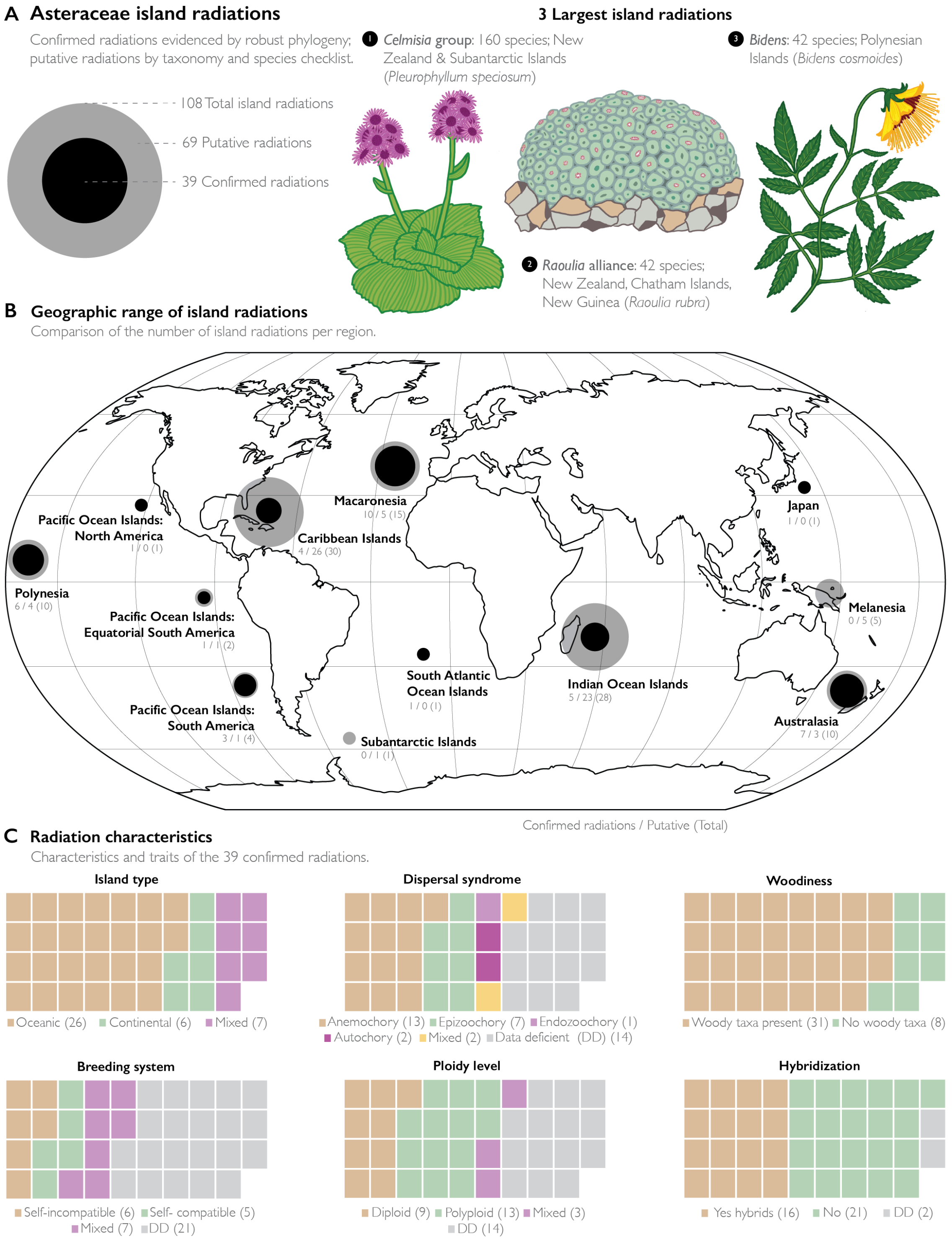

Figure 5: **Summary of island radiations within Asteraceae.** (A) Overview of the number of total, confirmed, and putative insular radiations within Asteraceae. The confirmed radiations have been evidenced by robust phylogenetic work and are represented by the black circles, and the putative radiations have been identified based on taxonomy and the island Asteraceae checklist and are represented by the gray circles (see methods for details on assessment criteria). Illustrations of species within the three largest island radiations. (B) Map compares the number of radiations between regions (defined in SD4); in cases where a radiation is distributed across multiple regions, it is included in the region where the most species diversity is located. Several island regions had no radiations (Mediterranean Islands, Micronesia) and are not included on the map. (C) The waffle charts summarize characteristics and traits of the confirmed radiations, where a single radiation is represented by one square. Traits were scored at the radiation level, and if there are multi-states in the radiation it is captured with the "Mixed" category. Full review of island radiations in Table SD4. Illustrations by Lizzie Roeble.

which is in agreement with recent research that secondary (insular) woodiness is associated with accelerated diversification rates and may be a key innovation for insular plants (Nürk et al., 2019). A diversity of dispersal syndromes - a key trait in determining island colonization - are represented in Asteraceae island radiations, with wind dispersal (anemochory) most common on less isolated archipelagos (e.g. Macaronesia) and bird dispersal (endozoochory and epizoochory) more common on isolated archipelagos (e.g. Polynesian islands). Hybridization and polyploidy are thought to be common features of adaptive radiations and linked to plant diversification on islands (Marques et al., 2019; Gillespie et al., 2020; Meudt et al., 2021; Cerca et al., 2023), and we found these two traits are somehow associated with island radiations in Asteraceae: both hybridization and polyploidy are documented in 40% of the confirmed radiations. While self-compatibility is often cited to be over-represented in island plants (Grossenbacher et al., 2017; Pannell et al., 2015), in our review of breeding systems (self-compatible, self-incompatible, or mixed), we found this trait to be surprisingly data deficient, indicating fertile ground for more research.

Conclusion

Our analysis of the global patterns of diversity and distribution of Asteraceae on islands is an essential first step towards unlocking further research on Asteraceae on islands, moving beyond classic well-studied oceanic islands (e.g., Canaries, Hawai'i) to cover less well-studied but also Asteraceae-rich regions such as the Caribbean, New Guinea, or the Mascarenes. Asteraceae diversity is unevenly distributed both geographically and across major clades in the family. This opens up the question of what intrinsic traits and external abiotic conditions are driving Asteraceae diversity on islands. The fact that Asteraceae follow key theoretical expectations of island biogeography and macroecology, suggests that they are not an outlier governed by their own biogeographical rules, highlighting their value as models for biogeography. In comparison with other groups, the key advantage of Asteraceae may lie in its unusually large sample sizes in terms of species and radiations, which may allow for circumventing a common limitation of studies of insular assemblages that are typically species-poor. Finally, the large number of potentially undiscovered radiations of Asteraceae suggests that many years of exciting discoveries on the evolution of this family lie ahead.

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Supplementary data

Table SD1: **Global checklist of Asteraceae native and endemic to islands.** The global checklist of insular Asteraceae extracted from GIFT with subsequent manual curation is structured by island geographic units. For each island in the data set, we have a checklist of Asteraceae species, name standardization (original name, WCVP name, and GCD name status), reference to the primary source, intrafamily taxonomic classification, the floristic status of the species (native, endemic, non-endemic) to that geographic unit, distribution, and conservation status.

Table SD2: **References for the global island Asteraceae checklist.** References of the primary regional checklists and floras from the Global Inventory of Floras and Traits (GIFT) used to compile the global checklist of Asteraceae native and endemic to islands.

Table SD3: **Dataset of islands with the number of native and endemic Asteraceae species and associated abiotic variables used in the mixed effects models.**

Table SD4: **Review of confirmed and putative island radiations in Asteraceae.** The data includes (1) a literature review of the confirmed radiations with associated trait and characteristic data, (2) a literature review of the putative radiations with notes summarizing current phylogenetic work on the group and evidence supporting putative radiation status, (3) criteria for assigning radiation status (confirmed, putative) and key definitions, (4) references for both confirmed and putative radiations.

Supplementary material (Extended Data)

Table S1: **Comparison of candidate models for native species richness (NSR) and the proportion of single-island endemics (pSIE).** For both response variables (NSR and pSIE), we built a range of candidate models to evaluate the relationship between insular diversity and different island environmental parameter combinations. The final model for NSR and pSIE was selected based on the best AIC (Akaike information criterion), AICc (Akaike information criterion corrected for sample size), and BIC (Bayesian information criterion) scores and is highlighted in bold. In the model formulas, the abbreviations are defined as: dist = distance, SLMP = surrounding landmass proportion, itype = island type (oceanic or continental), mxelv = maximum elevation, TRI = terrain ruggedness index, anntemp = mean annual temperature, annprecip = mean annual precipitation, tempseas = temperature seasonality, precipseas = precipitation seasonality, arch = archipelago, zi = zero-inflation.

	Model	Model type	AIC	AICc	BIC	R2 conditional	R2 marginal
1	NSR~area	glmmTMB	15935.7	15935.8	15944.2	NA	0.95
2	NSR~dist	glmmTMB	26378.8	26378.9	26387.3	NA	0.73
3	NSR~area+(1|arch)	glmmTMB	3773.7	3773.8	3790.7	0.91	0.25
4	NSR~area+(area||arch)	glmmTMB	3721.6	3721.7	3742.8	0.92	0.26
5	NSR~area+(area||arch); zi	glmmTMB	3723.6	3723.8	3749.1	0.60	0.17
6	NSR~area+dist+(area||arch)+(dist||arch)	glmmTMB	3709.8	3710	3743.7	0.88	0.52
7	NSR~area+dist+(area||arch)+(dist||arch); zi	glmmTMB	3711.8	3712.1	3749.9	0.48	0.29
8	NSR~area+dist+(1|arch)	glmmTMB	3771.1	3771.2	3792.3	0.90	0.27
9	NSR~area+SLMP+(1|arch)	glmmTMB	3701.8	3701.9	3723.0	0.89	0.45
10	NSR~area+SLMP+itype+(1|arch)	glmmTMB	3688.2	3688.4	3713.6	0.89	0.46
11	NSR~area+SLMP+itype+mxelv+(1|arch)	glmmTMB	3680.7	3680.9	3710.3	0.89	0.48
12	NSR~area+SLMP+itype+TRI+(1|arch)	glmmTMB	3683.2	3683.4	3712.8	0.89	0.48
13	NSR~area+SLMP+itype+mxelv+TRI+(1|arch)	glmmTMB	3682.5	3682.8	3716.4	0.89	0.48
14	NSR~area+SLMP+itype+mxelv+anntemp+(1|arch)	glmmTMB	3680.6	3680.9	3714.5	0.89	0.48
15	NSR~area+SLMP+itype+mxelv+annprecip+(1|arch)	glmmTMB	3682.0	3682.3	3715.9	0.89	0.48
16	NSR~area+SLMP+itype+mxelv+anntemp+annprecip+(1|arch)	glmmTMB	3682.1	3682.5	3720.3	0.89	0.47
17	**NSR~area+SLMP+itype+mxelv+tempseas+(1|arch)**	**glmmTMB**	**3661.4**	**3661.7**	**3695.3**	**0.90**	**0.56**
18	NSR~area+SLMP+itype+mxelv+precipseas+(1|arch)	glmmTMB	3682.6	3682.9	3716.5	0.89	0.48
19	NSR~area+SLMP+itype+mxelv+tempseas+precipseas+(1|arch)	glmmTMB	3662.5	3662.9	3700.7	0.90	0.56
1	pSIE~area	glmmTMB	250.5	250.6	259.0	NA	0.14
2	pSIE~dist	glmmTMB	265.2	265.2	273.7	NA	0.10
3	pSIE~area+(1|arch)	glmmTMB	1023.4	1023.5	1040.4	0.72	0.22
4	pSIE~area+dist+(1|arch)	glmmTMB	1013.9	1014.0	1035.1	0.70	0.29
5	pSIE~area+SLMP+(1|arch)	glmmTMB	994.6	994.8	1015.8	0.68	0.31
6	pSIE~area+SLMP+itype+(1|arch)	glmmTMB	987.3	987.5	1012.7	0.69	0.38
7	pSIE~area+SLMP+itype+mxelv+(1|arch)	glmmTMB	988.7	989.0	1018.4	0.69	0.39
8	pSIE~area+SLMP+itype+TRI+(1|arch)	glmmTMB	989.3	989.5	1018.9	0.69	0.38
9	pSIE~area+SLMP+itype+mxelv+TRI+(1|arch)	glmmTMB	989.3	989.6	1023.2	0.68	0.38
10	**pSIE~area+SLMP+itype+mxelv+anntemp+(1|arch)**	**glmmTMB**	**986.9**	**987.2**	**1020.8**	**0.69**	**0.40**
11	pSIE~area+SLMP+itype+mxelv+annprecip+(1|arch)	glmmTMB	990.7	991.0	1024.6	0.69	0.39
12	pSIE~area+SLMP+itype+mxelv+anntemp+annprecip+(1|arch)	glmmTMB	988.7	989.0	1026.8	0.68	0.41
13	pSIE~area+SLMP+itype+mxelv+tempseas+(1|arch)	glmmTMB	990.7	991.0	1024.6	0.69	0.39
14	pSIE~area+SLMP+itype+mxelv+precipseas+(1|arch)	glmmTMB	988.3	988.6	1022.2	0.68	0.40
15	pSIE~area+SLMP+itype+mxelv+tempseas+precipseas+(1|arch)	glmmTMB	990.3	990.6	1028.4	0.68	0.40

Table S2: **Summary of the island diversity data for the top ten angiosperm families across all islands (continental, oceanic, and mixed) and oceanic islands.** The total number of species native to islands and total number of species endemic to islands were calculated from the GIFT checklists and the overall number of species within each family is based on the World Checklist of Vascular Plants (WCVP). Proportion island refers to the number of species within each family that are native to islands. Stem ages for each family were extracted from the angiosperm dated phylogeny (relaxed calibration and complete fossil dataset) constructed in Ramírez-Barahona et al., 2020.

Family	Native island species	Endemic island species	Total species in family	Proportion island	Stem age (Mya)
All islands					
Orchidaceae	11,188	8,047	29,867	37%	133 (127-141)
Rubiaceae	6,188	4,740	14,083	44%	102 (90-115)
Asteraceae	6,135	3,535	33,994	18%	74 (72-78)
Fabaceae	4,169	1,773	22,187	19%	107 (93-119)
Poaceae	3,979	1,385	11,754	34%	94 (87-99)
Myrtaceae	2,389	1,808	6,186	39%	98 (84-112)
Cyperaceae	2,296	756	5,644	41%	85 (68-107)
Apocynaceae	2,288	1,633	6,487	35%	87 (70-104)
Euphorbiaceae	2,262	1,519	6,530	35%	80 (64-96)
Melastomataceae	1,954	1,617	5,844	33%	83 (65-102)
Oceanic islands					
Asteraceae	1,833	955	33,994	5%	74 (72-78)
Orchidaceae	1,776	708	29,867	6%	133 (127-141)
Poaceae	1,366	292	11,754	12%	94 (87-99)
Rubiaceae	1,343	871	14,083	10%	102 (90-115)
Fabaceae	1,141	287	22,187	5%	107 (93-119)
Cyperaceae	903	205	5,644	16%	85 (68-107)
Euphorbiaceae	653	287	6,530	10%	80 (64-96)
Myrtaceae	583	454	6,186	9%	98 (84-112)
Malvaceae	496	198	5,439	9%	92 (83-102)
Apocynaceae	480	256	6,487	7%	87 (70-104)

Table S3: **Binomial test for the ten most diverse angiosperm families on islands comparing the island proportion to the expected proportion of the family globally.** The total number of angiosperm species (n) on all islands is 99,659 species, and on oceanic islands 23,853 species. The sample estimate represents the estimated proportion of island species based on the observed data, and the 95% confidence interval is the range estimate for the true probability of success (i.e. the proportion of the family on islands). When the sample estimate is equal to the overall proportion of the family globally, the null hypothesis is accepted. The alternative hypothesis is accepted when the sample estimate is not equal to the overall proportion of the family globally, indicating a deviation from the expected proportion. If the sample estimate and 95% confidence interval are greater than the proportion of the family globally (p), then the family is more diverse on islands than expected, if they are lower than the proportion of the family globally, the family is less diverse on islands than expected given its global diversity.

	Binomial test parameters		Results		
Family	Native island species (x)	Proportion of family globally (p)	*p*-value	Sample estimate	95% confidence interval
All islands					
Orchidaceae	11,188	8.9	<0.001	11.23	11.03-11.42
Rubiaceae	6,188	4.2	<0.001	6.21	6.06-6.36
Asteraceae	6,135	10.2	<0.001	6.16	6.01-6.31
Fabaceae	4,169	6.6	<0.001	4.18	4.06-4.31
Poaceae	3,979	3.5	<0.001	3.99	3.87-4.12
Myrtaceae	2,389	1.9	<0.001	2.4	2.30-2.49
Cyperaceae	2,296	1.7	<0.001	2.3	2.21-2.40
Apocynaceae	2,288	1.9	<0.001	2.3	2.20-2.39
Euphorbiaceae	2,262	2.0	<0.001	2.27	2.18-2.36
Melastomataceae	1,954	1.8	<0.001	1.96	1.88-2.05
Oceanic islands					
Asteraceae	1,833	10.2	<0.001	7.68	7.35-8.03
Orchidaceae	1,776	8.9	<0.001	7.45	7.12-7.79
Poaceae	1,366	3.5	<0.001	5.73	5.44-6.03
Rubiaceae	1,343	4.2	<0.001	5.63	5.34-5.93
Fabaceae	1,141	6.6	<0.001	4.78	4.52-5.06
Cyperaceae	903	1.7	<0.001	3.79	3.55-4.04
Euphorbiaceae	653	2.0	<0.001	2.74	2.53-2.95
Myrtaceae	583	1.9	<0.001	2.44	2.25-2.65
Malvaceae	496	1.6	<0.001	2.08	1.90-2.27
Apocynaceae	480	1.9	0.439	2.01	1.84-2.20

Table S4: **Summary of island species diversity across Asteraceae subfamilies and tribes.** The proportion of island species is calculated as the number of native island species / total number of species in the tribe. The overall number of species in each tribe is based on the accepted number of species in the Global Compositae Database (GCD).

Tribe	Subfamily	Total species in tribe	Native island species	Endemic island species	Proportion island species
Barnadesieae	Barnadesioideae	92	0	0	0%
Famatinantheae	Famatinanthoideae	1	0	0	0%
Hyalideae	Stifftioideae	6	0	0	0%
Stifftieae	Stifftioideae	45	1	1	2%
Onoserideae	Mutisioideae	41	0	0	0%
Mutisieae	Mutisioideae	255	45	32	18%
Nassauvieae	Mutisioideae	328	27	5	8%
Wunderlichieae	Wunderlichioideae	36	0	0	0%
Cyclolepis	Gochnatioideae	1	0	0	0%
Gochnatieae	Gochnatioideae	102	36	33	35%
Hecastocleideae	Hecastocleidoideae	1	0	0	0%
Pertyeae	Pertyoideae	99	26	16	26%
Oldenburgieae	Tarchonanthoideae	4	0	0	0%
Tarchonantheae	Tarchonanthoideae	20	5	5	25%
Dicomeae	Dicomoideae	112	10	9	9%
Cardueae	Carduoideae	3,586	542	313	15%
Gymnarrheneae	Gymnarrhenoideae	2	0	0	0%
Eremothamneae	Vernonioideae	1	0	0	0%
Moquinieae	Vernonioideae	2	0	0	0%
Platycarpheae	Vernonioideae	3	0	0	0%
Distephaneae	Vernonioideae	43	37	36	86%
Liabeae	Vernonioideae	154	11	11	7%
Arctotideae	Vernonioideae	233	2	0	1%
Vernonieae	Vernonioideae	1,888	270	202	14%
Cichorieae	Cichorioideae	6,673	1,660	905	25%
Corymbieae	Corymbioideae	9	0	0	0%
Feddeeae	Asteroideae	1	1	1	100%
Polymnieae	Asteroideae	8	0	0	0%
Chaenactideae	Asteroideae	21	1	0	5%
Doroniceae	Asteroideae	39	7	1	18%
Perityleae	Asteroideae	78	8	3	10%
Athroismeae	Asteroideae	82	27	15	33%
Bahieae	Asteroideae	87	6	3	7%
Calenduleae	Asteroideae	118	10	2	8%
Helenieae	Asteroideae	138	6	1	4%
Neurolaeneae	Asteroideae	187	13	8	7%
Madieae	Asteroideae	227	63	38	28%
Tageteae	Asteroideae	266	56	22	21%
Millerieae	Asteroideae	477	29	8	6%
Coreopsideae	Asteroideae	523	122	86	23%
Inuleae	Asteroideae	659	206	91	31%
Heliantheae	Asteroideae	1,730	231	103	13%
Anthemideae	Asteroideae	1,955	354	147	18%
Gnaphalieae	Asteroideae	2,218	589	339	27%
Eupatorieae	Asteroideae	2,720	288	187	11%
Astereae	Asteroideae	3,586	793	465	22%
Senecioneae	Asteroideae	3,760	653	447	17%

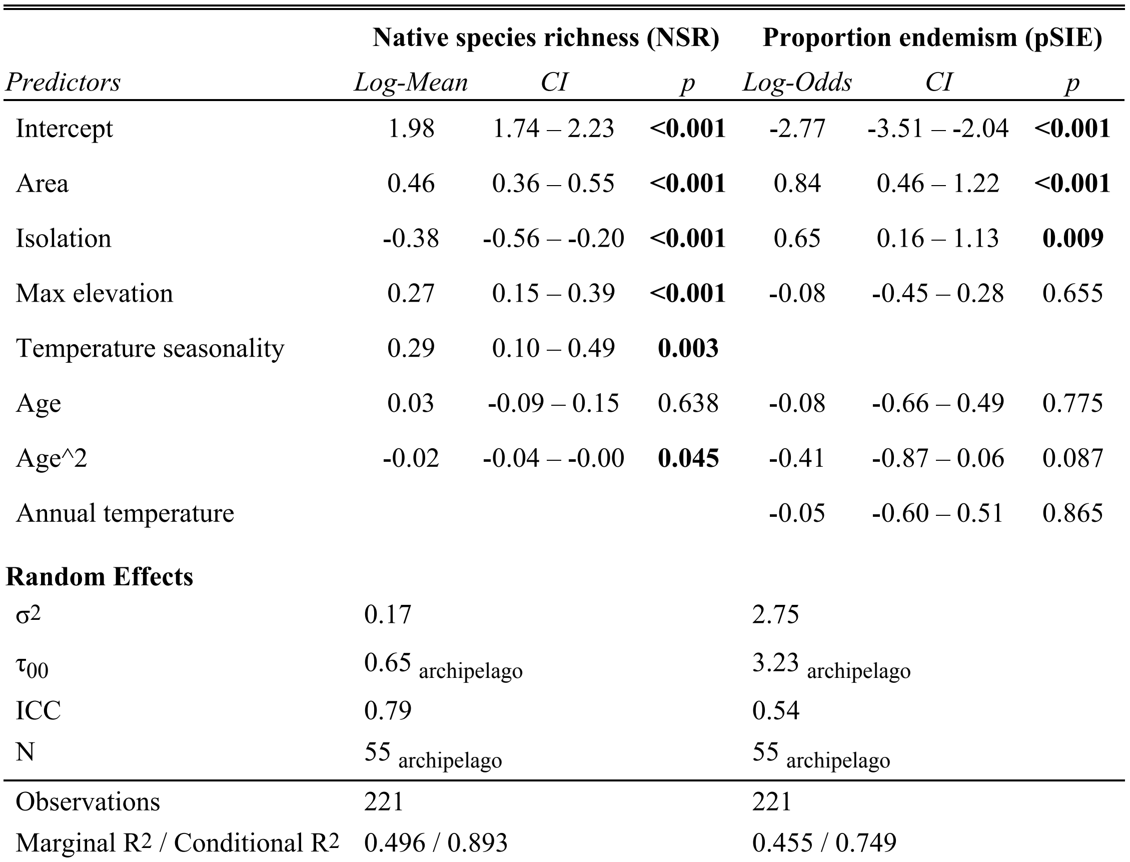
Table S5: **Binomial test for the tribes in Asteraceae comparing the island proportion to the expected proportion of the tribe globally.** The total number of Asteraceae species (n) on islands is 6,135 species. The sample estimate represents the estimated proportion of island species based on the observed data, and the 95% confidence interval is the range estimate for the true probability of success (i.e. the proportion of the tribe on islands). When the sample estimate is equal to the overall proportion of the tribe in Asteraceae (p), the null hypothesis is not rejected. The alternative hypothesis is accepted when the sample estimate is not equal to the overall proportion of the tribe globally, indicating a deviation from the expected proportion. If the sample estimate and 95% confidence interval are greater than the proportion of the tribe globally (*p*), then the tribe is more diverse on islands than expected, if they are lower than the proportion of the tribe globally, the tribe is less diverse on islands than expected given its global diversity. Significant deviations from the null expectation are highlighted in red (below expectation) and blue (above expectation).

Binomial test parameters			Results			
Tribe	Native island species (x)	Proportion of tribe in Aster. (p)	*p*-value	Sample estimate	Confidence interval	Significant deviation from null
Stifftieae	1	0.1	0.005	0.0	0-0.09	
Nassauvieae	27	1.0	<0.001	0.4	0.29-0.64	🟥
Mutisieae	45	0.8	0.941	0.7	0.54-0.98	
Gochnatieae	36	0.3	<0.001	0.6	0.41-0.81	🟦
Pertyeae	26	0.3	0.058	0.4	0.28-0.62	
Tarchonantheae	5	0.1	0.42	0.1	0.03-0.19	
Dicomeae	10	0.3	0.019	0.2	0.08-0.3	
Cardueae	542	10.5	<0.001	8.8	8.14-9.57	🟥
Arctotideae	2	0.7	<0.001	0.0	0-0.12	🟥
Liabeae	11	0.5	<0.001	0.2	0.09-0.32	🟥
Distephaneae	37	0.1	<0.001	0.6	0.42-0.83	🟦
Vernonieae	270	5.6	<0.001	4.4	3.9-4.94	🟥
Cichorieae	1,660	19.6	<0.001	27.1	25.95-28.19	🟦
Chaenactideae	1	0.1	0.198	0.0	0-0.09	
Feddeeae	1	0.0	0.165	0.0	0-0.09	
Bahieae	6	0.3	0.011	0.1	0.04-0.21	
Helenieae	6	0.4	<0.001	0.1	0.04-0.21	🟥
Doroniceae	7	0.1	1	0.1	0.05-0.23	
Perityleae	8	0.2	0.109	0.1	0.06-0.26	
Calenduleae	10	0.3	0.012	0.2	0.08-0.3	
Neurolaeneae	13	0.6	<0.001	0.2	0.11-0.36	🟥
Athroismeae	27	0.2	0.004	0.4	0.29-0.64	
Millerieae	29	1.4	<0.001	0.5	0.32-0.68	🟥
Tageteae	56	0.8	0.246	0.9	0.69-1.18	
Madieae	63	0.7	0.001	1.0	0.79-1.31	🟦
Coreopsideae	122	1.5	0.006	2.0	1.65-2.37	
Inuleae	206	1.9	<0.001	3.4	2.92-3.84	🟦
Heliantheae	231	5.1	<0.001	3.8	3.3-4.27	🟥
Eupatorieae	288	8.0	<0.001	4.7	4.18-5.25	🟥
Anthemideae	354	5.8	0.934	5.8	5.2-6.38	
Gnaphalieae	589	6.5	<0.001	9.6	8.87-10.37	🟦
Senecioneae	653	11.1	0.309	10.6	9.88-11.44	
Astereae	793	10.5	<0.001	12.9	12.1-13.79	🟦

Table S6: **Summary statistics of native species richness (NSR) and proportion of single-island endemic (pSIE) generalized mixed effect models.** The following predictor variables were log-transformed: area, isolation (-SLMP), maximum elevation, and temperature seasonality.

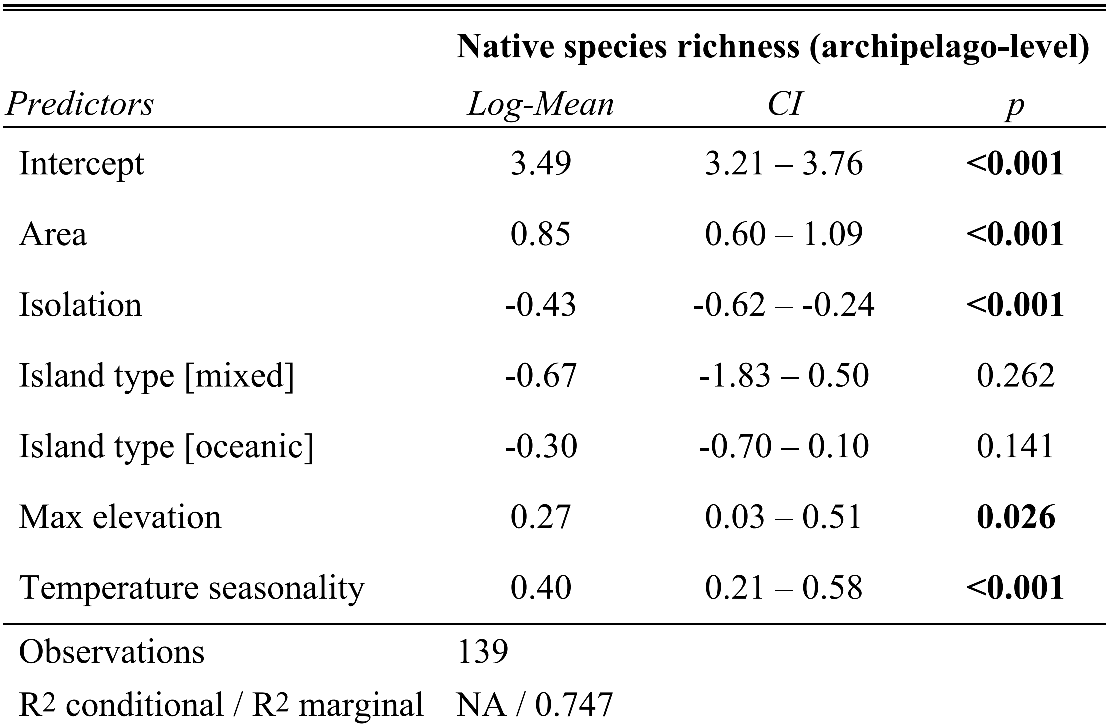
	Native species richness (NSR)			**Proportion endemism (pSIE)**		
Predictors	*Log-Mean*	*CI*	*p*	*Log-Odds*	*CI*	*p*
Intercept	2.76	2.57 – 2.96	**<0.001**	-4.97	-5.80 – -4.14	**<0.001**
Area	0.64	0.56 – 0.72	**<0.001**	1.55	1.17 – 1.94	**<0.001**
Isolation	-0.32	-0.45 – -0.19	**<0.001**	0.48	0.09 – 0.88	**0.017**
Island type [oceanic]	-0.38	-0.57 – -0.19	**<0.001**	1.36	0.48 – 2.23	**0.002**
Max elevation	0.13	0.05 – 0.22	**0.002**	0.18	-0.20 – 0.55	0.351
Temperature seasonality	0.34	0.20 – 0.48	**<0.001**			
Annual temperature				0.35	-0.00 – 0.70	0.051
Random Effects						
σ^2	0.18			3.09		
τ_{00}	$0.60_{\text{archipelago}}$			$2.78_{\text{archipelago}}$		
ICC	0.76			0.47		
N	$110_{\text{archipelago}}$			$110_{\text{archipelago}}$		
Observations	510			510		
Marginal R^2 / Conditional R^2	0.562 / 0.897			0.403 / 0.685		

Table S7: **Summary statistics of the island age subset models.** Subsets of the global models were run for (1) native species richness and (2) the proportion of single-island endemics that filtered to only oceanic islands and included Age+Age^2 as an additional fixed effect. The following predictor variables were log-transformed: area, isolation (-SLMP), maximum elevation, and temperature seasonality.



	Native species richness (NSR)			**Proportion endemism (pSIE)**		
Predictors	*Log-Mean*	*CI*	*p*	*Log-Odds*	*CI*	*p*
Intercept	1.98	1.74 – 2.23	**<0.001**	-2.77	-3.51 – -2.04	**<0.001**
Area	0.46	0.36 – 0.55	**<0.001**	0.84	0.46 – 1.22	**<0.001**
Isolation	-0.38	-0.56 – -0.20	**<0.001**	0.65	0.16 – 1.13	**0.009**
Max elevation	0.27	0.15 – 0.39	**<0.001**	-0.08	-0.45 – 0.28	0.655
Temperature seasonality	0.29	0.10 – 0.49	**0.003**			
Age	0.03	-0.09 – 0.15	0.638	-0.08	-0.66 – 0.49	0.775
Age^2	-0.02	-0.04 – -0.00	**0.045**	-0.41	-0.87 – 0.06	0.087
Annual temperature				-0.05	-0.60 – 0.51	0.865
Random Effects						
σ^2	0.17			2.75		
τ_{00}	0.65 $_{\text{archipelago}}$			3.23 $_{\text{archipelago}}$		
ICC	0.79			0.54		
N	55 $_{\text{archipelago}}$			55 $_{\text{archipelago}}$		
Observations	221			221		
Marginal R^2 / Conditional R^2	0.496 / 0.893			0.455 / 0.749		

Table S8: **Summary statistics for the native species richness on archipelagos generalized linear model.** In our global model for native species richness (Figure 4, Table S6), we found that the inclusion of archipelago as a random effect contributes substantially to the overall variance captured by the model (i.e. 0.56 marginal R^2 / 0.90 conditional R^2). To test the robustness of our general results, we aggregated the diversity and environmental data from the island level to the archipelago level and ran a generalized linear model. At the scale of the archipelago, the main model patterns do not change: area and isolation are the strongest predictors of native species richness, and the relationships between native species richness and environmental predictors remain the same. Notably for this model the marginal R^2 becomes 0.751, an increase from the 0.56 from the earlier model.



	Native species richness (archipelago-level)		
Predictors	*Log-Mean*	*CI*	*p*
Intercept	3.49	3.21 – 3.76	**<0.001**
Area	0.85	0.60 – 1.09	**<0.001**
Isolation	-0.43	-0.62 – -0.24	**<0.001**
Island type [mixed]	-0.67	-1.83 – 0.50	0.262
Island type [oceanic]	-0.30	-0.70 – 0.10	0.141
Max elevation	0.27	0.03 – 0.51	**0.026**
Temperature seasonality	0.40	0.21 – 0.58	**<0.001**
Observations	139		
R^2 conditional / R^2 marginal	NA / 0.747		

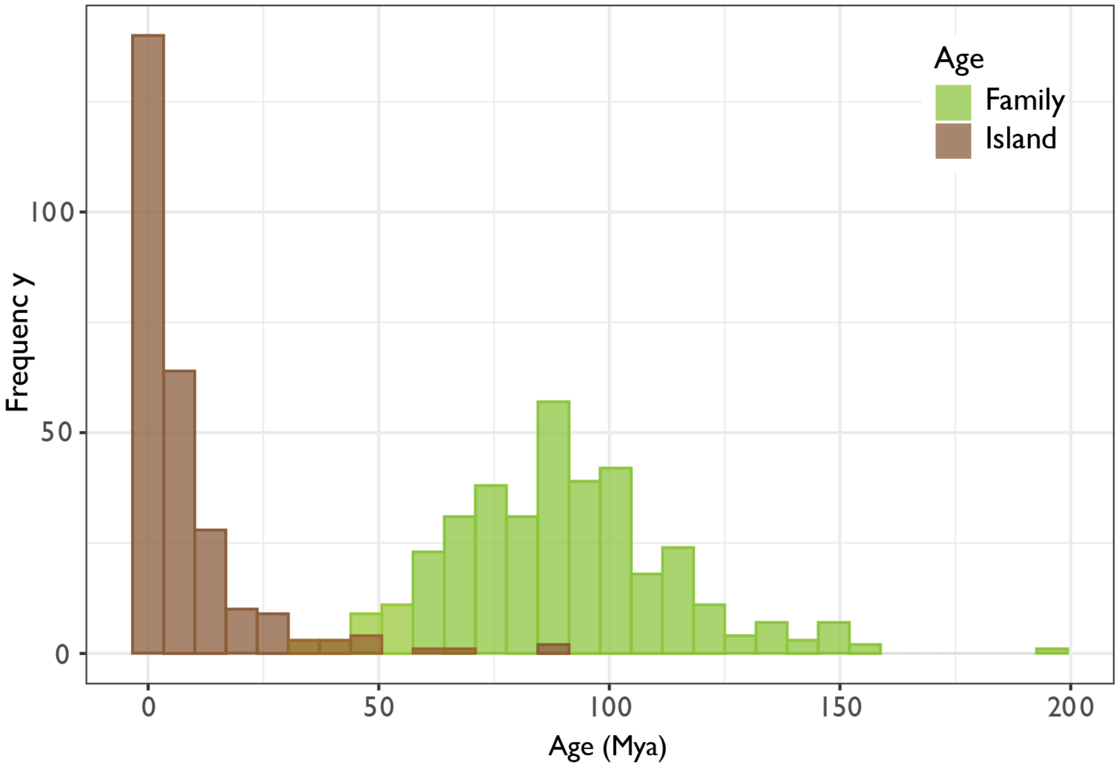


Figure S1: **Distribution of island and family ages.** The distribution of island ages (million years ago, Mya) is highlighted in brown. These are the islands in our dataset for which an age estimate is available. In green is the distribution of stem ages (Mya) for the plant families with native island species. Stem ages for each family were extracted from the angiosperm dated phylogeny (relaxed calibration and complete fossil dataset) constructed in Ramírez-Barahona et al., 2020.

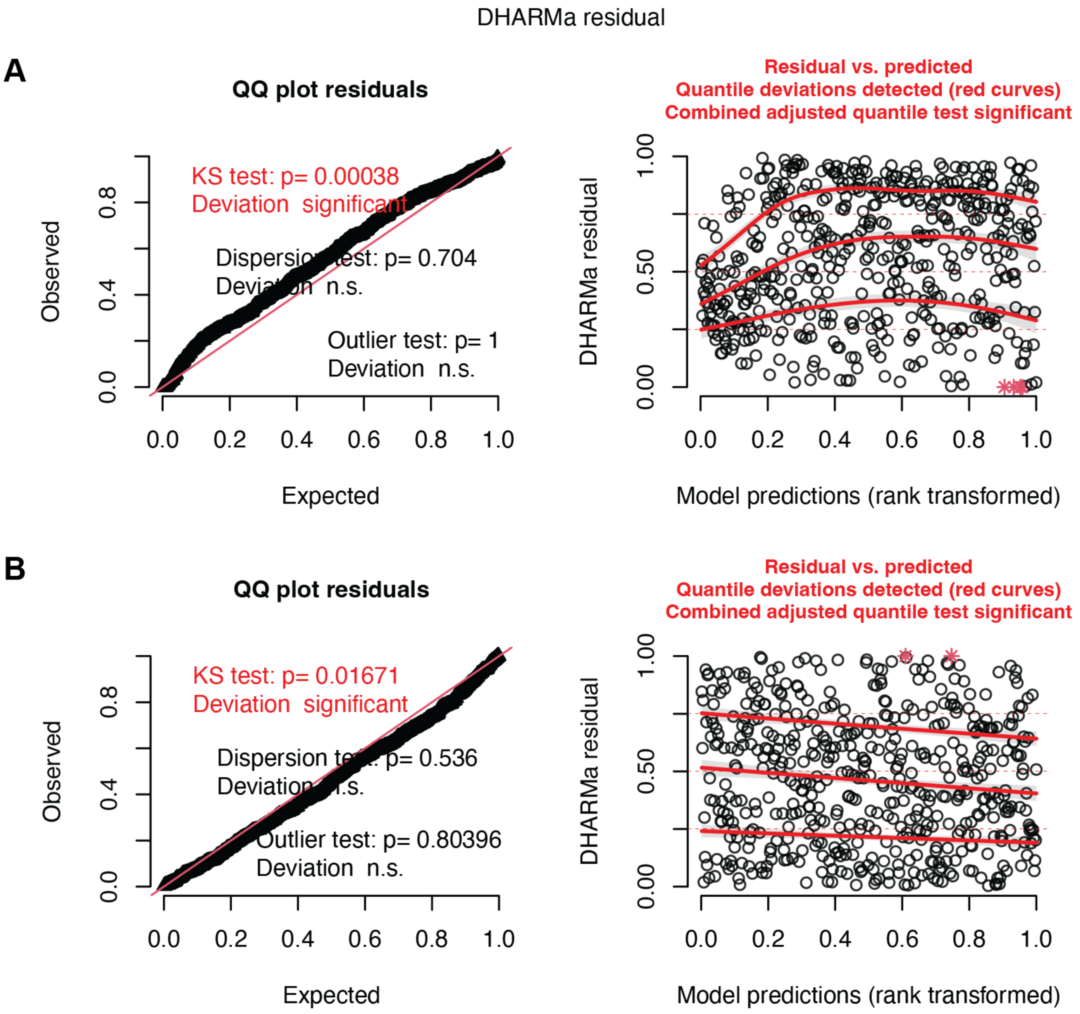


Figure S2: **Diagnostic plots of the scaled residuals for the fitted models for (A) Native species richness and (B) Proportion of single-island endemics.** We assessed the scaled residuals with the DHARMA package (Hartig, 2022), which simulates standardized residuals from the fitted model and can check for overdispersion and zero inflation. The QQ plots (left panel) detect deviations from the expected distribution, dispersions, and outliers; the residuals plot (right panel) shows the simulated residuals against the predicted values. For the NSR model (A), no significant outliers or overdispersion were detected. The simulated residuals indicate that the NSR model has difficulties predicting native species numbers for islands with a low number of native species (1-3) well. In particular, the model tends to overestimate these numbers. This is likely a reflection of sampling bias, where islands without any native species presence were filtered out of the data set and islands with few species possibly being poorly sampled locations or capturing possibly native (e.g. introduced species) species. Although deviations are marked as significant, they do not appear to be large. Furthermore, adding quadratic terms, splines or additional interactions did not significantly change the observed patterns. For the pSIE model (B), no significant outliers or overdispersion were detected. The simulated residuals for pSIE indicate heteroscedasticity but the effect is mild.

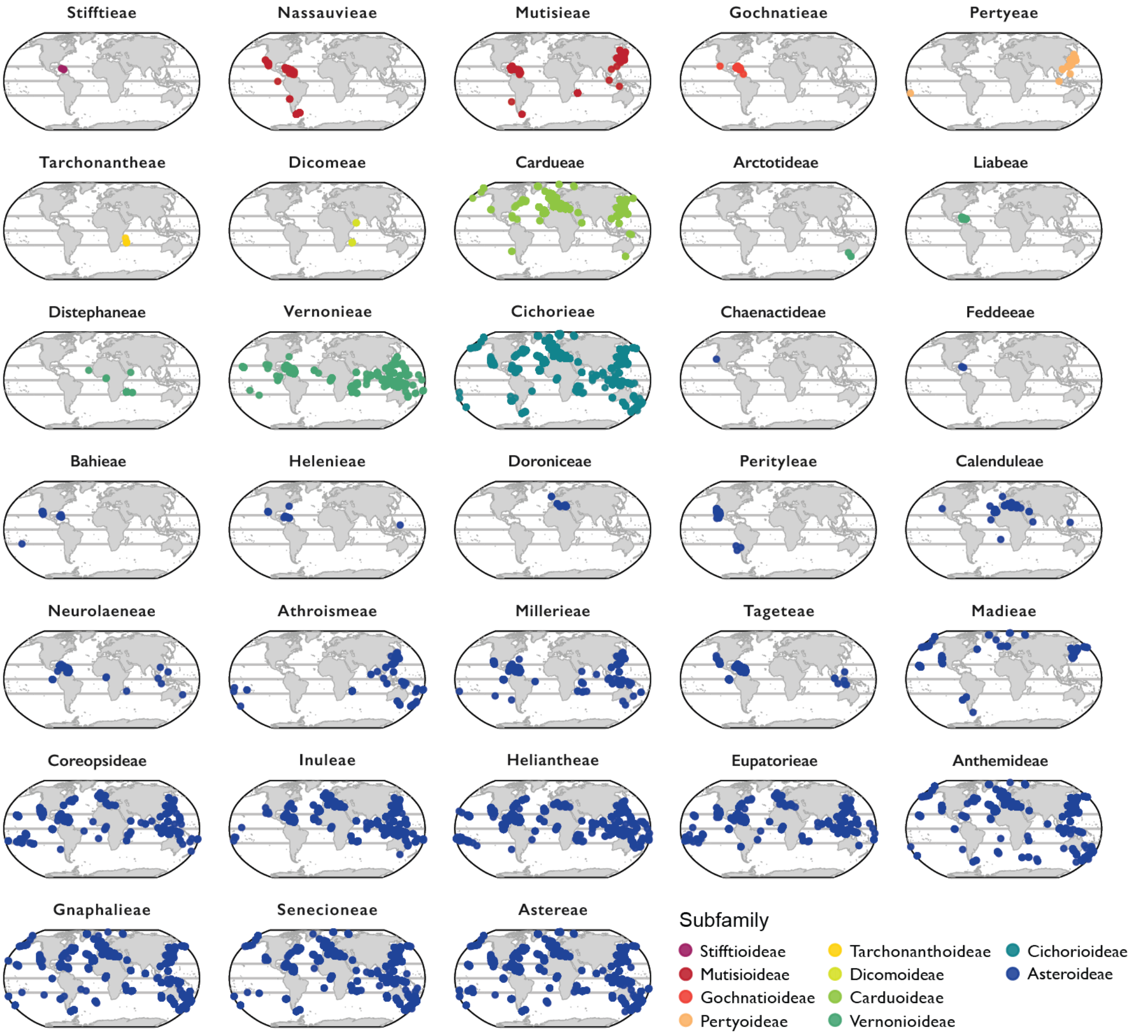


Figure S3: **Geographical distribution of native species on islands per tribe.** The tribes are colored and grouped by their subfamily.

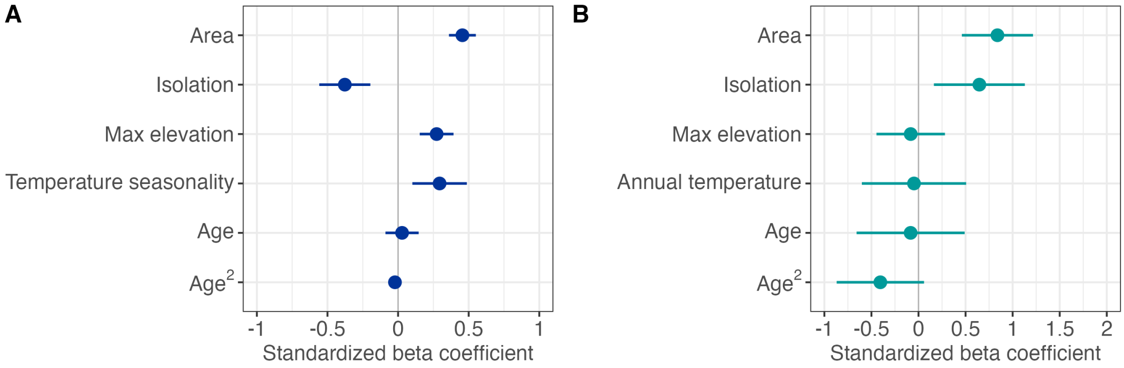


Figure S4: **Standardized coefficients for the island age subset models.** Coefficient estimates for the subset of global models for (A) native species richness (blue) and (B) the proportion of single-island endemics (green) including Age+Age^2 as an additional fixed effect. The bars around the coefficient estimates represent the standard error. The dark gray vertical intercept at 0 indicates no significant effect, and island variables with a positive coefficient estimate indicate an increase in native species richness or proportion endemism, whereas a negative coefficient estimate indicates a decrease in the response variables.

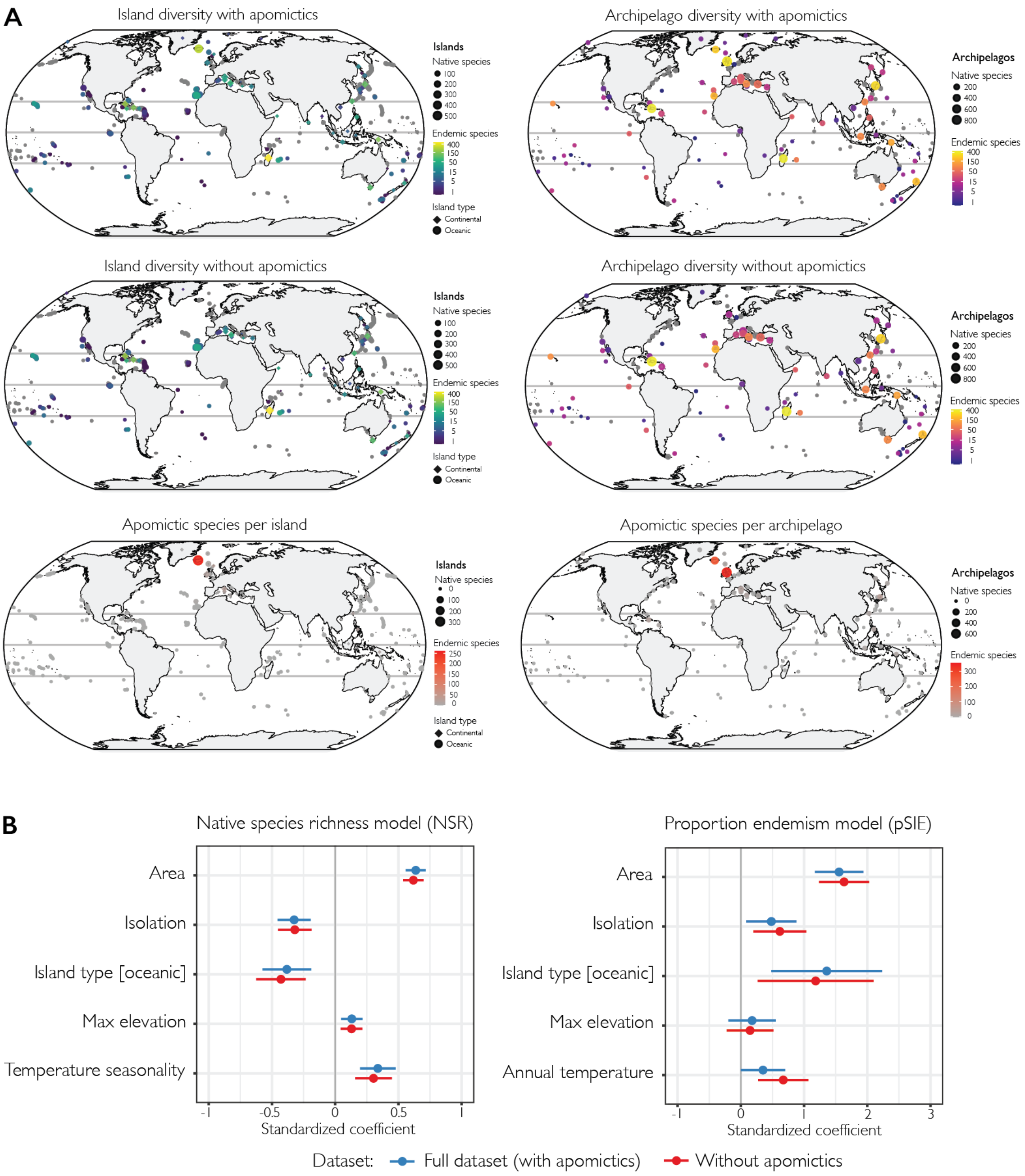


Figure S5: **Impact of apomictic species on family-level diversity analyses.** (Caption next page.)

Figure S5: **Impact of apomictic species on family-level diversity analyses.** (Previous page.) Here we evaluate the influence of apomictic species on family-level diversity analyses, focusing on two aspects: (1) geographic distribution and hotspots, and (2) island biogeographic patterns. Apomictic genera were filtered based on the Apomixis Database (https://www.uni-goettingen.de/de/apomixis+database/423360.html), an online database containing information on apomixis at the genus level in angiosperms. We examine the difference in diversity pattern using two datasets: one including all genera even putative apomictics (full dataset), and another with apomictic genera removed. (A) Geographic distribution and hotspots: The top row of maps presents the distribution with the full dataset on islands (left) and archipelagos (right), the middle row shows the distribution with apomictics excluded, and the third row shows the number of putative apomictic species per insular unit (island or archipelago). Most islands have no change in diversity due to apomictics, but the largest differences are on Iceland and the British Isles. (B) Island biogeographic patterns: we ran and compared generalized linear mixed effects models with both the full dataset and filtered dataset with apomictic genera removed to test whether the same global model was selected for both. There was no change in the best global model with the filtering of apomictics. We fit the global model for both datasets, and (in B) compare the standardized coefficients for the full dataset (blue) and dataset with apomictics removed (red). There is no significant change in predictor relationships when apomictic genera are removed.