










Autofertility and self-compatibility moderately benefit island colonization of plants

Mialy Razanajatovo¹  Mark van Kleunen^{1,2}  Holger Kreft^{3,4} 
Wayne Dawson⁵  Franz Essl^{6,7}  Jan Pergl⁸  Petr Pyšek^{8,9} 
Marten Winter¹⁰  Patrick Weigelt³ 

¹Ecology, Department of Biology, University of Konstanz, Konstanz, Germany

²Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, China

³Biodiversity, Macroecology & Biogeography, University of Göttingen, Göttingen, Germany

⁴Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen, Germany

⁵Department of Biosciences, Durham University, Durham, United Kingdom

⁶Division of Conservation, Vegetation and Landscape Ecology, University of Vienna, Wien, Austria

⁷Department of Botany and Zoology, Centre for Invasion Biology, Stellenbosch University, Matieland, South Africa

⁸Department of Invasion Ecology, Institute of Botany, The Czech Academy of Sciences, Průhonice, Czech Republic

⁹Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic

¹⁰German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

Correspondence

Mialy Razanajatovo, Ecology, Department of Biology, University of Konstanz, Universitätsstrasse 10, D-78457 Konstanz, Germany.
Email: mialy.razanajatovo@uni-konstanz.de

Funding information

Austrian Science Fund, Grant/Award Number: I 3757-B29; Deutsche Forschungsgemeinschaft, Grant/Award Number: 264740629, FZT 118 and RA 3009/1-1; Akademie Věd České Republiky, Grant/Award Number: RVO 67985939; Grantová Agentura České Republiky, Grant/Award Number: 14-36079G

Abstract

Aim: The current geographical distribution of species largely reflects colonization success after natural long-distance dispersal or introduction by humans. Plants with selfing ability should have an advantage when establishing on islands where mates and pollinators are limited (Baker's law). However, high percentages of dioecious and self-incompatible species have been reported for some islands, possibly resulting from post-colonization evolution. Given that such evolution is less likely to apply to alien species recently introduced to islands by humans, tests of Baker's law on islands need to consider both native and naturalized alien species.

Location: Global.

Time period: Undefined.

Major taxa studied: Angiosperms.

Methods: To test whether the colonization of islands is associated with selfing ability (self-compatibility and autofertility), we combined three comprehensive global databases: one on breeding systems of species, one on island and mainland distributions of native species and one on global naturalization of alien plants. We assigned each of a total of 1,752 species, from 161 angiosperm families, as mainland species, island colonists and/or island endemics (i.e., species that are restricted to islands). To assess potential relationships between island occurrence and selfing ability of species, we used multinomial logistic regressions.

Results: We found that species with high selfing ability were slightly more likely to be island colonist than mainland species. However, selfing ability did not increase the likelihood of being an island endemic in contrast to mainland species. Among island colonists, selfing ability did not differ between species on oceanic and on continental islands or between species native to islands and naturalized on islands.

Main conclusions: We performed a comprehensive test of Baker's law by considering many angiosperm families, using continuous metrics of self-compatibility and autofertility and including both native and naturalized species. We provide global evidence that high selfing ability may foster island colonization of angiosperms.

KEYWORDS

breeding system, exotic species, invasions, island biogeography, mating system, reproductive biology

1 INTRODUCTION

The geographical distribution of species on oceanic islands reflects colonization success after long-distance dispersal, subsequent evolution and radiation and, more recently, introduction by humans (MacArthur & Wilson, 1967; Moser et al., 2018; Whittaker & Fernández-Palacios, 2007). Although identifying the determinants of successful colonization is challenging, especially after rare events of long-distance dispersal, geographical patterns in species traits can provide valuable insights into determinants of colonization success. Baker's law refers to the advantage of species with a capacity for uniparental reproduction when colonizing new habitat after long-distance dispersal and when pollinators are limited (Baker, 1955, 1967). Baker's law may apply to metapopulation dynamics, natural range expansions, biological invasions and, in particular, the colonization of islands (Pannell et al., 2015). When plant propagules arrive on an island, the resulting plants are isolated from their source populations by oceans, and mates are likely to be limiting. In this circumstance, self-compatible species should have an advantage because they can reproduce from a single individual. Moreover, given that animal species in general, and major groups of pollinators in particular, are less frequent on islands than in mainland regions (Barrett, 1996), autofertile plants (i.e., self-compatible plants being able to self-pollinate) should have a particularly strong advantage when establishing on islands.

Baker's law has often been challenged owing to contradictory findings. Many studies found a prevalence of self-compatible species on islands, supporting Baker's law (Bernardello, Anderson, Stuessy, & Crawford, 2001; Chamorro, Heleno, Olesen, McMullen, & Traveset, 2012; Lord, 2015), whereas other studies found relatively high frequencies of self-incompatible and dioecious species in the floras of oceanic islands (Bawa, 1982; Carlquist, 1966; Sakai, Wagner, Ferguson, & Herbst, 1995). This apparent contradiction might result from the evolution of species reproductive traits after establishment (Pannell et al., 2015). On the one hand, the paucity of insect pollinators on islands has been suggested to favour the evolution of floral traits, such as reductions in flower size and anther–stigma separation, that increase selfing in self-compatible plants (Barrett, 1996). On the other hand, outcrossing should be advantageous for establishing in new environments, given that it avoids inbreeding depression and widens the gene pool, thus allowing for local adaptation (Charlesworth & Charlesworth, 1987). The selection of reduced selfing ability and enhanced outcrossing mechanisms, such as dioecy, herkogamy and dichogamy, might therefore be important for the subsequent radiation and diversification of species after establishment on islands (Barrett, 1996).

Recently, Gossenbacher et al. (2017) found a greater proportion of self-compatible species on islands than in mainland regions in a study on > 1,500 species. That study provides strong support for Baker's law, but it was restricted to three angiosperm families and did not look at autofertility, that is, the ability of self-compatible plants to self-pollinate. Moreover, it only differentiated between mainland

and island species, both including and excluding the island endemics, and did not test whether self-compatibility differed between island endemics and non-endemics (i.e., species that are not restricted to islands). In addition to differentiating between endemics and non-endemics among island species, testing Baker's law would benefit from inclusion of naturalized alien species, which established on islands relatively recently (i.e., in the last few centuries), because their potential for major evolutionary post-arrival transitions is minimal. More than 13,000 alien plant species have been introduced by humans to new regions where they have become part of the local flora (Pyšek et al., 2017; van Kleunen et al., 2015), and for most of these species the naturalization events happened in the last two centuries (Seebens et al., 2017, 2018). Therefore, the likelihood for evolutionary changes in self-compatibility and autofertility of these naturalized species is small. However, no study testing the applicability of Baker's law in the colonization of islands has included naturalized species so far; hence, we lack a comprehensive overview of the role of both self-compatibility and autofertility of species across a representative set of angiosperm families in island colonization.

The strength of the association between island colonization and selfing ability might depend on island geological history. Given that continental islands have been connected to the mainland in the past, mates and pollinators might be less likely to be lacking than on the usually much younger and more remote oceanic islands, which have never been connected to the mainland and where all species were new colonizers or their descendants. In line with this, Gossenbacher et al. (2017) found that for Asteraceae, Brassicaceae and Solanaceae, self-compatible species occurred more often on islands than self-incompatible ones did, and that this effect was stronger for oceanic than for continental islands. Whether this also holds true across other angiosperm families remains to be tested.

Selfing ability and other species characteristics associated with breeding system and colonization success are continuous (Raduski, Haney, & Igić, 2012; Razanajatovo et al., 2016), and treating them as such should provide a rigorous test of the relationship between breeding system and island colonization of plant species. Quantitative metrics of breeding-system traits should be more informative than the commonly used qualitative measures, such as self-compatible versus self-incompatible, when addressing general ecological questions related to plant reproductive strategies. However, previous studies testing the role of breeding systems in island colonization mainly relied on qualitative measures. Furthermore, other plant characteristics, such as life history, can be associated with the biogeographical patterns in plant breeding systems (Moeller et al., 2017; Razanajatovo et al., 2016). Therefore, in addition to using continuous metrics of self-compatibility and autofertility, it is important to account for life history when testing the relationship between island colonization and selfing ability.

Here, we combined three comprehensive global databases to test whether plant species with high self-compatibility and autofertility were more likely to occur on islands, as predicted by Baker's law. We assumed that species that colonized islands, either

naturally or after introduction by humans, arrived from the mainland. Thus, we considered that species currently occurring on the mainland and absent from island floras have failed to colonize islands (hereafter referred to as mainland species). Species that occur both on the mainland and on islands are likely to have succeeded in colonizing an island from the mainland (island colonists). Finally, species occurring only on islands are likely to have evolved there after arrival of a colonist ancestor (island endemics). We explicitly consider these different types of plant distributions (i.e., mainland species, island colonists and island endemics) and ask the following questions.

1. Are plant species with high selfing ability more likely to occur on both the mainland and islands than only on the mainland (i.e., to be island colonists)?
2. Are plant species with high selfing ability more likely to occur only on islands than only on the mainland (i.e., to be island endemics)?
3. Among the island colonists, is there a difference in selfing ability between species on oceanic islands and those on continental islands?
4. Is there a difference in selfing ability between species native to islands and those naturalized on islands?

2 METHODS

2.1 Species data

To test whether the colonization of islands by angiosperm species, irrespective of whether they are native or naturalized, is associated with selfing ability, we combined three comprehensive global plant databases: one on breeding systems of species, one on island and mainland distributions of native species (GIFT; <http://gift.uni-goettingen.de>) and one on global naturalization success of alien species (GloNAF; van Kleunen et al., 2015, 2018). To obtain information on the selfing ability of each species in the present study, we used a global database on breeding systems of angiosperms (for details on the compilation, see Razanajatovo et al., 2016). Briefly, selfing ability indices were calculated using fruit set and seed production after different breeding-system treatments. First, a self-compatibility index was obtained by dividing the outcome of self-pollination by the outcome of outcross pollination treatments. Second, an autofertility index was obtained by dividing the outcome of pollinator exclusion by that of outcross pollination treatments. This database includes self-compatibility and autofertility indices calculated for 1,752 angiosperm species from 161 families from all continents except Antarctica.

To obtain information on the native distribution of each species with quantitative breeding-system data on islands and mainlands, we used the Global Inventory of Floras and Traits (GIFT; Weigelt, König, & Kreft, 2017; <http://gift.uni-goettingen.de>), which to date includes regional plant species lists for 1,636 islands and 993 mainland regions globally. Depending on the plant taxonomic group, GIFT covers between 70 and

100% of the terrestrial surface of the world for native plant species. Given that GIFT does not have a global coverage for all species, 61.5% of the species in the present study did not have complete global island/mainland distribution information. For these species, if we had information on their occurrence only on islands, we could not rule out the possibility that they also occur in mainland regions, and if we had information on their occurrence only in mainland regions, we could not rule out the possibility that they occur also on islands. Nevertheless, given the comprehensive coverage of islands in GIFT, it is unlikely that a species occurs on any island, especially oceanic ones, if it is not listed in the floras of the islands included in GIFT. For species occurring on islands, we also obtained information on whether they occur on oceanic and/or continental islands from GIFT. In an additional analysis using a more conservative approach, we excluded species known to occur in either island or mainland regions, but for which information was missing about their occurrence in the other type of region.

To obtain information on the naturalized distribution of the species included in the present study, we used the Global Naturalized Alien Flora (GloNAF version 1.1; Pyšek et al., 2017; van Kleunen et al., 2015, 2018). This database includes 13,168 naturalized plant species and covers 362 islands and 481 mainland regions globally. We checked, for each naturalized species (i.e., listed in GloNAF; $n = 498$), whether it is naturalized on islands and/or in mainland regions.

2.2 Island and mainland occurrence of native and naturalized plant species

Using the information on the geographical distribution of the native and naturalized species from the GIFT and GloNAF databases, we assigned each species with breeding-system data to one of three categories according to their occurrence in mainland and island regions (mainland species, island colonists and island endemics). When a species was known to occur on an island but information was missing for its occurrence in mainland regions, we considered the species as not occurring in mainland regions. When a species was known to occur in mainland regions but information about island occurrences was missing, we assumed that they do not occur on islands.

In a first categorization, we considered each island regardless of whether it is an oceanic island or not. If the species was known to occur only in mainland regions as native or naturalized, we assigned it to mainland species. If a species was known to occur in mainland regions and in at least one island region, we assigned it to island colonists. If a species was known to occur in at least one island region and not known to occur in any mainland region, we assigned it to island endemics. In a second categorization, given that continental islands might have been colonized before they became islands, we assigned species distributions according to their occurrence on oceanic islands only.

2.3 Statistical analysis

To assess the selfing ability of species quantitatively, we used four selfing ability indices: two self-compatibility indices and two

autofertility indices calculated using fruit set and seed production (for details on the calculation of the different indices, see Razanajatovo et al., 2016). To assess potential relationships between island occurrence and selfing ability of species, we used multinomial logistic regressions (Ntzoufras, 2011). We used species distribution on the mainland and islands as a multi-categorical response variable. The response variable had the following three categories: (a) mainland species (species occurring only on the mainland); (b) island colonists (species occurring on both the mainland and islands); and (c) island endemics (species occurring only on islands). As explanatory variables, we used the self-compatibility or the autofertility index of species, scaled to a mean of zero and a standard deviation of one, their life history (annual/biennial or perennial, corresponding to monocarpic and polycarpic, respectively), and the interaction between self-compatibility or autofertility and life history. To account for non-independence of species owing to evolutionary relatedness, we used family as a random factor. We ran multinomial logistic regressions in WinBUGS (Lunn, Thomas, Best, & Spiegelhalter, 2000) from R version 2.15.3 (R Core Team, 2012), using the “R2WinBUGS” package (Sturtz, Ligges, & Gelman, 2005). The model parameters were estimated from Gibbs sampling of Markov chain Monte Carlo using three chains. For each dataset, 50,000 iterations were run after an initial burn-in phase of 1,000 iterations. To reduce the correlation between consecutive samples, only every fifth value was taken per chain. To assess the goodness-of-fit of the models, we compared the model predictions with the data graphically (Korner-Nievergelt et al., 2015). Separately for each category of the response variable (mainland species, island colonists and island endemics), we plotted, for each species, the probability of being in a certain category (i.e., the model predictions) on the x axis, and the observations (0 = not this category; 1 = this category) on the y axis. We added class-wise means of the observations within classes of width 0.1 of the model predictions. We also added the $y = x$ line. If the model fits the data well, the data would be on average equal to the model predictions, that is, the class-wise means should be close to the $y = x$ line.

To test whether autofertility is more strongly related to island occurrence than self-compatibility is, we used a subset of species for which both self-compatibility and autofertility indices were available. We ran similar multinomial logistic regressions as described above and compared the deviance information criterion (DIC) of the model with self-compatibility with the model having autofertility as an explanatory variable. Additionally, we ran multinomial logistic regressions, in which we included both self-compatibility and autofertility indices of species, scaled to a mean of zero and a standard deviation of one, the interaction between self-compatibility and autofertility, life history of the species (annual/biennial or perennial), the interaction between self-compatibility and life history, and the interaction between autofertility and life history as explanatory variables.

To test among the island colonists whether there is a difference in selfing ability between species that occur on oceanic islands and those that occur on continental islands, we fitted logistic regressions using

the `glmer` function of the “lme4” package (Bates, Maechler, Bolker, & Walker, 2015) in R. As the binary response variable, we used whether a species occurs on oceanic islands or not (yes/no). As explanatory variables, we included the self-compatibility or the autofertility index of the species, scaled to a mean of zero and a standard deviation of one, their life history (annual/biennial or perennial), and the interaction between self-compatibility or autofertility and life history. To test whether there is a difference in selfing ability between species native to islands and species naturalized on islands, we built logistic regressions, using the same terms as in the previous model. As the binary response variable, we used whether a species is naturalized on islands or not (yes/no). In these models, we also used family as a random factor. We tested for significance of the fixed terms using log-likelihood ratio tests (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

3 RESULTS

Of the 1,752 plant species included in this study, 1,129 are mainland species, 566 are island colonists, and 57 are island endemics. Of the 623 species occurring on islands, 242 occur on at least one oceanic island, 463 are native on islands, and 285 are naturalized on islands. Given that a species can be native to an island and naturalized on another island, the total number of species native to islands and that of species naturalized on islands do not add up to the total number of species occurring on islands. Given that annual and biennial species were more likely to be island colonists and less likely to be mainland species (Table 1; Supporting Information Figure S1), the results on self-compatibility and autofertility below have been corrected for differences in life history. Graphical assessment of model fits showed that the models fitted the data well (Supporting Information Figures S2–S6).

3.1 Association of island colonists and island endemics with selfing ability

When selfing ability indices based on fruit set were used, we found that species with high self-compatibility and autofertility indices were slightly more likely to be island colonists than mainland species (Table 1). An increase in 0.405 and 0.353 (one standard deviation) in the self-compatibility and autofertility index of a species increased its odds of being an island colonist by a factor of 1.21 and 1.43, respectively (Figures 1a, 2a and 3). Self-compatibility and autofertility, however, did not increase the likelihood of being an island endemic (Table 1; Figures 1b, 2b and 3). When selfing ability indices based on seed production ($n = 419$ for self-compatibility and $n = 284$ for autofertility index) instead of fruit set ($n = 1,184$ for self-compatibility and $n = 868$ for autofertility index) were used, the results were slightly different (compare Figure 1a,b with c,d; and compare Figure 2a,b with c,d). Self-compatibility still increased the likelihood of being an island colonist (Figures 1c and 3), but there was

TABLE 1 Association of island and mainland occurrence of species with selfing ability based on the non-conservative dataset

Multicategorical response variable with mainland species as a reference	Island colonist versus mainland species	Island endemic versus mainland species
Explanatory variables	Mean (2.5%, 97.5%)	Mean (2.5%, 97.5%)
Selfing ability indices based on fruit set		
Analysis with self-compatibility (DIC = 1794.930) [‡]		
Self-compatibility index	0.194 (0.042, 0.352)	0.282 (-0.100, 0.674)
Annual/biennial	1.058 (0.078, 2.093)	-2.126 (-6.017, 0.677)
Self-compatibility index × annual/biennial	0.010 (-0.907, 0.883)	-2.565 (-5.838, 0.409)
Family (random effect)	0.804 (0.420, 1.407)	0.054 (0.024, 0.101)
Analysis with autofertility (DIC = 1,297.600) [†]		
Autofertility index	0.359 (0.177, 0.542)	0.260 (-0.186, 0.672)
Annual/biennial	1.023 (0.200, 1.882)	-1.789 (-5.585, 0.930)
Autofertility index × annual/biennial	-0.063 (-0.632, 0.519)	-2.596 (-6.616, 0.151)
Family (random effect)	0.533 (0.269, 0.959)	0.057 (0.024, 0.109)
Selfing ability indices based on seed production		
Analysis with self-compatibility (DIC = 711.157) [‡]		
Self-compatibility index	0.300 (0.025, 0.582)	0.265 (-0.283, 0.845)
Annual/biennial	1.347 (0.180, 2.691)	1.101 (-1.195, 3.220)
Self-compatibility index × annual/biennial	-0.691 (-1.921, 0.401)	-2.799 (-5.175, -0.642)
Family (random effect)	0.952 (0.33, 2.351)	0.090 (0.024, 0.221)
Analysis with autofertility (DIC = 487.485) [§]		
Autofertility index	0.373 (-0.019, 0.693)	0.227 (-0.507, 0.947)
Annual/biennial	0.931 (-0.146, 2.060)	0.213 (-2.361, 2.317)
Autofertility index × annual/biennial	-0.309 (-1.160, 0.530)	-2.942 (-6.217, -0.787)
Family (random effect)	0.642 (0.211, 1.674)	0.095 (0.018, 0.276)

Abbreviation: DIC = deviance information criterion.

Note. The table shows logistic regression coefficients of four multinomial logistic regressions testing how the likelihood of being island colonists and island endemics compared with mainland species depends on the self-compatibility or the autofertility index of species, scaled to a mean of zero and a standard deviation of one, their life history (annual/biennial or perennial), and the interaction between self-compatibility or autofertility and life history. Shown are the mean and the 2.5 and 97.5 percentiles (95% credible intervals) of a sample of 29,400 posterior distributions of each model parameter.

[‡] $n_{\text{mainland species}} = 700$; $n_{\text{island colonists}} = 440$; $n_{\text{island endemics}} = 44$. [†] $n_{\text{mainland species}} = 517$; $n_{\text{island colonists}} = 315$; $n_{\text{island endemics}} = 36$. [‡] $n_{\text{mainland species}} = 207$; $n_{\text{island colonists}} = 199$; $n_{\text{island endemics}} = 13$. [§] $n_{\text{mainland species}} = 141$; $n_{\text{island colonists}} = 133$; $n_{\text{island endemics}} = 10$.

no relationship between the likelihood of being an island colonist and autofertility (Table 1; Figures 2c and 3). Overall, there was no interaction between self-compatibility or autofertility and life history (Table 1).

3.2 Association of the occurrence of species on oceanic versus continental islands with selfing ability

When only oceanic islands were considered, there was a weak but detectable positive relationship between the likelihood of being an island colonist (instead of a mainland species) and autofertility, but

self-compatibility did not increase the likelihood of being an island colonist (compare Table 1 with Supporting Information Table S1; and compare Figures 1 and 2 with Supporting Information Figure S7). The positive relationship between the likelihood of being an island colonist and autofertility tended to be weaker for annual and biennial species than for perennial species, as indicated by an interaction between autofertility index based on seed production and life history (Supporting Information Table S1). Among the island colonists, self-compatibility and autofertility did not differ between species that occur on oceanic islands and species that occur on continental islands (Table 2).

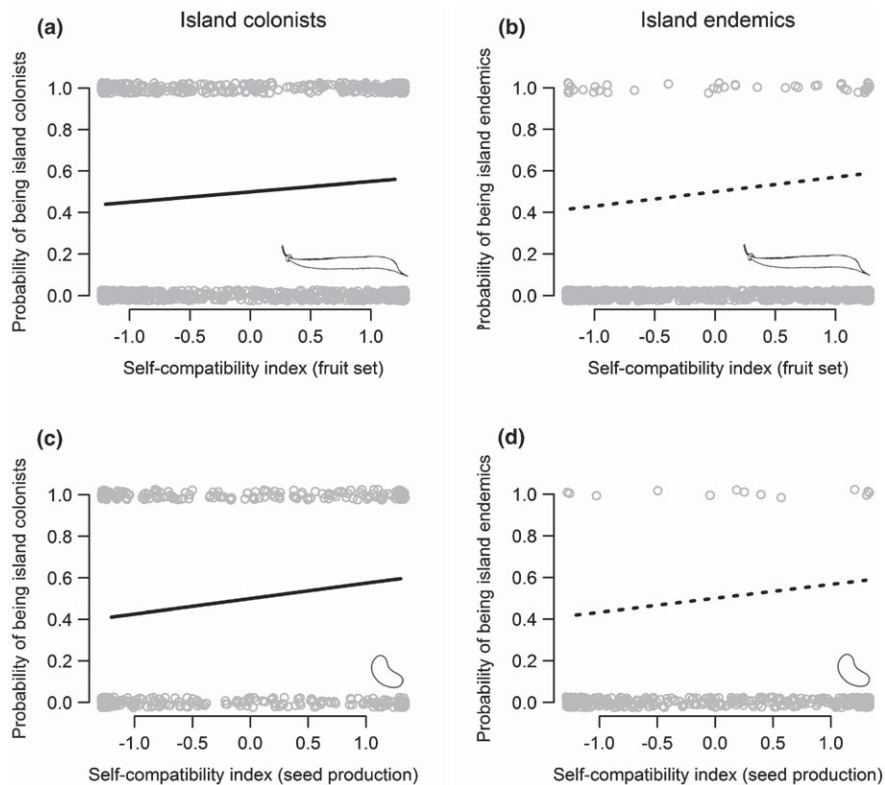


FIGURE 1 Island and mainland occurrence of plant species in relationship to self-compatibility based on the non-conservative dataset. (a–d) Results of two multinomial logistic regressions testing how the occurrence of native and naturalized plant species on both the mainland and islands (island colonists) and only on islands (island endemics) compared with only on the mainland depends on self-compatibility of species. Each row corresponds to a model. Selfing ability of species was measured as follows: (a, b) a self-compatibility index calculated based on fruit set ($n = 1,184$); or (c, d) a self-compatibility index calculated based on seed production ($n = 419$). Self-compatibility indices were standardized to a mean of zero and a standard deviation of one. Sample sizes refer to the total number of species from individual studies in the breeding system database. Continuous curves and dotted curves indicate that the posterior distribution of the model parameter overlaps with zero and does not overlap with zero, respectively

3.3 Association of the occurrence of native versus naturalized species on islands with selfing ability

Among the island colonists, species native to islands and species naturalized on islands did not differ in their degrees of self-compatibility and autofertility (Table 3).

3.4 Autofertility versus self-compatibility as a driver of island occurrence

Within the subset of species for which both self-compatibility and autofertility indices were available, when indices were based on fruit set we found that there was a tendency for species with high self-compatibility and autofertility indices to be island colonists rather than mainland species. However, the DIC of the model with autofertility was lower than that of the model with self-compatibility (Supporting Information Table S2), indicating a better fit. When indices based on seed production were used, there was no relationship between the likelihood of being an island colonist and autofertility (Supporting Information Table S2). When both self-compatibility and

autofertility indices were included in a model, there was still a positive relationship between the likelihood of being an island colonist and autofertility, at least in the analysis with indices based on fruit set (Supporting Information Table S3).

3.5 Species with incomplete data on mainland and island distribution excluded

In an additional analysis, taking a more conservative approach, when species with incomplete data on mainland and island distribution were excluded, the results were slightly different. Then, species with high autofertility were slightly more likely to be island colonists than mainland species, but there was no relationship between the likelihood of being an island colonist and self-compatibility (compare Table 1 with Supporting Information Table S4; compare Figures 1 and 2 with Supporting Information Figure S8). Moreover, the positive relationship between the likelihood of being an island colonist and autofertility tended to be stronger for annual and biennial species than for perennial species, as indicated by an interaction between autofertility index based on fruit set and life history (Supporting Information Table S4).

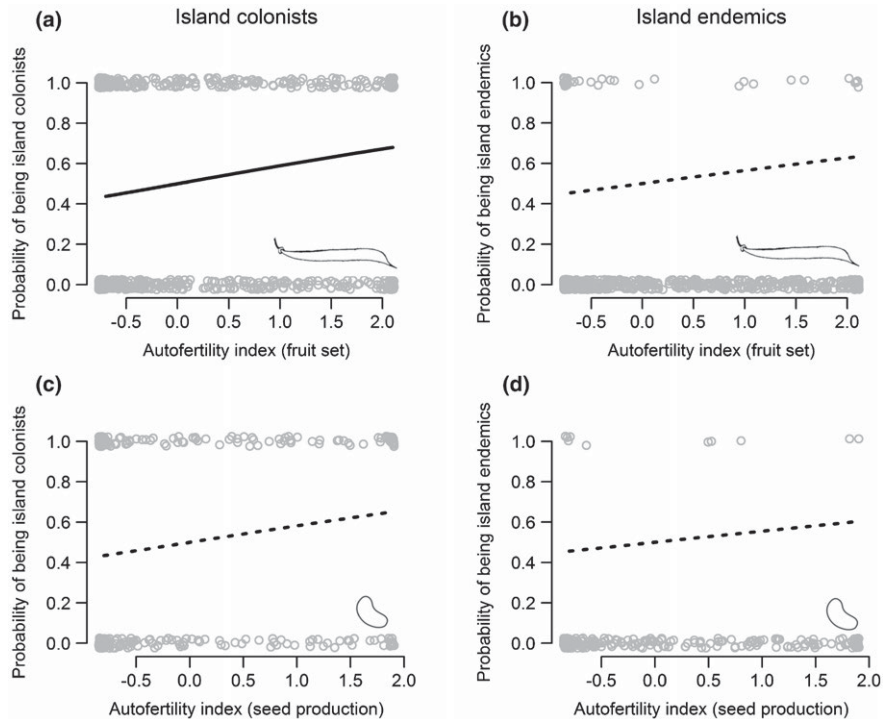


FIGURE 2 Island and mainland occurrence of plant species in relationship to autofertility based on the non-conservative dataset. (a–d) Results of two multinomial logistic regressions testing how the occurrence of native and naturalized plant species on both the mainland and islands (island colonists) and only on islands (island endemics) compared with only on the mainland depends on autofertility of species. Each row corresponds to a model. Selfing ability of species was measured as follows: (a, b) an autofertility index calculated based on fruit set ($n = 868$); or (c, d) an autofertility index calculated based on seed production ($n = 284$). Autofertility indices were standardized to a mean of zero and a standard deviation of one. Sample sizes refer to the total number of species from individual studies in the breeding system database. Continuous curves and dotted curves indicate that the posterior distribution of the model parameter overlaps with zero and does not overlap with zero, respectively

4 DISCUSSION

This is the first test of Baker's law to consider a large set of angiosperm families using continuous metrics of self-compatibility and autofertility and including both native and naturalized species. Despite some variation in the results of the different tests and subsets of data, plant species with high selfing ability, regardless of being native or naturalized, tended generally to be island colonists rather than mainland species, supporting Baker's law. We found similar patterns of association between island occurrence and selfing ability, whether we considered all islands or only oceanic islands.

We found that both self-compatible and autofertile plant species were more likely to be island colonists. Even if self-compatibility and autofertility are not independent, the model with autofertility gave a better fit than the one with self-compatibility (Supporting Information Table S2), and in the model with both self-compatibility and autofertility there was still a positive relationship between the likelihood of being an island colonist and autofertility (Supporting Information Table S3). This suggests that autofertility, which requires both autonomous self-fertilization and self-compatibility (or apomixis), is a stronger driver of island colonization than self-compatibility alone. These findings corroborate previous ones on the

role of autofertility in the colonization of new regions in different contexts. For example, in North America, the over-representation of autonomously selfing plants in populations of *Campanula americana* at the northern and the western range edges has been suggested to be the result of post-glacial recolonization from southern refugia (Koski, Grossenbacher, Busch, & Galloway, 2017). Although a previous review by Pannell et al. (2015) proposed a restriction of the scope of Baker's law to the consequences of mate rather than pollinator limitation, besides the benefit of overcoming mate limitation by self-compatibility, autofertile species also have the advantage of overcoming pollinator limitation when establishing in new regions, especially on islands where the major groups of pollinators are usually scarce.

We did not find an association between selfing ability and island endemics, in contrast to mainland species. With the exception of a few relict endemics (i.e., species that went extinct elsewhere), island endemic species might have arisen from different modes of speciation, such as cladogenetic and anagenetic speciation (Stuessy, Crawford, & Marticorena, 1990). Whichever is the mode of speciation, island endemics might have evolved different breeding systems compared with their mainland ancestors. The colonizers from which the endemics evolved might also have gone through mate and

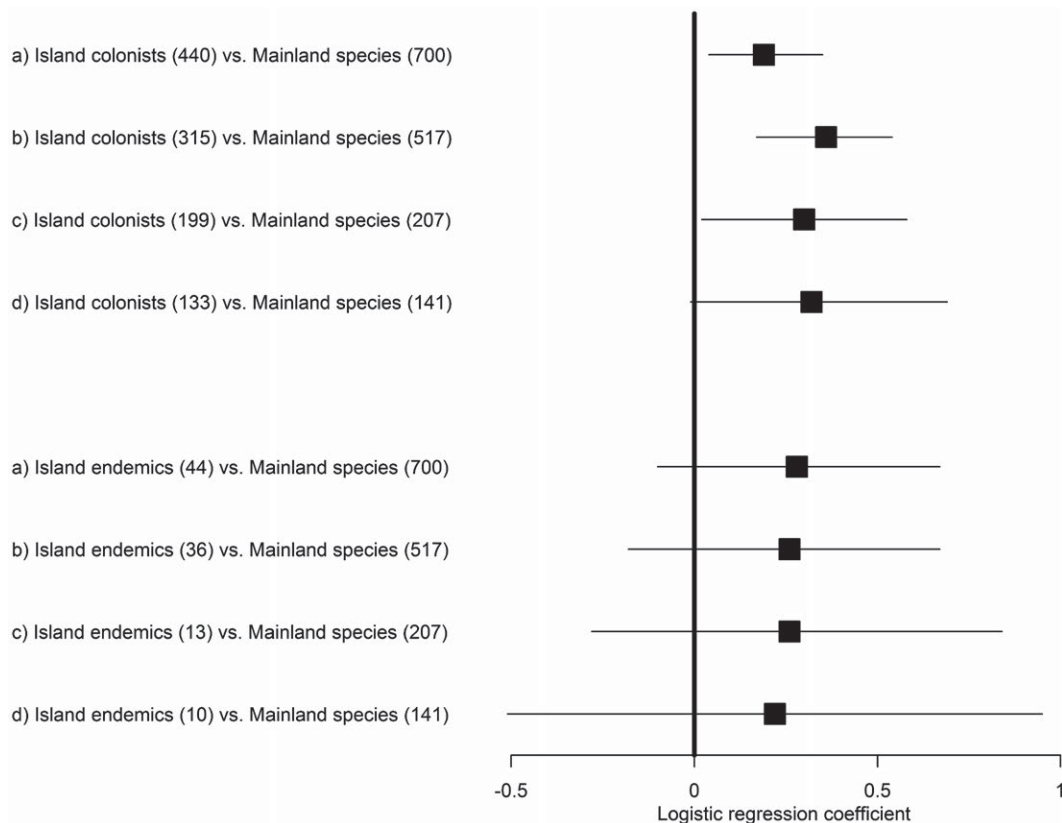


FIGURE 3 Association of island and mainland occurrence of species with selfing ability based on the non-conservative dataset. (a–d) Posterior distribution of the logistic regression coefficients of four multinomial logistic regressions testing how the occurrence of native and naturalized plant species on both the mainland and islands (island colonists) and only on islands (island endemics) compared with only on the mainland (mainland species) depends on selfing ability of species. The selfing ability of species was measured as follows: (a) as an index of self-compatibility calculated based on fruit set ($n = 1,184$); (b) as an index of autofertility calculated based on fruit set ($n = 868$); (c) as a self-compatibility index calculated based on seed production ($n = 419$); or (d) as an autofertility index calculated based on seed production ($n = 284$). Sample sizes, given in parentheses, refer to the total number of species from individual studies in the breeding system database

pollinator limitation filters, and, similar to the island colonists, might have had a higher selfing ability than mainland species. A subsequent evolution of reduced selfing ability and more outcrossing or dioecy compared with the mainland species might then have balanced out the influence of the filtering. Nevertheless, given that island endemics accounted for only a relatively small number of species in our database ($n = 57$), the question of whether island endemic species have generally evolved higher or reduced selfing ability remains to be tested more rigorously.

We found that selfing ability did not differ between native and naturalized island colonists, suggesting that high selfing ability might also help alien species to become naturalized on islands where suitable mates and pollinators are more limiting than on the mainland. Some plants that were introduced by humans to both island and mainland regions from mainland regions have previously been shown to exhibit higher selfing ability on islands than on the mainland, such as for *Nicotiana glauca* on two of the California Channel Islands compared with the California mainland (Schueller, 2004). *Nicotiana glauca* is pollinated by hummingbirds and sunbirds in regions where it was introduced and where such birds are present, but it is largely selfing in regions where bird pollinators are absent, such as on the

island of Tenerife (Ollerton et al., 2012). In contrast, multiple introductions of alien species have been shown to have alleviated mate limitation during establishment (Dlugosch & Parker, 2008; Pannell et al., 2015). In line with these case studies and the previous finding that species with selfing ability were more likely to become naturalized (Razanajatovo et al., 2016), our results also suggest that selfing ability might benefit the establishment of alien species on islands.

Correlations among and trade-offs between different species traits complicate the detectability of Baker's law. Life history and growth form have been shown to play a major role in the geographical distribution of plant species (Moeller et al., 2017; Razanajatovo et al., 2016). We found that annual and biennial species were more likely to be island colonists. Perennial species have more time to reproduce than annual and biennial species, and might therefore overcome mate and pollinator limitations more easily (Pannell et al., 2015). Nevertheless, after accounting for life history, we still found an association between selfing ability and island occurrence. Other reproductive traits, whether associated with selfing ability or not, can also contribute to variation in species distribution patterns. For example, given that polyploidy can be important for the evolution and diversification of the colonists' progeny, polyploid species may have larger

TABLE 2 Association of the occurrence of species on oceanic or continental islands with selfing ability

Explanatory variables	Analysis with self-compatibility			Analysis with autofertility		
	d.f.	χ^2	<i>p</i>	d.f.	χ^2	<i>p</i>
Selfing ability indices based on fruit set						
Selfing ability index	1	0.849	.357	1	0.002	.964
Annual/biennial	1	6.884	.009	1	4.792	.029
Selfing ability × annual/biennial	1	4.153	.041	1	1.497	.221
Random effect	<i>SD</i>	<i>SD</i> _{residuals}	<i>n</i>	<i>SD</i>	<i>SD</i> _{residuals}	<i>n</i>
Family	1.182	1.028	388	1.128	1.005	274
Selfing ability indices based on seed production						
Selfing ability index	1	1.248	.264	1	1.367	.242
Annual/biennial	1	6.053	.014	1	3.963	.046
Selfing ability × annual/biennial	1	3.833	.050	1	2.014	.156
Random effect	<i>SD</i>	<i>SD</i> _{residuals}	<i>n</i>	<i>SD</i>	<i>SD</i> _{residuals}	<i>n</i>
Family	0.725	1.055	171	1.138	0.953	113

Note. Results of four logistic regressions testing how the occurrence of island colonist species on oceanic islands depends on self-compatibility or the autofertility index of species, scaled to a mean of zero and a standard deviation of one, their life history (annual/biennial or perennial), and the interaction between self-compatibility or autofertility and life history. Shown are the degrees of freedom (d.f.), χ^2 values and *p*-values from log-likelihood ratio tests.

TABLE 3 Association of the occurrence of native versus naturalized species on islands with selfing ability

Explanatory variables	Analysis with self-compatibility			Analysis with autofertility		
	d.f.	χ^2	<i>p</i>	d.f.	χ^2	<i>p</i>
Selfing ability indices based on fruit set						
Selfing ability index	1	0.462	.497	1	0.146	.703
Annual/biennial	1	10.123	.001	1	14.039	< .001
Selfing ability × annual/biennial	1	0.028	.867	1	1.254	.262
Random effect	<i>SD</i>	<i>SD</i> _{residuals}	<i>n</i>	<i>SD</i>	<i>SD</i> _{residuals}	<i>n</i>
Family	0.707	1.049	440	0.887	0.989	315
Selfing ability indices based on seed production						
Selfing ability index	1	0.710	.399	1	0.342	.559
Annual/biennial	1	8.735	.003	1	11.980	<.001
Selfing ability × annual/biennial	1	0.044	.833	1	1.746	.186
Random effect	<i>SD</i>	<i>SD</i> _{residuals}	<i>n</i>	<i>SD</i>	<i>SD</i> _{residuals}	<i>n</i>
Family	0.856	1.023	199	0.874	1.010	133

Note. Results of four logistic regressions testing how the naturalization status of island colonist species depends on the self-compatibility or the autofertility index of species, scaled to a mean of zero and a standard deviation of one, their life history (annual/biennial or perennial), and the interaction between self-compatibility or autofertility and life history. Shown are the degrees of freedom (d.f.), χ^2 values and *p*-values from log-likelihood ratio tests.

ranges than the diploid ones (Lowry & Lester, 2006). Clonality can also help species without selfing ability to establish populations in new environments (Pyšek, 1997; Vallejo-Marín & O'Brien, 2007), and this

trait is also implied in the capacity for uniparental reproduction proposed by Baker's law (Pannell et al., 2015). Furthermore, traits related to dispersal ability can confer advantages in the colonization of islands.

The relatively high frequencies of dioecious species on islands may, for example, be linked to fleshy and many-seeded fruits (Vamosi, Zhang, & Wilson, 2007), increasing the number of seeds dispersed by seed dispersal mutualists. Therefore, both dispersal and breeding-system traits can affect colonization success.

Our results were somewhat different depending on whether we included or excluded the species with incomplete data on island/mainland distribution (compare Table 1 with Supporting Information Table S4). If excluded, the association between occurrence on islands and selfing ability was weaker (i.e., less often positive). However, this more conservative dataset might be biased toward island species, because the GIFT database started with the compilation of island floras (Weigelt et al., 2017). Given that only a few mainland species remained in this dataset, that is, most species were island colonists, the comparison between island and mainland occurrences might have been less powerful than when all species were included. Nevertheless, whenever we found an association between island occurrence and selfing ability, it was positive, and thus in line with Baker's law (Supporting Information Table S4).

Our results were also somewhat different depending on whether we used selfing ability indices calculated using fruit set or seed production. Although seed production would be a preferable proxy for maternal fitness, it is challenging in practice to measure seed production, especially for non-herbaceous species. For this reason, compared with seed production, fruit set has been the most commonly measured variable for reproductive success in pollination studies (Knight et al., 2005; Razanajatovo et al., 2016). Nevertheless, fruit set and seed production can show similar patterns, as was found for pollen limitation (Knight et al., 2005). For the subset of species for which we had selfing ability indices based on fruit set and seed production, the two indices were highly correlated (self-compatibility index: Pearson's $r = 0.833$, $p < .0001$, $n = 384$, Supporting Information Figure S9a; and autofertility index: Pearson's $r = 0.835$, $p < .0001$, $n = 263$, Supporting Information Figure S9b). As a result of the much larger sample sizes in our analyses with selfing ability indices based on fruit set compared with those based on seed production (e.g., $n = 1,184$ vs. 419 for self-compatibility index, and $n = 868$ vs. 284 for autofertility index in the non-conservative dataset), the analyses with indices based on fruit set should have more power (van Kleunen, Dawson, Bossdorf, & Fischer, 2014). Furthermore, when we found an association between island occurrence and selfing ability indices based on seed production, it was positive (Figures 1 and 2; Supporting Information S7), thus supporting Baker's law.

5 CONCLUSION

Our comprehensive test of Baker's law shows that selfing ability may influence the colonization of islands by plants, both naturally after long-distance dispersal and with the help of humans. The ability to reproduce is critical for establishment in new environments, and reproductive traits involving the breeding system can be vital. The role of the breeding system might be especially notable in the colonization of islands, because colonists have fewer opportunities

to find mates than on the mainland, and on islands the major groups of pollinators are often impoverished. Our results suggest that both mate and pollinator limitations might act as filters to the successful colonization of islands by plant species.

ACKNOWLEDGMENTS

We thank Dr Fränzi Korner-Nievergelt for statistical advice. M.R., M.v.K. and M.W. thank the German Research Foundation DFG for funding (RA 3009/1-1; 264740629; M.W. via iDiv FZT 118). P.P. and J.P. were supported by project no. 14-36079G Centre of Excellence PLADIAS (Czech Science Foundation) and long-term research development project RVO 67985939 (The Czech Academy of Sciences). F.E. acknowledges funding by the Austrian Science Foundation FWF (project no. I 3757-B29).

ORCID

Mialy Razanajatovo  <https://orcid.org/0000-0001-9181-7363>

Mark van Kleunen  <http://orcid.org/0000-0002-2861-3701>

Holger Kreft  <http://orcid.org/0000-0003-4471-8236>

Wayne Dawson  <http://orcid.org/0000-0003-3402-0774>

Franz Essl  <https://orcid.org/0000-0001-8253-2112>

Jan Pergl  <http://orcid.org/0000-0002-0045-1974>

Petr Pyšek  <http://orcid.org/0000-0001-8500-442X>

Marten Winter  <http://orcid.org/0000-0002-9593-7300>

Patrick Weigelt  <https://orcid.org/0000-0002-2485-3708>

REFERENCES

- Baker, H. G. (1955). Self-compatibility and establishment after "long-distance" dispersal. *Evolution*, 9, 347–349. [10.2307/2405656](https://doi.org/10.2307/2405656) <https://doi.org/10.1111/j.1558-5646.1955.tb01544.x>
- Baker, H. G. (1967). Support for Baker's law—as a rule. *Evolution*, 21, 853–856. <https://doi.org/10.1111/j.1558-5646.1967.tb03440.x>
- Barrett, S. C. (1996). The reproductive biology and genetics of island plants. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351, 725–733. <https://doi.org/10.1098/rstb.1996.0067>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Bawa, K. (1982). Outcrossing and the incidence of dioecism in island floras. *The American Naturalist*, 119, 866–871. <https://doi.org/10.1086/283960>
- Bernardello, G., Anderson, G. J., Stuessy, T. F., & Crawford, D. J. (2001). A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernandez Islands (Chile). *The Botanical Review*, 67, 255–308.
- Carlquist, S. (1966). The biota of long-distance dispersal. IV. Genetic systems in the floras of oceanic islands. *Evolution*, 20, 433–455. <https://doi.org/10.1111/j.1558-5646.1966.tb03379.x>

- Chamorro, S., Heleno, R., Olesen, J. M., McMullen, C. K., & Traveset, A. (2012). Pollination patterns and plant breeding systems in the Galápagos: A review. *Annals of Botany*, 110, 1489–1501. <https://doi.org/10.1093/aob/mcs132>
- Charlesworth, D., & Charlesworth, B. (1987). Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics*, 18, 237–268. <https://doi.org/10.1146/annurev.es.18.110187.001321>
- Dlugosch, K., & Parker, I. (2008). Founding events in species invasions: Genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology*, 17, 431–449. <https://doi.org/10.1111/j.1365-294X.2007.03538.x>
- Grossenbacher, D. L., Brandvain, Y., Auld, J. R., Burd, M., Cheptou, P.-O., Conner, J. K., ... Goldberg, E. E. (2017). Self-compatibility is over-represented on islands. *New Phytologist*, 215, 469–478. <https://doi.org/10.1111/nph.14534>
- Knight, T. M., Steets, J. A., Vamosi, J. C., Mazer, S. J., Burd, M., Campbell, D. R., ... Ashman, T.-L. (2005). Pollen limitation of plant reproduction: Pattern and process. *Annual Review of Ecology, Evolution, and Systematics*, 36, 467–497. <https://doi.org/10.1146/annurev.ecolsys.36.102403.115320>
- Korner-Nievergelt, F., Roth, T., Von Felten, S., Guélat, J., Almasi, B., & Korner-Nievergelt, P. (2015). *Bayesian data analysis in ecology using linear models with R, BUGS, and Stan*. Amsterdam, the Netherlands: Academic Press.
- Koski, M. H., Grossenbacher, D. L., Busch, J. W., & Galloway, L. F. (2017). A geographic cline in the ability to self-fertilize is unrelated to the pollination environment. *Ecology*, 98, 2930–2939. <https://doi.org/10.1002/ecy.2001>
- Lord, J. M. (2015). Patterns in floral traits and plant breeding systems on Southern Ocean Islands. *AoB Plants*, 7, plv095. <https://doi.org/10.1093/aobpla/plv095>
- Lowry, E., & Lester, S. (2006). The biogeography of plant reproduction: Potential determinants of species' range sizes. *Journal of Biogeography*, 33, 1975–1982. <https://doi.org/10.1111/j.1365-2699.2006.01562.x>
- Lunn, D. J., Thomas, A., Best, N., & Spiegelhalter, D. (2000). WinBUGS - A Bayesian modelling framework: Concepts, structure, and extensibility. *Statistics and Computing*, 10, 325–337.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Moeller, D. A., Briscoe Runquist, R. D., Moe, A. M., Geber, M. A., Goodwillie, C., Cheptou, P.-O., ... Winn, A. A. (2017). Global biogeography of mating system variation in seed plants. *Ecology Letters*, 20, 375–384. <https://doi.org/10.1111/ele.12738>
- Moser, D., Lenzner, B., Weigelt, P., Dawson, W., Kreft, H., Pergl, J., ... Essl, F. (2018). Remoteness promotes biological invasions on islands worldwide. *Proceedings of the National Academy of Sciences of the USA*, 115, 9270–9275. <https://doi.org/10.1073/pnas.1804179115>
- Ntzoufras, I. (2011). *Bayesian modeling using WinBUGS*. Hoboken, NJ: John Wiley & Sons.
- Ollerton, J., Watts, S., Connerty, S., Lock, J., Parker, L., Wilson, I., ... Izhaki, I. (2012). Pollination ecology of the invasive tree tobacco *Nicotiana glauca*: Comparisons across native and non-native ranges. *Journal of Pollination Ecology*, 9, 85–95.
- Pannell, J. R., Auld, J. R., Brandvain, Y., Burd, M., Busch, J. W., Cheptou, P. O., ... Grossenbacher, D. L. (2015). The scope of Baker's law. *New Phytologist*, 208, 656–667. <https://doi.org/10.1111/nph.13539>
- Pyšek, P. (1997). Clonality and plant invasions: Can a trait make a difference. In H. de Kroon & J. van Groenendael (Eds.), *The ecology and evolution of clonal plants* (pp. 405–427). Leiden, the Netherlands: Backhuys Publishers.
- Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Kreft, H., ... van Kleunen, M. (2017). Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. *Preslia*, 89, 203–274. <https://doi.org/10.23855/preslia.2017.203>
- R Core Team. (2012). *A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raduski, A. R., Haney, E. B., & Igić, B. (2012). The expression of self-incompatibility in angiosperms is bimodal. *Evolution*, 66, 1275–1283. <https://doi.org/10.1111/j.1558-5646.2011.01505.x>
- Razanajatovo, M., Maurel, N., Dawson, W., Essl, F., Kreft, H., Pergl, J., ... van Kleunen, M. (2016). Plants capable of selfing are more likely to become naturalized. *Nature Communications*, 7, 13313. <https://doi.org/10.1038/ncomms13313>
- Sakai, A. K., Wagner, W. L., Ferguson, D. M., & Herbst, D. R. (1995). Origins of dioecy in the Hawaiian flora. *Ecology*, 76, 2517–2529. <https://doi.org/10.2307/2265825>
- Schueller, S. K. (2004). Self-pollination in island and mainland populations of the introduced hummingbird-pollinated plant, *Nicotiana glauca* (Solanaceae). *American Journal of Botany*, 91, 672–681.
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., ... Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8, 14435. <https://doi.org/10.1038/ncomms14435>
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., ... Essl, F. (2018). Global rise in emerging alien species results from increased accessibility of new source pools. *Proceedings of the National Academy of Sciences of the USA*, 115, E2264–E2273. <https://doi.org/10.1073/pnas.1719429115>
- Stuessy, T. F., Crawford, D. J., & Marticorena, C. (1990). Patterns of phylogeny in the endemic vascular flora of the Juan Fernandez Islands, Chile. *Systematic Botany*, 15, 338–346. <https://doi.org/10.2307/2419187>
- Sturtz, S., Ligges, U., & Gelman, A. (2005). R2WinBUGS: A package for running WinBUGS from R. *Journal of Statistical Software*, 12, 1–16.
- Vallejo-Marín, M., & O'Brien, H. E. (2007). Correlated evolution of self-incompatibility and clonal reproduction in *Solanum* (Solanaceae). *New Phytologist*, 173, 415–421.
- Vamosi, J. C., Zhang, Y., & Wilson, W. G. (2007). Animal dispersal dynamics promoting dioecy over hermaphroditism. *The American Naturalist*, 170, 485–491. <https://doi.org/10.1086/519856>
- van Kleunen, M., Dawson, W., Bossdorf, O., & Fischer, M. (2014). The more the merrier: Multi-species experiments in ecology. *Basic and Applied Ecology*, 15, 1–9. <https://doi.org/10.1016/j.baae.2013.10.006>
- van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., ... Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, 525, 100–103. <https://doi.org/10.1038/nature14910>
- van Kleunen, M., Pyšek, P., Dawson, W., Essl, F., Kreft, H., Pergl, J., ... Winter, M. (2018). The Global Naturalized Alien Flora (GloNAF) database. *Ecology*, in press. <https://doi.org/10.1002/ecy.2542>
- Weigelt, P., König, C., & Kreft, H. (2017). The Global Inventory of Floras and Traits (GIFT) database. Retrieved from <http://gift.uni-goettingen.de>
- Whittaker, R. J., & Fernández-Palacios, J. M. (2007). *Island biogeography: Ecology, evolution, and conservation*. New York, NY: Oxford University Press.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A., & Smith, G. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.

BIOSKETCH

MIALY RAZANAJATOVO is an ecologist whose work investigates the role of reproductive characteristics in the establishment and persistence of plants in novel environments. Mialy's interests have been focused mainly on the naturalization success of alien species but have also included the survival and persistence of species under climate change. Currently, Mialy investigates the importance of phylogenetic distance and the dissimilarity of floral traits in the formation of novel plant–pollinator interactions.

