Flower size evolution in the Southwest Pacific

Abstract

Despite accelerating interest in the island syndrome, the evolutionary trajectories of island flowers remain poorly understood. Here, we derive a new dataset from the Southwest Pacific to evaluate how flower size evolves on islands. Specifically, we tested whether flowers with different pollination modes followed the island rule or evolved convergently toward gigantism or dwarfism. Results indicate that flower size follows the island rule. However, patterns differed significantly between pollination modes. Animal-pollinated flowers followed the island rule, while wind-pollinated flowers showed evidence for gigantism. Both of these trends were mirrored by evolutionary changes in flower-correlated traits. Overall, we provide the first test for an island syndrome in flower size and found that flowers with different pollination modes exhibited markedly different evolutionary trajectories. These results suggest that overall trends in the evolution of flower size on islands might be a byproduct of selection acting on flower-correlated traits.

Keywords

Island rule; flower size; island biogeography; plant evolution; Southwest Pacific

Introduction

Island flowers often differ from their mainland relatives, being typically dull-coloured and inconspicuous (Whittaker et al., 2023). They are often self-compatible and possess generalized morphologies that allow pollination by a wide array of pollinators (Baker, 1967; Carlquist, 1974; Barrett, 1996; Crawford et al., 2011; Burns, 2019). These differences suggest the existence of an island floral syndrome (i.e. a set of predictable differences between island and mainland flowers) which is still largely unexplored (Whittaker et al., 2023).

The island floral syndrome can arise from evolutionary processes and/or from insular assembly rules (i.e. patterns arising from biased colonization/establishment) (Whittaker et al., 2023). At the moment, most components of the island floral syndrome are regarded as insular assembly rules (Hetherington-Rauth and Johnson, 2020). For example, plants capable of self-fertilization are overrepresented on islands as they can establish new populations more readily (Baker, 1967; Pannel et al., 2015; Burns, 2019). In turn, self-compatible plants typically have smaller flowers (Goodwillie et al., 2010). Whether components of the island floral syndrome can arise from in-situ evolutionary processes is still unclear (Bernardello et al., 2001; Newstrom and Robertson, 2005; Burns, 2019).

Island evolutionary processes can be directional or stabilizing. Directional selection can lead to overall trends toward gigantism or dwarfism (Burns et al., 2012; Kavanagh and Burns, 2014), while stabilizing selection can result in the ‘island rule’, causing small organisms to become larger and large organisms to become smaller. While it remains one of the most controversial topics in biogeography (Van Valen, 1973; Lomolino, 2005; Meiri et al., 2008; Lomolino et al., 2012; Faurby and Svenning, 2016; Itescu et al., 2018; Rebouças et al., 2018; Lokatis and Jeschke, 2018; Benitez-Lopez et al., 2021), evidence for the island rule has recently been found for plant stature and leaf area on islands in the Southwest Pacific (Biddick et al., 2019).

The size of island flowers could be under either directional or stabilizing selection. Islands are known for their paucity of pollinators (Burns, 2019; Whittaker et al., 2023). Changes in pollinator abundance between islands and the mainland could generate directional selective pressures in floral display (i.e. flower size · number of flowers per individual), causing animal-pollinated floral displays to increase/decrease and wind-pollinated floral displays to remain unchanged (Parachnowitsch and Kessler, 2010; Caruso et al., 2019; Brunet et al., 2021). If floral display varies through changes in flower size, pollen limitation could intensify selection of traits promoting outcrossing through increased floral display leading to larger flowers (Harder et al., 2010; Thomann et al., 2013; Panique and Caruso, 2020). Alternatively, pollinator decline and mate limitation could select for selfing mechanisms, leading to smaller floral displays and smaller flowers (Elle and Carney, 2003; Thomann et al., 2013).

Flower size of both animal- and wind-pollinated species could follow the island rule as a by-product of stabilizing selection acting on flower-correlated traits. Since many plant traits are known to covary with flower size were shown to evolve predictably on islands (Niklas, 1994; Burns et al., 2012; Biddick et al., 2019; E-Vojtkó et al., 2022; Whittaker et al., 2023), flower size could follow the island rule because of its allometric relationships. Under this hypothesis, both animal- and wind-pollinated island flowers should differ from their mainland relatives. Additionally, if the two pollination modes exhibited different evolutionary trajectories, these should be mirrored by their correlated traits.

Different plant lineages can respond independently to insular selective pressures. For example, the genetic, morphological and evolutionary history of certain taxonomic families make them more likely to evolve generalized floral structures or to break down mechanisms of self-incompatibility (Goldberg et al., 2010; Minelli, 2018; Cossard et al., 2021). Similarly, plants with different breeding systems are typically characterized by different flowers (Krizek

and Anderson, 2013; Salisbury et al., 2017) and might respond to insular conditions in a distinct way. Additionally, evolutionary pressures will vary depending on the abiotic and biotic characteristics of the islands themselves (MacArthur and Wilson, 1967; Whittaker et al., 2023). Consequently, to test for flower size evolution on islands, it is vital to include multiple plant lineages with different pollination modes, evolutionary histories and breeding systems that occur across multiple archipelagos.

In this study, we used a phylogenetic comparative approach to test whether island animal-pollinated and wind-pollinated flowers evolve toward gigantism/dwarfism or follow the island rule. Specifically, using a newly derived dataset representing 131 independent colonization events on 10 archipelagos in the Southwest Pacific, which we then used to answer three questions: I) Do animal-pollinated flowers increase or decrease in size while wind-pollinated flowers remain unchanged? II) Do both animal-pollinated and wind-pollinated flowers evolve to follow the island rule? And if so, III) are these trajectories mirrored by their correlated traits?

Methods

Study area

We focused on the endemic flora of 10 archipelagos distributed across 25° of latitude (29°04’ S - 54°37’ S) around New Zealand (Fig 1). The island groups can roughly be divided into the sub-tropical archipelagos of Lord Howe, Norfolk, Kermadec, and Three Kings, and the cool-temperate/subantarctic archipelagos of Chatham, Snares, Antipodes, Auckland, Campbell and Macquarie. All island systems are oceanic in origin, with faunas and floras derived by overwater dispersal from New Zealand and Australia or vicariance (Chown et al., 1998; Rutledge et al., 2003; Pendlebury and Barnes-Keoghan, 2007; Lord, 2015; Fitzgerald, 2020).

We restricted analyses to these island systems so that our set of island taxa would be

derived from a few well-known mainland floras, sharing similar ecological, geological and evolutionary histories. Chatham, Snares, Antipodes, Auckland, Campbell, Three Kings, Kermadec and Macquarie were included as most of their endemic species originated from the New Zealand mainland. Lord Howe and Norfolk islands were included as most of their endemic species originated from Australia (Supplementary S2). We included endemics from 2 mainland sources to increase the number of taxonomic families present and to account for the possibility that endemics originating from very different mainland source pools (i.e. New Zealand and Australia) would respond differently to insular environments.

Species selection

To test flower size evolution in animal- and wind-pollinated species, we compiled a list of island/mainland pairs of taxa. Each mainland taxon is the sister group of the island taxon so that each pair represents a phylogenetically independent comparison.

We first compiled a list of endemic species and subspecies on each archipelago using the most recent data available (Oliver, 1948; Godley, 1969; Taylor, 1971; Johnson and Campbell, 1975; Meurk, 1977; Sykes, 1977; Godley, 1989; Wright, 1983; Green, 1994; Meurk et al., 1994; Sykes and West, 1996; Amey et al., 2007; De Lange et al., 2011; Lord et al., 2013; De Lange, 2014; De Salas and Baker, 2015). Because botanical sources varied widely in age, all species names were cross-checked for synonymy, keeping the New Zealand Plant Conservation Network (2023) and the Atlas of Living Australia (2023) as taxonomic references.

We then identified the mainland sister taxon of each island taxon using published molecular phylogenies. We searched Google Scholar for phylogenies using the species or genus name and the Boolean operator “AND” along the term “phylogen*” (e.g. *Coprosma* AND phylogen*). When multiple phylogenies were available, we selected the phylogeny that

used the most comprehensive genetic dataset, used either Bayesian inference or Maximum likelihood for phylogenetic reconstruction, and showed the strongest support at each node (supplementary material S3). Species names were standardized following the New Zealand Plant Conservation Network (2023) and Atlas of Living Australia (2023). When molecular phylogenies were unavailable, sister taxa were identified based on morphological evidence. As without phylogenies we could not identify the closest relative with certainty, multiple mainland species within the genus were selected and their floral traits averaged. If the genus comprised less than five species on the mainland (e.g. genus *Streblus*), all species were included as mainland relatives. If the genus comprised more than five species on the mainland (e.g. genus *Exocarpos*), we included as mainland relatives up to five species based on morphological affinities. (Supplementary material S3). We excluded island taxa if mainland taxa could not be identified using either phylogeny or taxonomy.

Trait measurements

Each island/mainland pair was categorized as animal-pollinated or wind-pollinated, and as monomorphic (including hermaphroditic, monoecious, andromonoecious, and gynomonoecious species) or dimorphic (including dioecious and gynodioecious species) using McGlone and Richardson (2023), Atlas of Living Australia (2023), Flora of New South Wales Online (2023) and the New Zealand Plant Conservation Network (2023).

For animal-pollinated flowers, to obtain a measure of floral display, we counted the number of flowers per individual. When unavailable, we used the number of flowers per inflorescence as an estimate of floral display. This can be a reliable estimate as inflorescences typically behave as autonomous modules among which resources cannot be reallocated (Herrera, 1991; Torices and Mendez, 2014; Dai et al., 2018).

For animal-pollinated flowers, we identified the unit of pollination (i.e. the unit of pollinator attraction, sensu Faegri and Van der Pijl, 1979) and we characterized the organs involved in pollinator attraction (i.e. possessing an advertisement function). For radially symmetric flowers with fused petals and petal lobes (e.g. Plantaginaceae, genus *Veronica*), we characterized lobe length, lobe width, or corolla diameter. Tube length was collected but not included in the analysis as it is not a measure of advertisement but of accessibility (Dafni, 1992). For radially symmetric flowers with free petals, we characterized petal length, petal width or corolla diameter. For zygomorphic flowers, we used the length and width of the organs most involved in advertisement (e.g. banner and wing of Fabaceae flowers). For the Myrtaceae family, we characterized both stamen length and petal length, as in this family the stamens are often involved in pollinator attraction (Vasconcelos et al., 2019). For Asteraceae, we collected ray floret length, disk diameter or capitulum diameter. For dimorphic taxa, we always used measurements from male flowers, as we expect the male perianth to be the one under stronger selective pressures (Barbot et al., 2023) (supplementary material S2).

For wind-pollinated flowers, we used the sterile parts of flowers. For radially symmetric flowers with fused petals (e.g. Plantaginaceae, genus *Plantago*), we characterized lobe length, lobe width, or corolla diameter. For radially symmetric flowers with free petals (e.g. Arecaceae) we characterized petal length or corolla diameter. For flowers with undifferentiated sepals and petals (e.g. Juncaceae), we used tepal length. For Poaceae, we used glume, lemma, palea or lodicule length. For Cyperaceae, we used glume length. For dimorphic taxa (e.g. Rubiaceae, genus *Coprosma*) we characterized both male and female flowers.

To test our first hypothesis, floral display was defined as flower number · flower size. Flower size was measured on the floral trait bearing the primary attractiveness function (e.g. petals), so that each trait had a comparable biological function across families. To test our

second hypothesis, we measured any non-fertile trait of the flower as proxy for flower size. For all analyses, we used the same trait for all species within a family (e.g. capitulum diameter for all Asteraceae). If missing, another flower trait was used in its place. Before using multiple traits, and to make sure that single traits could be reliable indicators of flower size, a Pearson's correlation test was run to assess collinearity, setting 0.7 as a cut-off (Berry and Feldman, 1985). Only traits above the cut-off value were considered (Table S4).

To test whether the evolutionary trajectories of flower size were mirrored by the correlated traits, we also measured leaf area and seed dry mass for all species. These two traits were selected because, among the studied traits of island plants, they are the ones most clearly under direct selective pressures (Kavanagh and Burns, 2014; Biddick et al., 2019; Whittaker et al., 2023; Ciarle et al., 2024).

Leaf area was estimated from leaf length and width using the equation:

$$A = \frac{Ll}{2} \times \frac{Lw}{2} \times \pi$$

where A is the estimated leaf area, Ll is leaf length and Lw is leaf width. Seed mass was estimated from seed length using the equation:

$$m = 0.1329 sl^{2.2243}$$

where m is the estimated seed mass, sl is the seed length and the two numeric values are constants. The equation was parametrized based on a linear model with both variables log-transformed, a sample size of 695 species with directly measured seed mass (74% of which are native species) across 297 genera and 100 families, and a fit of R squared = 0.865 (Sarah Richardson, personal communication, May 20, 2020).

All traits were extracted from the Floras of New Zealand and Australia series (Allan, 1961; Moore and Edgar, 1970; Webb et al., 1988; Edgar et al., 2010) and additional online sources (New Zealand Plant Conservation Network, 2023; Atlas of Living Australia, 2023; and New South Wales Flora Online, 2023). We searched the primary literature when data

were missing. When online data was unavailable, we manually measured floral traits from herbaria in the Botany collection of Te Papa Tongarewa Museum of New Zealand. For each species trait, 5 to 10 specimens with multiple, well-preserved flowers were sampled. Three to five measurements were then taken for each specimen and averaged.

Statistical analyses

To test whether floral display (i.e. flower size · number of flowers per inflorescence) followed the island rule, we computed a floral display log ratio (fdLR) for each island/mainland pair of animal-pollinated plants as log(mean island floral display/mean mainland floral display). We then conducted three major axis regressions using fdLR as dependent variable and average values of mainland relatives as independent variables. The three regressions accounted for all plant species, animal-pollinated and wind-pollinated species respectively. Slopes significantly lower than zero would be evidence for the island rule. Slopes indistinguishable from zero would denote morphological isometry (Lomolino et al., 2013). The analysis was then repeated without the fdLR ratio, with island floral display as the dependent variable and mainland floral display as the independent variable. Slopes indistinguishable from one would denote morphological isometry. Intercepts above or below zero would be evidence for gigantism or dwarfism respectively (Burns 2022).

The same analyses were repeated for flower size by computing a flower size log ratio (fsLR). We conducted three separate reduced major axis regressions, accounting for all plant species, animal-pollinated and wind-pollinated species respectively. We used fsLR values as dependent variable and average values of mainland relatives as independent variable in all regressions.

To test whether flower-correlated traits (i.e. leaf area and seed mass) mirrored the evolutionary trajectories of flower size, we computed a leaf area and a seed mass log ratios

(laLR and smLR respectively). We then conducted two separate major axis regressions using laLR and smLR as dependent variables and average values of mainland relatives as independent variables.

Mixed effect models were used to control for potential confounding factors. Because flower size may differ between plants with different breeding strategies, the breeding system was included as a fixed factor with two categories: monomorphic and dimorphic. Because flowers from different mainlands may respond differently to insular systems, mainland source was included as a fixed factor with two categories: Australia and New Zealand. Because we expect fully differentiated species to exhibit more pronounced insular trends compared to partially differentiated species (i.e. subspecies), taxonomic differentiation was included as a fixed effect with two categories: partially differentiated and fully differentiated. To control for phylogenetic conservatism, taxonomic families were included as a random effect. To avoid singularity, only taxonomic families with three or more island/mainland pairs were included. To control for environmental and ecological differences among islands, islands were included as a random effect. Since flower size may differ between different flower morphologies of animal-pollinated species, flower type was included as a fixed effect with three categories: actinomorphic flowers with fused petals; actinomorphic flowers with free petals, and zigomorphic flowers.

To test whether floral display, flower size, leaf area, and seed mass of island species were consistently larger or smaller than their mainland relatives, we used one-sided t-tests to determine whether mean fdLR and fsLR values differed significantly from zero. Kruskal-Wallis analysis of variance was used to assess significant differences in fdLR and fsLR means among breeding systems, mainland sources, degree of taxonomic differentiation, taxonomic families (i.e. phylogenetic conservatism), and islands.

All analyses were conducted in the R environment version 4.3.1 (R Core Team, 2022). Reduced major axis regressions were conducted using the R package *lmodel2* (Legendre and Oksanen, 2018). Mixed effect models were conducted using the R packages *nlme* (Pinhero et al., 2017) and lme4 (Bates et al., 2009). When used as the independent variable, mainland flower size was log-transformed to avoid heteroskedasticity. *ggplot2* was used for data visualization (Wickham et al., 2016).

Results

We identified 155 endemic island species, representing 139 independent colonization events. From these, we could compile island/mainland pairs for 149 species belonging to 43 families and representing 131 phylogenetically independent events. We identified 92 animal-pollinated pairs and 40 wind-pollinated pairs. Data for 104 pairs was gathered from online sources, while data for the remaining 27 pairs was manually measured from herbaria specimens (Supplementary material S2). Within each family for which multiple traits were measured, Pearson's correlation test revealed all traits to strictly correlate (Table S5).

Floral display in all species exhibited no pattern toward gigantism or dwarfism (n = 103, LR mean = 0.06, t = 1.75, p-value = 0.08) (Fig S1). This remains true when considering animal-pollinated species (n = 75, LR mean = -0.011, t = -0.36, p-value = 0.72). However, wind-pollinated floral display exhibited a trend toward gigantism (n = 29, LR mean = 0.09, t = 2.48, p-value = 0.02). Flower number alone exhibited no pattern (Table S1).

Flower size followed the island rule, with a slope lower than zero (n = -7.68, 95% confidence interval = -18.61, -4.28; p-value < 0.01) (Fig 2a). Results differed significantly between pollination modes. Flowers of animal-pollinated plants did not get larger (n = 87, LR mean = -0.005, t = 0.15, p-value = 0.82) but followed the island rule (n = -6.87, 95% confidence interval = -19.78, -3.82; p-value < 0.01) (Fig 2b). Instead, wind-pollinated flowers

did not follow the island rule (n = -0.01, 95% confidence interval = -0.13, 0.10; p-value = 0.81) but evolved toward gigantism (n = 39, LR mean = 0.060, t = 3.28, p-value = 0.002) (Fig 2c).

Differences in flower size evolution between pollination modes were mirrored by differences in the evolution of leaf area and seed mass. In animal-pollinated species, leaf area followed the island rule (n = -1.85, 95% confidence interval = -4.70, -0.83; p-value = 0.01) while seed mass exhibited no predictable pattern (n = 61, LR mean = 0.17, t = 1.44, p-value = 0.155) (Fig 3a-c). In wind-pollinated species, leaf area followed no predictable pattern (n = -0.24, 95% confidence interval = -1.00, 0.53; p-value = 0.53) while seed mass consistently evolved toward gigantism (n = 31, LR mean = 0.44, t = 3.49, p-value < 0.001) (Fig 3d-f).

Results for the island rule did not vary when island flower size was used as the dependent variable instead of LR (Supplementary material S1). Results remained unchanged after controlling for breeding system, mainland source, degree of taxonomic differentiation, phylogenetic conservatism (i.e. taxonomic families), and islands (p-values = 0.02 and 0.81 respectively) (Table S2). Results were less robust for animal-pollinated flowers, where the LR mean did not vary significantly among mainland sources, taxonomic families, and degrees of taxonomic differentiation, but did vary among breeding systems and islands (Figure S2, Table S3). The LR mean of wind-pollinated flowers did not vary significantly between breeding system, mainland source, degree of taxonomic differentiation, taxonomic families, and islands (Figure S2, Table S3).

Discussion

We provided the first evidence of *in-situ* evolution of flower size on islands and the first test for the island rule in flowers. We found no evidence for increased floral display in animal-pollinated species. Instead, while overall flower size followed the island rule, different

pollination modes followed different evolutionary trajectories. Animal-pollinated flowers followed the island rule. Conversely, wind-pollinated flowers became consistently larger on islands. These differences between pollination modes were mirrored by flower-correlated traits, with leaf area of animal-pollinated species following the island rule and seed mass of wind-pollinated species evolving toward gigantism. These patterns were robust across breeding systems, mainland sources, degree of taxonomic differentiation, taxonomic families and islands.

The floral display of animal-pollinated species exhibited no recognizable pattern, becoming neither larger nor smaller. Resources allocated to flowers need to increase reproductive success, which is pollinator-driven. Flowers are also subjected to non-pollinator selective pressures such as predators and environmental stresses, which determine flower maintenance costs. If pollinators decline, but reproductive success still increases at a higher rate than maintenance costs, selection will favour increased pollinator attraction. Only when pollinators become too scarce and/or mating partners are limited will selection favour individuals that rely on abiotic vectors/self-fertilization (Maciel et al., 2020; Roddy et al., 2021). Consequently, depending on the biotic and abiotic factors of islands, pollinator paucity could result in showy flowers, inconspicuous flowers, or neither. Our results indicate that, if pollinators do decline on the islands of the Southwest Pacific, differences in pollinator pressures between islands and the mainland could be negligible and/or countered by differences in flower maintenance costs.

Flower size of animal-pollinated flowers followed the island rule. This was likely a by-product of selection acting on leaf area (Fig 3b). Flower size is known to correlate with other plant traits, including leaf area (Bawa et al., 2019; Roddy et al., 2021; E□Vojtkó et al., 2022). Thus, selection acting on a correlated trait could result in the evolution of flower size (Niklas, 1994; Burns et al., 2012).

Results for animal-pollinated plants varied significantly between breeding systems (Figure S2). Pollinator selection acts more strongly on dimorphic species (Geber et al., 2012). Larger flowers in males of dimorphic animal-pollinated island plants may therefore reflect evolution in a depauperate environment where every possibility of attracting pollinators needs to be exploited (Godley, 1979). Additionally, while females allocate more to reproduction in dimorphic animal-pollinated plants, in wind-pollinated species the reproductive costs of males may exceed or match those of females, potentially causing plants with different pollination modes to follow different evolutionary trajectories (Harris and Pannell, 2008; Liu et al., 2021; Roddy et al., 2021; but see Midgley, 2022).

Flower size of wind-pollinated species did not follow the island rule but evolved to be consistently larger on islands. Floral display too evolved toward gigantism. As flower number alone shows no predictable pattern (Table S1), this is likely the by-product of gigantism in flower size. As seed gigantism is a hallmark of New Zealand's outlying islands (Kavanagh and Burns, 2014; Biddick et al., 2019), larger wind-pollinated flowers might be a by-product of selection acting on seed mass (Fig 3f). But while it is true that flower size and seed mass can positively correlate (Roddy et al., 2021; E□Vojtkó et al., 2022), this explanation faces two key challenges.

First, wind-pollinated plants typically benefit from producing many small, uniovulate, inexpensive flowers. This is because numerous flowers can sample more of the airstream and maximize pollen capture and seed production (Sakai and Sakai, 1995; Friedman and Barrett, 2011). According to this model, producing larger, more expensive flowers would reduce maternal fitness. This could be prevented only if island plants possessed more resources available for flower and seed production than their mainland relatives, allowing them to produce larger flowers and seeds without reducing flower number.

Second, larger seeds can coevolve with smaller flowers. Larger seeds can lead to increased within-fruit sibling competition. One of the strategies adopted by plant species to counter sibling competition is to reduce the number of seeds per fruit (Bawa, 2016). While this potentially reduces fitness, it also reduces flower and pollinator investment, allowing plants to produce small flowers that are wind-pollinated or that rely on generalist pollinators (Bawa et al., 2019). In other words, as seed size increases, flower size of wind-pollinated plants might decline, which is not what we observe. Again, perhaps insular wind-pollinated plants allocate resources differently than their mainland counterparts, promoting consistent positive flower/seed correlations. The reason behind it though remains unclear.

Finally, why animal- and wind-pollinated species should exhibit different island syndromes is puzzling. Differences in the agents of pollination may cause the two groups to follow different evolutionary trajectories. But beyond pollination mode, the two groups seem rather heterogeneous. For example, they both contain animal- and wind-dispersed species spanning multiple plant families, with several families featuring in both groups. It is therefore unclear why traits performing functions unrelated to pollination (e.g. seed dispersal) should evolve according to pollinator-selected traits. This difference may just be an idiosyncrasy of our system. Further studies should be conducted on other island systems to test this possibility.

Burns (2019) proposed that flower size may follow the island rule because of flower-pollinators size-coupling. Considering that size-coupling is an important aspect of plant-pollinator mutualism in specialized flowers (Dalsgaard et al. 2009; Maglianesi et al. 2014; Biddick and Burn, 2018), a reduction in pollinators' diversity and size range could select for reduced flower diversity, causing specialized flowers to follow the island rule (Hiraiwa and Ushimaru, 2017; Burns, 2019). While intriguing, we were not able to test this hypothesis as most of our species possessed open, radial, generalist flowers that would likely not comply

with size changes in pollinators (Faure et al., 2022). As pollinator specialists are rare on islands (Olesen et al., 2002; Traveset et al., 2016; Wang et al., 2020), testing this hypothesis would likely require a global dataset.

Our analysis encompasses only a portion of the Southwest Pacific. First, the study does not include any tropical islands. Ecologically, tropical systems might operate differently than non-tropical ones. For instance, while pollination networks seem to be structurally similar in tropical and non-tropical areas (Vizentin-Bugoni et al., 2018), many plant traits follow a latitudinal gradient, including flower morphological diversity (Currie and Paquin, 1987; Chen et al., 2017; Chartier et al., 2021). Additionally, tropical systems are underrepresented in the literature (Culumber et al., 2019). Secondly, our study focuses on small, isolated archipelagos with relatively small species pools. As the ecological and evolutionary dynamics of islands vary markedly with area and isolation (MacArthur and Wilson, 1967; Whittaker et al., 2023), these results may not apply to larger and less isolated archipelagos.

In this study, we accounted for phylogenetic relatedness through paired taxonomic comparisons and by adding taxonomic family as a random effect in our mixed models. To make sure that flower size evolution was widespread among flowering plants we included multiple families and two mainland source pools. However, accounting for relatedness using a systematic approach, such as a phylogenetic generalized least square model, would have likely yielded more accurate results. This was not possible as a well-resolved phylogeny for the investigated species is not currently available.

In this study, we focused on many island/mainland pairs of species, spanning several families. However, many of the families included in the analysis were only represented by one or a few species, making it difficult to evaluate within family trends. Moreover, focusing on island/mainland pairs implies that we did not account for intraspecific variance. It is

possible that accounting for such variance would alter the observed patterns. Finally, while our study focused on flower size, future research should aim for a multi-trait approach capable of encompassing the plant island syndrome in its entirety.

In conclusion, we provided the first test for the island rule in flowers, and the first evidence of *in-situ* evolution of flower size on islands. Results indicate that, while *in situ* evolution of flower size is widespread on islands in the Southwest Pacific, species belonging to different pollination modes exhibit markedly different evolutionary trajectories. Flower size may evolve as a by-product of selection acting on non-flower correlated traits. These results combine with a growing body of literature investigating the island syndrome in plants (Burns, 2019; Schrader et al., 2021; Delavaux et al., 2021; Meudt et al., 2021; Zizka et al., 2022; Whittaker et al., 2023), and provide a much-needed insight into the evolution of plants on islands.

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Ethics

This work did not require ethical approval from a human subject or animal welfare committee.

Declaration of AI use

We have not used AI-assisted technologies in creating this article.

Data availability Statement

Code, plant species lists, flower traits measured, and models used for the analysis are available in the supplementary materials of this article.

Conflict of Interest Declaration

The authors declare no conflict of interest.

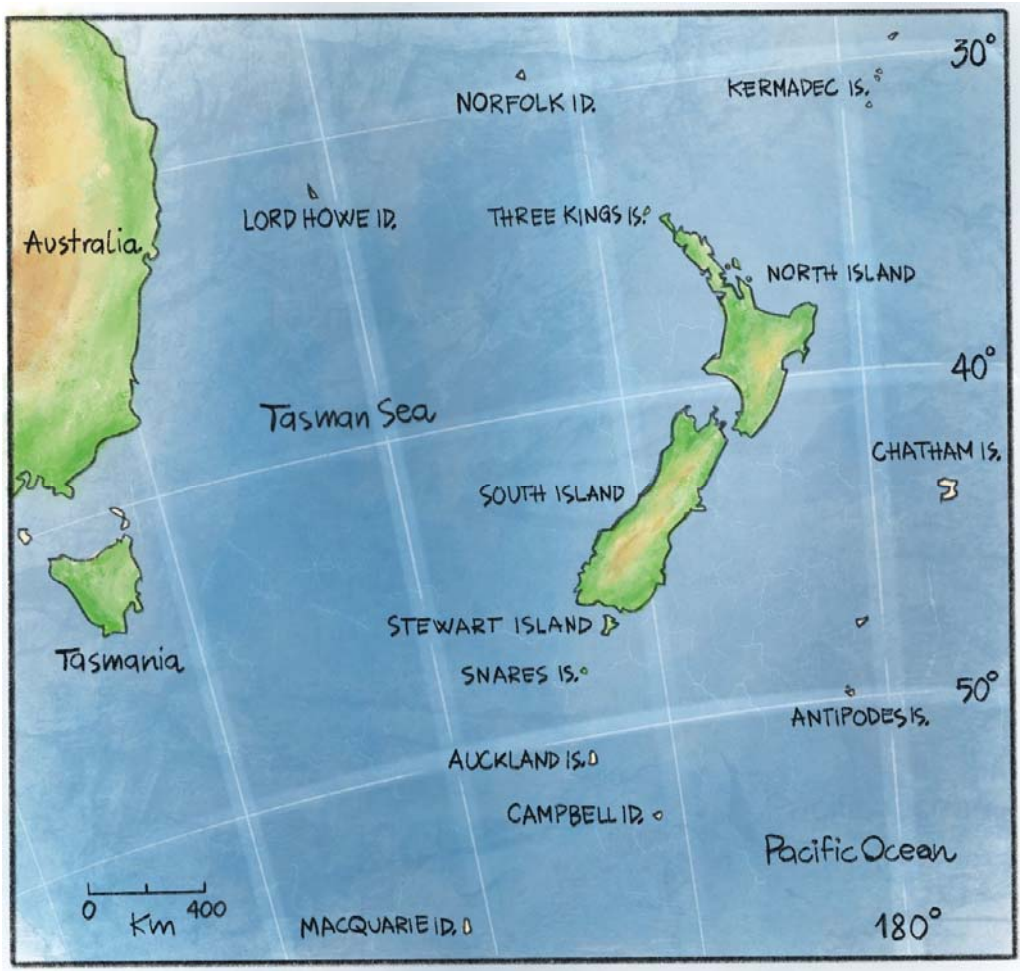
Figure legends

Figure 1 Map of the studied archipelagos.

Figure 2 LR of flower size (y-axis) varying as a function of log mainland values (x-axis) for a) all flowers, b) animal-pollinated and c) wind-pollinated flowers. Each point denotes an island/mainland pairing. A horizontal line intercepting the y-axis at 0 denotes morphological isometry. For all and animal-pollinated flowers, the slope is significantly smaller than 0, giving support for the island rule. For wind-pollinated flowers, the slope does not vary significantly from 0, but most points are above the horizontal line, indicating that island flowers are larger than their mainland relatives. Opposing arrows denote the island rule. Single, upward arrows denote gigantism.

Figure 3 LR of flower size (fsLR), leaf area (laLR) and seed mass (smLR) (y-axes) varying as a function of log mainland values (x-axis) for animal-pollinated (a-c) and wind-pollinated (d-f) species. Each point denotes an island/mainland pairing. A horizontal line intercepting the y-axis at 0 denotes morphological isometry. For animal-pollinated species, flower size and leaf area follow the island rule while seed mass follows no pattern. For wind-pollinated species, flower size and seed mass evolve toward gigantism while leaf area follows no pattern. Opposing arrows denote the island rule. Single, upward arrows denote gigantism.

Fig. 1


30°
NORFOLK ID.
KERMADEC IS.
LORD HOWE ID.
THREE KINGS IS.
Australia
NORTH ISLAND
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Tasman Sea
CHATHAM IS.
SOUTH ISLAND
STEWART ISLAND
Tasmania
SNARES IS.
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ANTIPODES IS.
AUCKLAND IS.
CAMPBELL ID.
Pacific Ocean
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MACQUARIE ID.
180°

Fig 2.

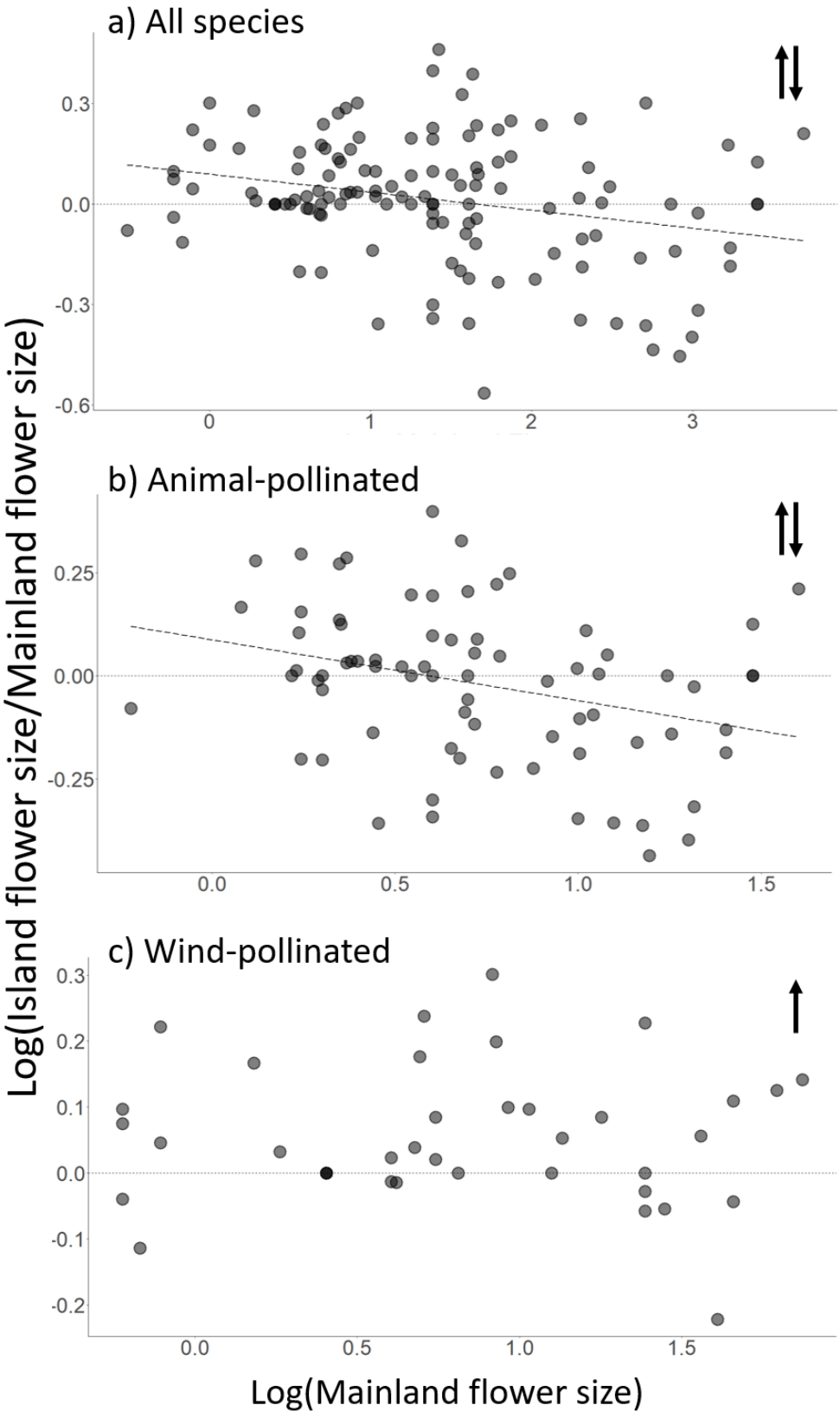
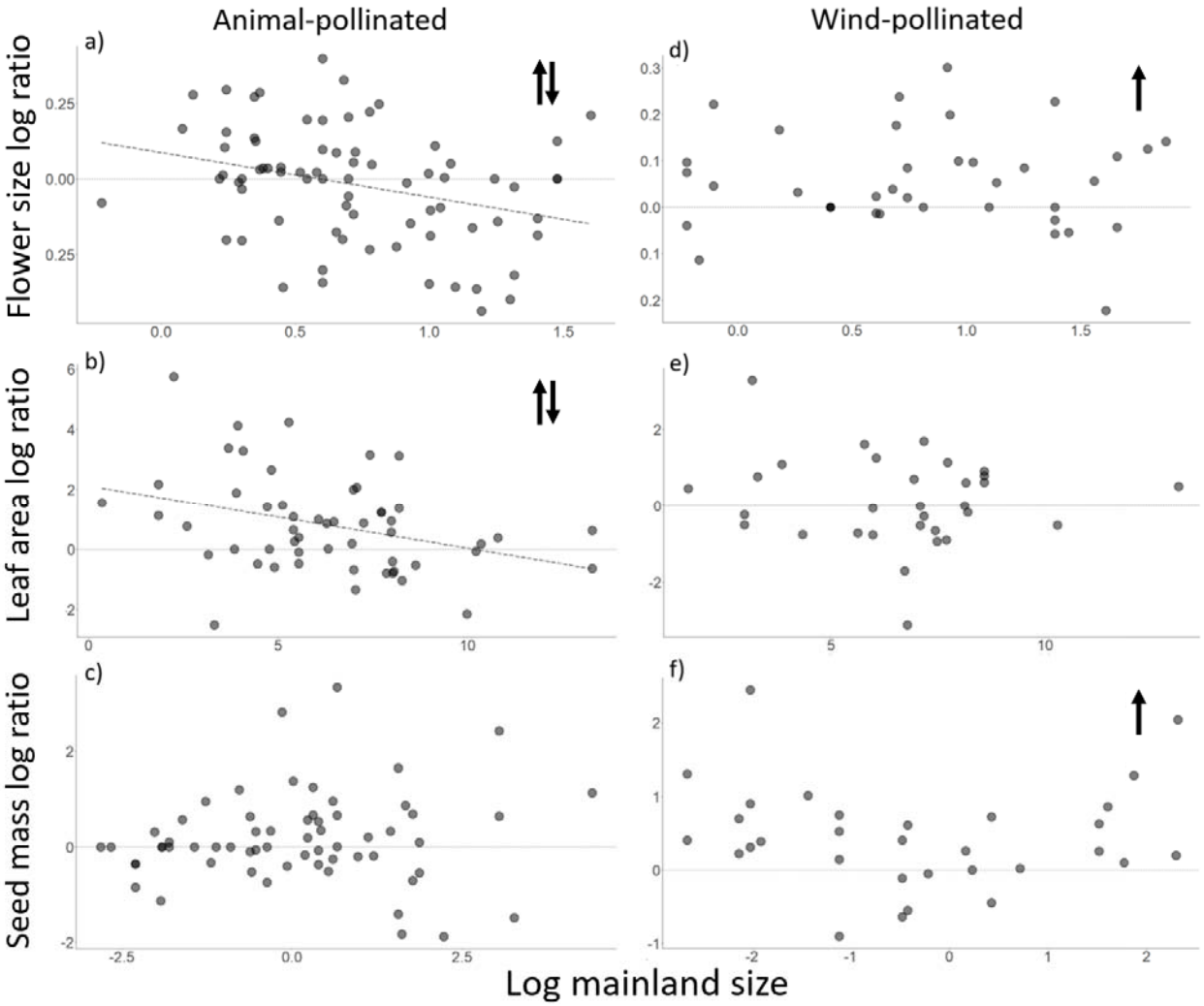

a) All species
0.3
0.0
-0.3
-0.6
0
1
2
3
b) Animal-pollinated
0.25
0.00
-0.25
0.0
0.5
1.0
1.5
c) Wind-pollinated
0.3
0.2
0.1
0.0
-0.1
-0.2
0.0
0.5
1.0
1.5
Log(Island flower size/Mainland flower size)
Log(Mainland flower size)

Fig 3.


Animal-pollinated
Wind-pollinated
a)
b)
c)
d)
e)
f)
Flower size log ratio
Leaf area log ratio
Seed mass log ratio
Log mainland size