Flower size evolution in the Southwest Pacific

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Abstract

The island rule is arguably the most controversial topic in evolutionary biogeography. Previous work has focused almost exclusively on vertebrates. Little is known about the island rule in plants, and no previous study has tested for the island rule in flower size. Here, we provide the first test of the island rule in flowers. Using a newly derived dataset from the Southwest Pacific, we tested whether animal-pollinated and wind-pollinated flowers follow the island rule, or whether they exhibit directional size changes (i.e. gigantism or dwarfism). Results indicate that animal-pollinated flowers follow the island rule, while wind-pollinated flowers do not. Instead, they became consistently larger on islands. We conclude that, while *in situ* evolution of flower size is widespread on islands in the Southwest Pacific, species belonging to different pollination syndromes exhibit markedly different evolutionary trajectories.

Keywords

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

Introduction

Evolutionary size changes are common on islands. After island colonization, some organisms get bigger, such as the Moas of New Zealand and the elephant birds of Madagascar. Paradoxically, other organisms get smaller, such as the pygmy elephants of the Mediterranean islands and the hobbit of Flores (Benitez-Lopez et al., 2021).

Van Valen recognized that the directionality of body size changes was related to body size itself. He termed this phenomenon ‘island rule’ stating that, after island colonization, small organisms evolve to become larger while large organisms evolve to become smaller (Van Valen, 1973; Lomolino et al., 2012). Whether the island rule provides a general explanation for the evolutionary trajectories of island life has been fiercely debated for decades (Lomolino, 2005; Meiri et al., 2008; Faurby and Svenning, 2016; Itescu et al., 2018; Rebouças et al., 2018; Lokatis and Jeschke, 2018; Benitez-Lopez et al., 2021). To date, the island rule remains one of the most controversial topics in biogeography.

Most work on the island rule focuses on animals, mainly vertebrates (Meiri et al., 2008; Benitez-Lopez et al., 2021; Ciarle et al., 2023; Whittaker et al., 2023). Little is known about the island rule in plants (Burns, 2019). Studies conducted in the Southwest Pacific found evidence for the island rule in plant stature and leaf area but not in seed size (Kavanagh and Burns, 2014; Biddick et al., 2019). Similar evolutionary trajectories might be followed by other plant traits, including flower size. Differences in the size of flowers between island and mainland populations have been investigated in the past (Bernardello et al., 2001; Newstrom and Robertson, 2005; Hetherington-Rauth and Johnson, 2020). However, no previous study has tested for the island rule in flower size.

Two main evolutionary processes may cause flower size to follow the island rule. One is the reduction of pollinator diversity and size range on islands. Considering that size-coupling is an important aspect of plant-pollinator mutualism (Biddick and Burn, 2018), a

reduction in pollinators' diversity and size range could select for reduced flower diversity, causing animal-pollinated flowers to follow the island rule (Hiraiwa and Ushimaru, 2017; Burns, 2019). Under this hypothesis, only animal-pollinated flowers should be under selection. Wind-pollinated flowers should not differ in size when compared to their mainland relatives.

Alternatively, changes in flower size could be a by-product of selection acting on a non-flower correlated trait. Since plant traits 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), flower size could follow the island rule simply because of its allometric relationships. Under this hypothesis, both animal- and wind-pollinated island flowers should differ from their mainland relatives.

Distinct plant lineages will respond differently to insular selective pressures. For example, the genetic, morphology and evolutionary history of certain taxonomic families makes 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 the island rule in flower size, it is vital to include multiple plant lineages with different pollination syndromes, evolutionary histories and breeding systems spanning multiple archipelagos.

In this study, we used a phylogenetic comparative approach to test whether island animal-pollinated and wind-pollinated flowers follow the island rule. Specifically, using a newly derived dataset representing 131 independent colonization events on 10 archipelagos

in the Southwest Pacific, we tried to answer the following questions: I) Do Island animal-pollinated and wind-pollinated flowers evolve to follow the island rule? II) Do they evolve to become larger or smaller? III) Do flowers with different pollination syndromes follow different evolutionary trajectories?

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 mainlands (i.e. New Zealand and Australia) would respond differently to insular environments.

Species selection

To test whether island animal- and wind-pollinated flowers follow the island rule, 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, 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 part 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 collected glume length. For dimorphic taxa (e.g. Rubiaceae, genus *Coprosma*) we characterized both male and female flowers.

For the analysis, 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, 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 S3).

We extracted floral traits 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 wind-pollinated and animal-pollinated island flowers followed the island rule, we computed a log ratio (LR) for each island/mainland pair as log(mean island flower size/mean mainland flower size). We then conducted two separate reduced major axis regressions. We used LR values as dependent variables and average values of mainland relatives as independent variables. 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 LR ratio, with island flower size as the dependent variable and mainland flower size as the independent variable. Slopes indistinguishable from zero would denote morphological isometry. Intercepts above or below zero would be evidence for gigantism or dwarfism respectively (Burns et al., 2012).

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 animal-pollinated and wind-pollinated island flowers were consistently larger or smaller than their mainland relatives, we used one-sided t-tests to determine whether mean LR values differed significantly from zero. Kruskal-Wallis analysis of variance was used to assess significant differences in LR 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).

Animal-pollinated flowers followed the island rule, with a slope that was weakly but significantly lower than 0 (n = -0.17, 95% confidence interval = -0.39, -0.05; p-value = 0.01) (Fig 2a). Wind-pollinated flowers did not follow the island rule, with a slope that was not significantly different from 0 (n = -0.01, 95% confidence interval = -0.13, 0.10; p-value = 0.81) (Fig2b). Results 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 S1).

Animal-pollinated flowers were not consistently larger or smaller than mainland relatives (n = 87, LR mean = -0.005, t = 0.15, p-value = 0.82). Conversely, wind-pollinated

flowers exhibited a trend toward gigantism, being generally larger than mainland relatives (n = 39, LR mean = 0.060, t = 3.28, p-value = 0.002). For animal-pollinated flowers, the LR mean did not vary significantly among mainland sources, taxonomic families and degrees of taxonomic differentiation. However, it did vary among breeding systems and islands (Figure S1, 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 S1, Table S3).

Discussion

We provided the first test for the island rule in flowers and the first evidence of *in-situ* evolution of flower size on islands. The size of flowers both obeyed and disobeyed the island rule, and species with different pollination syndromes followed different evolutionary trajectories. We found significant, albeit weak, support for the island rule in animal-pollinated flowers. Conversely, wind-pollinated flowers did not follow the island rule but were consistently larger on islands. This pattern was robust across breeding systems, mainland sources, degree of taxonomic differentiation, taxonomic families and islands.

Animal-pollinated flowers obey the island rule. Perhaps this is because of reduced pollinator diversity on islands. As pollinator diversity declines, so should the overall size range of pollinator species (Burns, 2019). Size coupling is an important aspect of pollination mutualisms, as smaller flowers tend to be pollinated by smaller pollinators and larger flowers by larger pollinators (Kuriya et al., 2015; Biddick and Burn, 2018). Consequently, the reduced size range of island pollinators may in turn reduce the flower-size diversity of animal-pollinated island flowers.

This explanation faces two key challenges. First, we assume that pollinator size follows the island rule, but no one has ever tested for the island rule in insect or vertebrate

pollinators in the Southwest Pacific (Burns, 2019). Secondly, plant stature and leaf area were shown to follow the island rule (Biddick et al., 2019). As flower size scales positively with these plant traits (Lambrecht and Dawson, 2007; Gomez et al., 2009; E-Vojtkó et al., 2022; Genty et al., 2023), animal-pollinated flower size may follow the island rule just as a by-product of selection acting of plant stature and/or leaf area. However, trait correlation could explain the evolution of both animal-pollinated and wind-pollinated flowers, in which case the reason why these groups evolve differently on islands becomes puzzling. Biddick et al. (2019) did not account for pollination syndrome, and it is therefore possible that animal-pollinated and wind-pollinated plant species exhibit different patterns in stature and leaf area.

Results for animal-pollinated plants varied significantly among islands and breeding systems (Figure S1). Differences among islands in animal-pollinated plants could be explained by different pollinator communities. For example, Campbell Island hosts various plants with spectacular, large inflorescences (Lord et al., 2013; Buxton et al., 2019). The nocturnal weta (*Notoplectron campbellensis)*, a giant flightless cricket, is thought to play an important role in their pollination (Lord et al., 2013). The Antipodes Islands mostly lack plants with large inflorescences (Ciarle and Burns, 2023). Accordingly, they also lack an endemic species of weta (Richards, 1974).

Differences between dimorphic and monomorphic plants in animal-pollinated species were unexpected. Larger flowers in males of dimorphic animal-pollinated island plants may 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 syndromes to follow different evolutionary trajectories (Harris and Pannell, 2008; Liu et al., 2021; Roddy et al., 2021; but see Midgley, 2022).

Wind-pollinated flowers did not follow the island rule but were consistently larger on islands. Larger wind-pollinated flowers might be a by-product of selection acting on a correlated trait. Flower size correlates with other plant traits (Bawa et al., 2019; Roddy et al., 2021; E-Vojtkó et al., 2022), and thus selection acting on a correlated trait could result in the evolution of flower size (Niklas, 1994; Burns et al., 2012).

On islands, seeds consistently become larger (Kavanagh and Burns, 2014; Biddick et al., 2019). Larger seeds might constrain the plant into producing larger fruits and flowers (Sakai and Sakai, 1995). Conversely, larger seeds may 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 also decline, which is not what we observe. 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.

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 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.

We encourage future work to seek alternative explanations. We currently lack alternative hypotheses to explain the *in-situ* evolution of island flowers, likely due to most peculiarities of such flowers being viewed as assembly rules (i.e. a products of biased colonization/establishment) rather than evolutionary processes (Lord, 2015; Pannell et al., 2015; Burns, 2019; Hetherington-Rauth and Johnson, 2020). Finally, while our study focused exclusively 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 syndromes exhibit markedly different evolutionary trajectories. 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 (y-axis) varying as a function of log mainland values (x-axis) for a) animal-pollinated and b) wind-pollinated flowers. Each point denotes an island/mainland pairing. A horizontal line intercepting the y-axis at 0 denotes morphological isometry. For 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.

Fig. 1

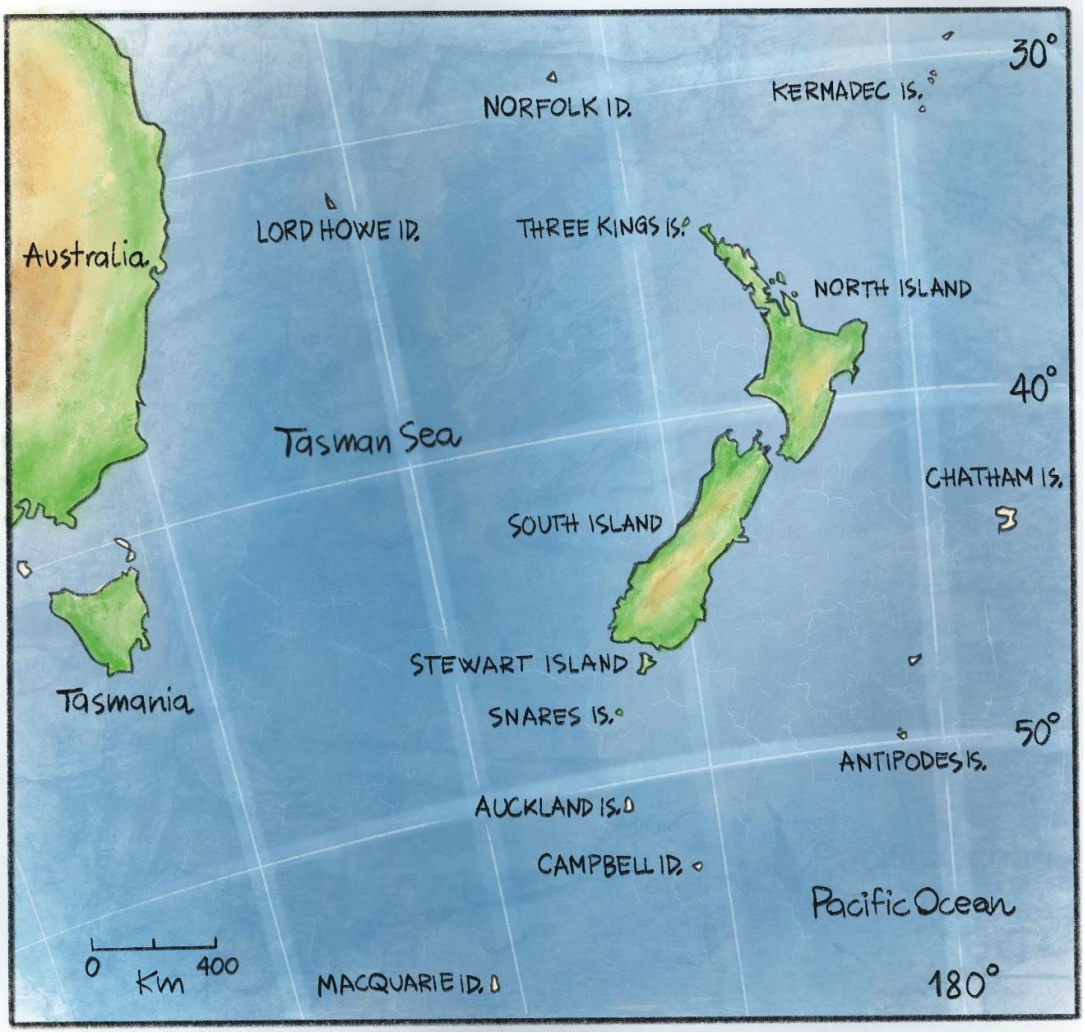
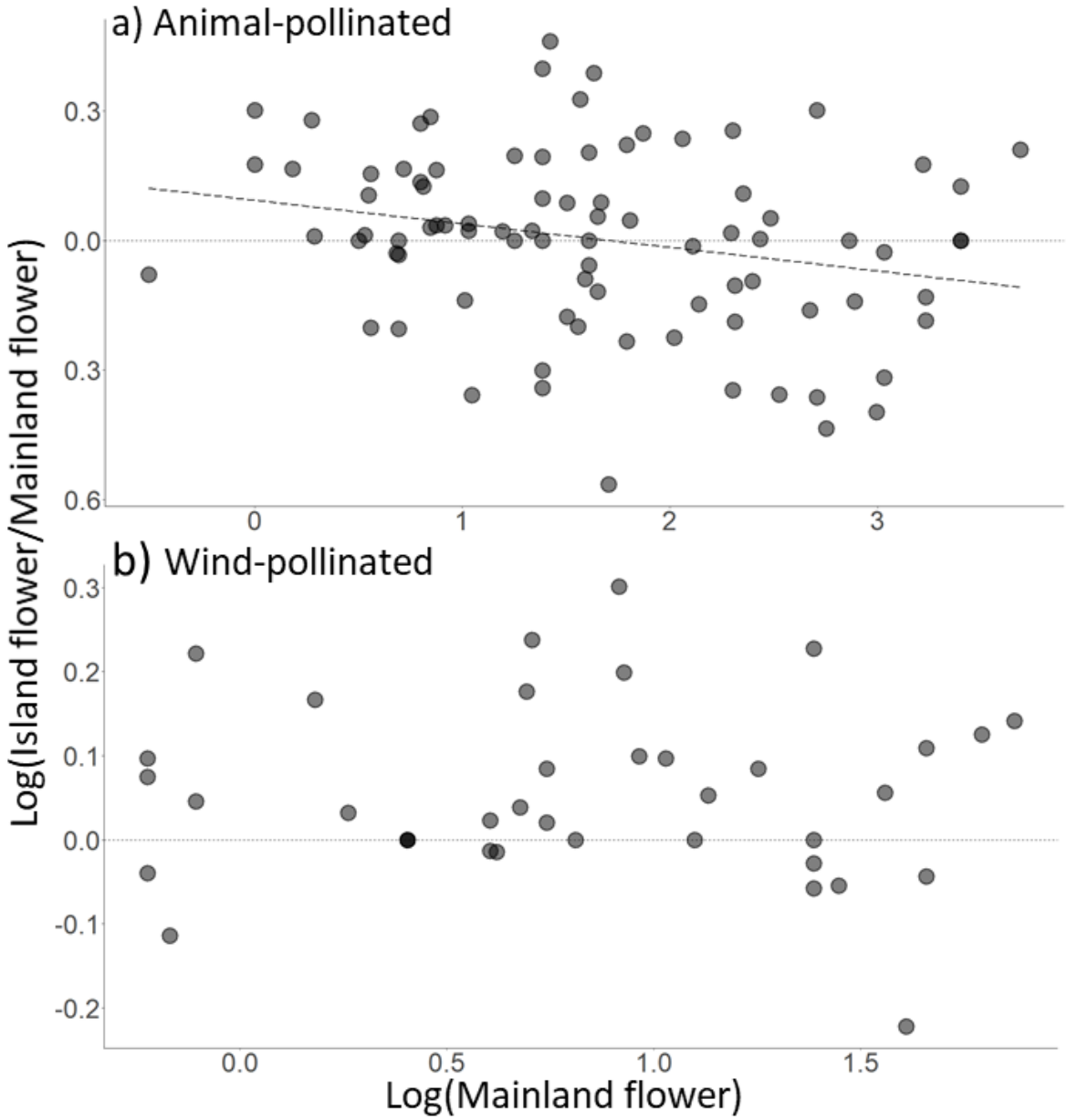

30°
NORFOLK ID.
KERMADEC IS.
LORD HOWE ID.
THREE KINGS IS.
Australia
NORTH ISLAND
40°
Tasman Sea
CHATHAM IS.
SOUTH ISLAND
STEWART ISLAND
Tasmania
SNARES IS.
50°
ANTIPODES IS.
AUCKLAND IS.
CAMPBELL ID.
Pacific Ocean
0 Km 400
MACQUARIE ID.
180°

Fig 2.


a) Animal-pollinated
0.3
0.0
0.3
0.6
0
1
2
3
b) 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/Mainland flower)
Log(Mainland flower)