

1 **Autofertility and self-compatibility moderately benefit island colonization**  
2 **of plants**

3 *Running title:* Selfing ability benefits island colonization

4 **Abstract**

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

13 **Location:** Global.

14 **Time period:** Undefined.

15 **Major taxa studied:** Angiosperms.

16 **Methods:** To test whether the colonization of islands is associated with selfing ability  
17 (self-compatibility and autofertility), we combined three comprehensive global databases: one  
18 on breeding systems of species, one on island and mainland distributions of native species  
19 (GIFT) and one on global naturalization of alien plants (GloNAF). We assigned each of a  
20 total of 1,752 species, from 161 angiosperm families, as mainland species, island colonists or

21 island endemics (i.e. species that are restricted to islands). To assess potential relationships  
22 between island occurrence and selfing ability of species, we used multinomial logistic  
23 regressions.

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

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

33 *Keywords:* Breeding system; exotic species; invasions; island biogeography; mating system;  
34 reproductive biology.

## 35 **Introduction**

36           The geographic distribution of species on oceanic islands reflects colonization success  
37 after long-distance dispersal, subsequent evolution and radiation, and – more recently –  
38 introduction by humans (MacArthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007;  
39 Moser *et al.*, 2018). Although identifying the determinants of successful colonization is  
40 challenging, especially after rare events of long-distance dispersal, geographic patterns in  
41 species traits can provide valuable insights into determinants of colonization success. Baker’s  
42 Law refers to the advantage of species with a capacity for uniparental reproduction when  
43 colonizing new habitat after long-distance dispersal and when pollinators are limited (Baker,  
44 1955, 1967). Baker’s Law may apply to metapopulation dynamics, natural range expansions,  
45 biological invasions and particularly the colonization of islands (Pannell *et al.*, 2015). When  
46 plant propagules arrive on an island, the resulting plants are isolated from their source  
47 populations by oceans, and mates are likely to be limiting. Under such circumstance, self-  
48 compatible species should have an advantage because they can reproduce from a single  
49 individual. Moreover, as animal species in general, and major groups of pollinators in  
50 particular, are less frequent on islands than in mainland regions (Barrett, 1996), autofertile  
51 plants (i.e. self-compatible plants being able to self-pollinate) should have a particularly  
52 strong advantage when establishing on islands.

53           Baker’s Law has often been challenged due to contradictory findings. Many studies  
54 found a prevalence of self-compatible species on islands, supporting Baker’s Law  
55 (Bernardello *et al.*, 2001; Chamorro *et al.*, 2012; Lord, 2015), while other studies found  
56 relatively high frequencies of self-incompatible and dioecious species in the floras of oceanic  
57 islands (Carlquist, 1966; Bawa, 1982; Sakai *et al.*, 1995). This apparent contradiction might  
58 result from the evolution of species reproductive traits following establishment (Pannell *et al.*,

59 2015). On the one hand, the paucity of insect pollinators on islands has been suggested to  
60 favor the evolution of floral traits, such as reductions in flower size and anther-stigma  
61 separation, that increase selfing in self-compatible plants (Barrett, 1996). On the other hand,  
62 outcrossing should be advantageous for establishing in new environments given that it avoids  
63 inbreeding depression and widens the gene pool, thus allowing for local adaptation  
64 (Charlesworth & Charlesworth, 1987). The selection of reduced selfing ability and enhanced  
65 outcrossing mechanisms such as dioecy, herkogamy and dichogamy may therefore be  
66 important for the subsequent radiation and diversification of species following establishment  
67 on islands (Barrett, 1996).

68         Recently, Grossenbacher *et al.* (2017) found a greater proportion of self-compatible  
69 species on islands than in mainland regions in a study on >1,500 species. This study provides  
70 strong support for Baker's Law, but it was restricted to three angiosperm families, and did not  
71 look at autofertility, i.e. the ability of self-compatible plants to self-pollinate. Moreover, it  
72 only differentiated between mainland and island species, both including and excluding the  
73 island endemics, and did not test whether self-compatibility differed between island endemics  
74 and non-endemics (i.e. species that are not restricted to islands). In addition to differentiating  
75 between endemics and non-endemics among island species, testing Baker's Law would  
76 benefit from including naturalized alien species, which established on islands relatively  
77 recently (i.e. in the last few centuries), since their potential for major evolutionary post-arrival  
78 transitions is minimal. More than 13,000 alien plant species have been introduced by humans  
79 to new regions where they have become part of the local flora (van Kleunen *et al.*, 2015;  
80 Pyšek *et al.*, 2017), and most of these species naturalization events happened in the last two  
81 centuries (Seebens *et al.*, 2017; Seebens *et al.*, 2018). Therefore, the likelihood for  
82 evolutionary changes in self-compatibility and autofertility of these naturalized species is  
83 small. However, no study testing the applicability of Baker's Law in the colonization of

84 islands has included naturalized species so far. We hence lack a comprehensive overview of  
85 the role of both self-compatibility and autofertility of species across a representative set of  
86 angiosperm families of angiosperms in island colonization.

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

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

108           Here we combined three comprehensive global databases to test whether plant species  
109 with high self-compatibility and autofertility were more likely to occur on islands, as  
110 predicted by Baker's Law. We assumed that species that colonized islands, either naturally or  
111 after introduction by humans, arrived from the mainland. Thus, we considered that species  
112 currently occurring on the mainland and absent from island floras have failed to colonize  
113 islands (hereafter referred to as mainland species). Species that occur both on the mainland  
114 and on islands are likely to have succeeded in colonizing an island from the mainland (island  
115 colonists). Finally, species occurring only on islands are likely to have evolved there after  
116 arrival of a colonist ancestor (island endemics). We explicitly consider these different types of  
117 plant distributions (i.e. mainland species, island colonists, island endemics), and ask: 1) Are  
118 plant species with high selfing ability more likely to occur on both the mainland and islands  
119 than only on the mainland (i.e. to be island colonists)? 2) Are plant species with high selfing  
120 ability more likely to occur only on islands than only on the mainland (i.e. to be island  
121 endemics)? 3) Among the island colonists, is there a difference in selfing ability between  
122 species on oceanic islands and those on continental islands? 4) Is there a difference in selfing  
123 ability between species native to islands and those naturalized on islands?

## 124 **Methods**

### 125 **Species data**

126           To test whether the colonization of islands by angiosperm species, irrespective of  
127 whether they are native or naturalized, is associated with selfing ability, we combined three  
128 comprehensive global plant databases: one on breeding systems of species, one on island and  
129 mainland distributions of native species (GIFT; [gift.uni-goettingen.de](http://gift.uni-goettingen.de)) and one on global  
130 naturalization success of alien species (GloNAF; van Kleunen *et al.*, 2015). To obtain

131 information on the selfing ability of each species in this study, we used a global database on  
132 breeding systems of angiosperms (for details on the compilation see Razanajatovo *et al.*,  
133 2016). Briefly, selfing-ability indices were calculated using fruit set and seed production after  
134 different breeding-system treatments. First, a self-compatibility index was obtained by  
135 dividing the outcome of self-pollination by the outcome of outcross-pollination treatments.  
136 Second, an autofertility index was obtained by dividing the outcome of pollinator exclusion  
137 by that of outcross-pollination treatments. This database includes self-compatibility and  
138 autofertility indices calculated for 1,752 angiosperm species from 161 families from all  
139 continents except Antarctica.

140 To obtain information on the native distribution of each species with quantitative  
141 breeding-system data on islands and mainlands, we used the Global Inventory of Floras and  
142 Traits (GIFT; (Weigelt *et al.*, 2017); <http://gift.uni-goettingen.de>), which to date included  
143 regional plant species lists for 1,636 islands and 993 mainland regions globally. Depending on  
144 the plant taxonomic group, GIFT covers between 70% and 100% of the terrestrial surface of  
145 the world for native plant species. Because GIFT does not have a global coverage for all  
146 species, 61.5 % of the species in this study did not have complete global island/mainland  
147 distribution information. For these species, if we had only information on their occurrence on  
148 islands, we could not rule out the possibility that they also occur in mainland regions, and if  
149 we had only information on their occurrence in mainland regions, we could not rule out the  
150 possibility that they occur also on islands. Nevertheless, given the comprehensive coverage of  
151 islands in GIFT, it is unlikely that a species occurs on any island, especially oceanic ones, if it  
152 is not listed in the floras of the islands included in GIFT. For species occurring on islands, we  
153 also obtained information on whether they occur on oceanic and/or continental islands from  
154 GIFT. In an additional analysis using a more conservative approach, we excluded species

155 known to occur in either island or mainland regions but for which information was missing  
156 about their occurrence in the other region type.

157 To obtain information on the naturalized distribution of the species included in this  
158 study, we used the Global Naturalized Alien Flora (GloNAF version 1.1; van Kleunen *et al.*,  
159 2015; Pyšek *et al.*, 2017). This database includes 13,168 naturalized plant species and covers  
160 362 islands and 481 mainland regions globally. We checked for each naturalized species (i.e.  
161 listed in GloNAF; n=498), whether it is naturalized on islands and/or in mainland regions.

### 162 **Island and mainland occurrence of native and naturalized plant species**

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

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

## 179 **Statistical analysis**

180 To quantitatively assess selfing ability of species, we used four selfing-ability indices:  
181 two self-compatibility indices and two autofertility indices calculated using fruit set and seed  
182 production (see (Razanajatovo *et al.*, 2016) for details on the calculation of the different  
183 indices). To assess potential relationships between island occurrence and selfing ability of  
184 species, we used multinomial logistic regressions (Ntzoufras, 2011). We used species  
185 distribution on the mainland and islands as a multi-categorical response variable. The  
186 response variable had the following three categories: (1) mainland species (species occurring  
187 only on the mainland), (2) island colonists (species occurring on both the mainland and  
188 islands), and (3) island endemics (species occurring only on islands). As explanatory  
189 variables, we used the self-compatibility or the autofertility index of species, scaled to a mean  
190 of zero and a standard deviation of one, their life history (annual/biennial or perennial,  
191 corresponding to monocarpic and polycarpic, respectively), and the interaction between self-  
192 compatibility or autofertility and life history. To account for non-independence of species due  
193 to evolutionary relatedness, we used family as a random factor. We ran multinomial logistic  
194 regressions in WinBUGS (Lunn *et al.*, 2000) from R version 2.15.3 (R Core Team, 2012),  
195 using the 'R2WinBUGS' package (Sturtz *et al.*, 2005). The model parameters were estimated  
196 from Gibbs sampling of Markov chain Monte Carlo (MCMC) using three chains. For each  
197 dataset, 50,000 iterations were run after an initial burn-in phase of 1,000 iterations. To reduce  
198 the correlation between consecutive samples, only every fifth value was taken per chain. To  
199 assess the goodness-of-fit of the models, we compared the model predictions with the data  
200 graphically (Korner-Nievergelt *et al.*, 2015). Separately for each category of the response  
201 variable (mainland species, island colonists and island endemics), we plotted for each species  
202 the probability to be a certain category (i.e. the model predictions) on the x-axis, and the  
203 observations (0=not this category, 1=this category) on the y-axis. We added class-wise means

204 of the observations within classes of width 0.1 of the model predictions. We also added the  
205  $y=x$  line. If the model fits the data well, the data would be on average equal to the model  
206 predictions, i.e. the class-wise means should be close to the  $y=x$  line.

207 To test whether autofertility is more strongly related to island occurrence than self-  
208 compatibility is, we used a subset of species for which both self-compatibility and  
209 autofertility indices were available. We ran similar multinomial logistic regressions as  
210 described above, and compared the Deviance Information Criterion (DIC) of the model with  
211 self-compatibility to that with autofertility as explanatory variable. Additionally, we ran  
212 multinomial logistic regressions in which we included both self-compatibility and autofertility  
213 indices of species, scaled to a mean of zero and a standard deviation of one, the interaction  
214 between self-compatibility and autofertility, species' life history (annual/biennial or  
215 perennial), the interaction between self-compatibility and life history, and the interaction  
216 between autofertility and life history as explanatory variables.

217 To test among the island colonists whether there is a difference in selfing ability  
218 between species that occur on oceanic islands and those that occur on continental islands, we  
219 fitted logistic regressions using the `glmer` function of the 'lme4' package (Bates *et al.*, 2015)  
220 in R. As the binary response variable, we used whether a species occurs on oceanic islands or  
221 not (yes/no). As explanatory variables, we included the self-compatibility or the autofertility  
222 index of the species, scaled to a mean of zero and a standard deviation of one, their life  
223 history (annual/biennial or perennial), and the interaction between self-compatibility or  
224 autofertility and life history. To test whether there is a difference in selfing ability between  
225 species native to islands and species naturalized on islands, we built logistic regressions, using  
226 the same terms as in the previous model. As the binary response variable, we used whether a  
227 species is naturalized on islands or not (yes/no). In these models, we also used family as a

228 random factor. We tested for significance of the fixed terms using log-likelihood ratio tests  
229 (Zuur *et al.*, 2009).

## 230 **Results**

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

### 241 *Association of island colonists and island endemics with selfing ability*

242         When selfing-ability indices based on fruit set were used, we found that species with  
243 high self-compatibility and autofertility indices were slightly more likely to be island colonist  
244 than mainland species (Table 1). An increase of 0.405 and 0.353 (one standard deviation) in  
245 self-compatibility and autofertility index of a species increased its odds of being an island  
246 colonist by a factor of 1.21 and 1.43, respectively (Figures 1a, 2a, and 3). Self-compatibility  
247 and autofertility, however, did not increase the likelihood of being an island endemic (Table  
248 1; Figures 1b, 2b and 3). When selfing-ability indices based on seed production (n=419 for  
249 self-compatibility and n=284 for autofertility index) instead of fruit set (n=1184 for self-  
250 compatibility and n=868 for autofertility index) were used, the results were slightly different

251 (compare Figures 1a-b and 1c-d; 2a-b and 2c-d). Self-compatibility still increased the  
252 likelihood of being an island colonist (Figures 1c and 3), but there was no relationship  
253 between the likelihood of being an island colonist and autofertility (Table 1; Figures 2c and  
254 3). Overall, there was no interaction between self-compatibility or autofertility and life history  
255 (Table 1).

#### 256 *Association of the occurrence of species on oceanic vs. continental islands with selfing ability*

257         When only oceanic islands were considered, there was a weak but detectable positive  
258 relationship between the likelihood of being an island colonist (instead of a mainland species)  
259 and autofertility, but self-compatibility did not increase the likelihood of being an island  
260 colonist (compare Tables 1 and S1; Figures 1-2 and S7). The positive relationship between the  
261 likelihood of being an island colonist and autofertility tended to be weaker for annual and  
262 biennial species than for perennial species, as indicated by an interaction between autofertility  
263 index based on seed production and life history (Table S1). Among the island colonists, self-  
264 compatibility and autofertility did not differ between species that occur on oceanic islands and  
265 species that occur on continental islands (Table 2).

#### 266 *Association of the occurrence of native vs. naturalized species on islands with selfing ability*

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

#### 269 *Autofertility vs. self-compatibility as a driver of island occurrence*

270         Within the subset of species for which both self-compatibility and autofertility indices  
271 were available, when indices were based on fruit set, we found that there was a tendency for  
272 species with high self-compatibility and autofertility indices to be island colonists rather than  
273 mainland species. However, the Deviance Information Criterion (DIC) of the model with  
274 autofertility was lower than that of the model with self-compatibility (Table S2), indicating a

275 better fit. When indices based on seed production were used, there was no relationship  
276 between the likelihood of being an island colonist and autofertility (Table S2). When both  
277 self-compatibility and autofertility indices were included in a model, there was still a positive  
278 relationship between the likelihood of being an island colonist and autofertility, at least so in  
279 the analysis with indices based on fruit set (Table S3).

#### 280 *Species with incomplete data on mainland and island distribution excluded*

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

## 289 **Discussion**

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

297           We found that both self-compatible and autofertile plant species were more likely to  
298 be island colonists. Even if self-compatibility and autofertility are not independent, the model  
299 with autofertility gave a better fit than the one with self-compatibility (Table S2), and in the  
300 model with both self-compatibility and autofertility, there was still a positive relationship  
301 between the likelihood of being an island colonist and autofertility (Table S3). This suggests  
302 that autofertility, which requires both autonomous self-fertilization and self-compatibility (or  
303 apomixis), is a stronger driver of island colonization than self-compatibility alone. These  
304 findings corroborate previous ones on the role of autofertility in the colonization of new  
305 regions in different contexts. For example, in North America, the over-representation of  
306 autonomously selfing plants in populations of *Campanula americana* at the northern and the  
307 western range edges has been suggested to be the result of post-glacial recolonization from  
308 southern refugia (Koski *et al.*, 2017). Although a previous review by Pannell *et al.* (2015)  
309 proposed a restriction of the scope of Baker's Law to the consequences of mate rather than  
310 pollinator limitation, besides the benefit of overcoming mate limitation by self-compatibility,  
311 autofertile species also have the advantage of overcoming pollinator limitation when  
312 establishing in new regions, especially on islands where the major groups of pollinators are  
313 usually scarce.

314           We did not find an association between selfing ability and island endemics in contrast  
315 with mainland species. With the exception of a few relict endemics (i.e. species that went  
316 extinct elsewhere), island endemic species might have arisen from different modes of  
317 speciation such as cladogenetic and anagenetic speciation (Stuessy *et al.*, 1990). Whichever is  
318 the mode of speciation, island endemics might have evolved different breeding systems  
319 compared to their mainland ancestors. The colonizers that the endemics evolved from may  
320 also have gone through mate and pollinator limitation filters, and, similarly to the island  
321 colonists, have had a higher selfing ability than mainland species. A subsequent evolution of

322 reduced selfing ability and more outcrossing or dioecy compared to the mainland species  
323 might then have balanced out the influence of the filtering. Nevertheless, as island endemics  
324 accounted only for a relatively small number of species in our database (n=57), the question  
325 whether island endemic species have generally evolved higher or reduced selfing ability  
326 remains to be tested more rigorously.

327         We found that selfing ability did not differ between native and naturalized island  
328 colonists suggesting that high selfing ability might also help alien species to become  
329 naturalized on islands where suitable mates and pollinators are more limiting than on the  
330 mainland. Some plants that were introduced by humans to both island and mainland regions  
331 from mainland regions have previously been shown to exhibit higher selfing ability on islands  
332 than on the mainland, as for *Nicotiana glauca* on two of the California Channel Islands  
333 compared to on the California mainland (Schueller, 2004). *Nicotiana glauca* is pollinated by  
334 hummingbirds and sunbirds in regions where it was introduced and where such birds are  
335 present, but it is largely selfing in regions where bird pollinators are absent, such as on the  
336 island of Tenerife (Ollerton *et al.*, 2012). On the other hand, multiple introductions of alien  
337 species have been shown to have alleviated mate limitation during establishment (Dlugosch &  
338 Parker, 2008; Pannell *et al.*, 2015). In line with these case studies and the previous finding  
339 that species with selfing ability were more likely to become naturalized (Razanajatovo *et al.*,  
340 2016), our results also suggest that selfing ability may benefit the establishment of alien  
341 species on islands.

342         Correlations among and trade-offs between different species traits complicate the  
343 detectability of Baker's Law. Life history and growth form have been shown to play a major  
344 role in the geographic distribution of plant species (Razanajatovo *et al.*, 2016; Moeller *et al.*,  
345 2017). We found that annual and biennial species were more likely to be island colonists.  
346 Perennial species have more time to reproduce than annual and biennial species, and might

347 therefore more easily overcome mate and pollinator limitations (Pannell *et al.*, 2015).  
348 Nevertheless, after accounting for life history, we still found an association between selfing  
349 ability and island occurrence. Other reproductive traits, associated or not with selfing ability,  
350 can further contribute to variation in species distribution patterns. For example, as polyploidy  
351 can be important for the evolution and diversification of the colonists' progeny, polyploid  
352 species may have larger ranges than the diploid ones (Lowry & Lester, 2006). Clonality can  
353 also help species without selfing ability to establish populations in new environments (Pyšek,  
354 1997; Vallejo-Marín & O'Brien, 2007), and this trait is also implied in the capacity for  
355 uniparental reproduction proposed by Baker's Law (Pannell *et al.*, 2015). Furthermore, traits  
356 related to dispersal ability can confer advantages in the colonization of islands. The relatively  
357 high frequencies of dioecious species on islands may, for example, be linked to fleshy and  
358 many-seeded fruits (Vamosi *et al.*, 2007), increasing the number of seeds dispersed by seed  
359 dispersal mutualists. Therefore, both dispersal and breeding system traits can affect  
360 colonization success.

361         Our results were partly different depending on whether we included or excluded the  
362 species with incomplete data on island/mainland distribution (compare Tables 1 and S4). If  
363 excluded, the association between occurrence on islands and selfing ability was weaker (i.e.  
364 less often positive). However, this more conservative dataset may be biased towards island  
365 species, as the GIFT database started with the compilation of island floras (Weigelt *et al.*,  
366 2017). Because only a few mainland species remained in this dataset, i.e. most species were  
367 island colonists, the comparison between island and mainland occurrences might have been  
368 less powerful than when all species were included. Nevertheless, whenever we found an  
369 association between island occurrence and selfing ability, it was positive, and thus in line with  
370 Baker's Law (Table S4).

371 Our results were also partly different depending on whether we used selfing ability  
372 indices calculated by using fruit set or seed production. Although seed production would be a  
373 preferable proxy for maternal fitness, it is practically challenging to measure seed production  
374 especially for non-herbaceous species. For this reason, compared to seed production, fruit set  
375 has been the most commonly measured variable for reproductive success in pollination  
376 studies (Knight et al., 2005; Razanajatovo et al., 2016). Nevertheless, fruit set and seed  
377 production can show similar patterns, as was found for pollen limitation (Knight et al., 2005).  
378 For the subset of species for which we had selfing ability indices based on fruit set and seed  
379 production, the two indices were highly correlated (self-compatibility index: Pearson's  
380  $r=0.833$ ,  $p<0.0001$ ,  $n=384$ , Figure S9a; autofertility index: Pearson's  $r=0.835$ ,  $p<0.0001$ ,  
381  $n=263$ , Figure S9b). Because of the much larger sample sizes in our analyses with selfing  
382 ability indices based on fruit set compared to those based on seed production (e.g.  $n=1184$  vs.  
383  $419$  for self-compatibility index, and  $n=868$  vs.  $284$  for autofertility index in the non-  
384 conservative dataset), the analyses with indices based on fruit set should have more power  
385 (van Kleunen et al., 2014). Furthermore, when we found an association between island  
386 occurrence and selfing ability indices based on seed production, it was positive (Figures 1, 2  
387 and S7), thus supporting Baker's Law.

### 388 *Conclusion*

389 Our comprehensive test of Baker's Law shows that selfing ability may influence the  
390 colonization of islands by plants, both naturally after long-distance dispersal and with the help  
391 of humans. The ability to reproduce is critical for establishment in new environments, and  
392 reproductive traits involving the breeding system can be vital. The role of breeding system  
393 might be especially notable in the colonization of islands, as colonists have fewer  
394 opportunities to find mates than on the mainland, and on islands the major groups of

395 pollinators are often impoverished. Our results suggest that both mate- and pollinator  
396 limitations may act as filters to the successful colonization of islands by plant species.

## 397 **References**

398 Baker, H.G. (1955) Self-compatibility and establishment after long distance dispersal.  
399 *Evolution*, 9, 347-349.

400 Baker, H.G. (1967) Support for Baker's law as a rule. *Evolution*, 21, 853-856.

401 Barrett, S.C. (1996) The reproductive biology and genetics of island plants. *Philosophical*  
402 *Transactions of the Royal Society B: Biological Sciences*, 351, 725-733.

403 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models  
404 using lme4. *Journal of Statistical Software*, 67, 1-48.

405 Bawa, K. (1982) Outcrossing and the incidence of dioecism in island floras. *The American*  
406 *Naturalist*, 119, 866-871.

407 Bernardello, G., Anderson, G.J., Stuessy, T.F. & Crawford, D.J. (2001) A survey of floral  
408 traits, breeding systems, floral visitors, and pollination systems of the angiosperms of  
409 the Juan Fernandez Islands (Chile). *The Botanical Review*, 67, 255-308.

410 Carlquist, S. (1966) The biota of long-distance dispersal. IV. Genetic systems in the floras of  
411 oceanic islands. *Evolution*, 20, 433-455.

412 Chamorro, S., Heleno, R., Olesen, J.M., McMullen, C.K. & Traveset, A. (2012) Pollination  
413 patterns and plant breeding systems in the Galápagos: a review. *Annals of Botany*,  
414 110, 1489-1501.

415 Charlesworth, D. & Charlesworth, B. (1987) Inbreeding depression and its evolutionary  
416 consequences. *Annual Review of Ecology and Systematics*, 18, 237-268.

417 Dlugosch, K. & Parker, I. (2008) Founding events in species invasions: genetic variation,  
418 adaptive evolution, and the role of multiple introductions. *Molecular Ecology*, 17,  
419 431-449.

420 Grossenbacher, D.L., Brandvain, Y., Auld, J.R., Burd, M., Cheptou, P.-O., Conner, J.K.,  
421 Grant, A.G., Hovick, S.M., Pannell, J.R., Pauw, A., Petanidou, T., Randle, A.M.,  
422 Rubio de Casas, R., Vamosi, J., Winn, A., Igic, B., Busch, J.W., Kalisz, S. &  
423 Goldberg, E.E. (2017) Self-compatibility is over-represented on islands. *New*  
424 *Phytologist*, 215, 469-478.

425 Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash,  
426 M.R., Johnston, M.O., Mitchell, R.J. & Ashman, T.-L. (2005) Pollen limitation of  
427 plant reproduction: pattern and process. *Annual Review of Ecology, Evolution, and*  
428 *Systematics*, 36, 467-497.

429 Korner-Nievergelt, F., Roth, T., Von Felten, S., Guélat, J., Almasi, B. & Korner-Nievergelt,  
430 P. (2015) *Bayesian data analysis in ecology using linear models with R, BUGS, and*  
431 *Stan*. Academic Press, Amsterdam.

432 Koski, M.H., Grossenbacher, D.L., Busch, J.W. & Galloway, L.F. (2017) A geographic cline  
433 in the ability to self-fertilize is unrelated to the pollination environment. *Ecology*, 98,  
434 2930-2939.

435 Lord, J.M. (2015) Patterns in floral traits and plant breeding systems on Southern Ocean  
436 Islands. *AoB Plants*, 7, plv095.

437 Lowry, E. & Lester, S. (2006) The biogeography of plant reproduction: potential determinants  
438 of species' range sizes. *Journal of Biogeography*, 33, 1975-1982.

439 Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. (2000) WinBUGS-a Bayesian modelling  
440 framework: concepts, structure, and extensibility. *Statistics and Computing*, 10, 325-  
441 337.

442 MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton  
443 University Press, New Jersey.

444 Moeller, D.A., Briscoe Runquist, R.D., Moe, A.M., Geber, M.A., Goodwillie, C., Cheptou,  
445 P.-O., Eckert, C.G., Elle, E., Johnston, M.O., Kalisz, S., Ree, R.H., Sargent, R.D.,  
446 Vallejo-Marin, M. & Winn, A.A. (2017) Global biogeography of mating system  
447 variation in seed plants. *Ecology Letters*, 20, 375-384.

448 Moser, D., Lenzner, B., Weigelt, P., Dawson, W., Kreft, H., Pergl, J., Pyšek, P., van Kleunen,  
449 M., Winter, M., Capinha, C., Cassey, P., Dullinger, S., Economo, E.P., García-Díaz,  
450 P., Guénard, B., Hofhansl, F., Mang, T., Seebens, H. & Essl, F. (2018) Remoteness  
451 promotes biological invasions on islands worldwide. *Proceedings of the National*  
452 *Academy of Sciences*, DOI: 10.1073/pnas.1804179115.

453 Ntzoufras, I. (2011) *Bayesian modeling using WinBUGS*. John Wiley & Sons, New Jersey.

454 Ollerton, J., Watts, S., Connerty, S., Lock, J., Parker, L., Wilson, I., Schueller, S.K., Nattero,  
455 J., Cocucci, A.A. & Izhaki, I. (2012) Pollination ecology of the invasive tree tobacco  
456 *Nicotiana glauca*: comparisons across native and non-native ranges. *Journal of*  
457 *Pollination Ecology*, 9, 85-95.

458 Pannell, J.R., Auld, J.R., Brandvain, Y., Burd, M., Busch, J.W., Cheptou, P.O., Conner, J.K.,  
459 Goldberg, E.E., Grant, A.G. & Grossenbacher, D.L. (2015) The scope of Baker's law.  
460 *New Phytologist*, 208, 656-667.

461 Pyšek, P. (1997) Clonality and plant invasions: can a trait make a difference. *The ecology and*  
462 *evolution of clonal plants*, eds. de Kroon H. & van Groenendael J., Backhuys  
463 Publishers Leiden, pp. 405-427.

464 Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Kreft, H., Weigelt, P., Maurel, N. &  
465 van Kleunen, M. (2017) Naturalized alien flora of the world: species diversity,  
466 taxonomic and phylogenetic patterns, geographic distribution and global hotspots of  
467 plant invasion. *Preslia*, 89, 203-274.

468 R Core Team (2012) *A language and environment for statistical computing*. R Foundation for  
469 Statistical Computing, Vienna, Austria.

470 Raduski, A.R., Haney, E.B. & Igić, B. (2012) The expression of self-incompatibility in  
471 angiosperms is bimodal. *Evolution*, 66, 1275-1283.

472 Razanajatovo, M., Maurel, N., Dawson, W., Essl, F., Kreft, H., Pergl, J., Pyšek, P., Weigelt,  
473 P., Winter, M. & van Kleunen, M. (2016) Plants capable of selfing are more likely to  
474 become naturalized. *Nature Communications*, 7, 13313.

475 Sakai, A.K., Wagner, W.L., Ferguson, D.M. & Herbst, D.R. (1995) Origins of dioecy in the  
476 Hawaiian flora. *Ecology*, 76, 2517-2529.

477 Schueller, S.K. (2004) Self-pollination in island and mainland populations of the introduced  
478 hummingbird-pollinated plant, *Nicotiana glauca* (Solanaceae). *American Journal of*  
479 *Botany*, 91, 672-681.

480 Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad,  
481 S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G.,  
482 Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H.,  
483 Kartesz, J., Kenis, M., Kreft, H., Kühn, I., Lenzner, B., Liebhold, A., Mosena, A.,  
484 Moser, D., Nishino, M., Pearman, D., Pergl, J., Rabitsch, W., Rojas-Sandoval, J.,  
485 Roques, A., Rorke, S., Rossinelli, S., Roy, H.E., Scalera, R., Schindler, S., Štajerová,  
486 K., Tokarska-Guzik, B., van Kleunen, M., Walker, K., Weigelt, P., Yamanaka, T. &  
487 Essl, F. (2017) No saturation in the accumulation of alien species worldwide. *Nature*  
488 *Communications*, 8, 14435.

489 Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad,  
490 S., Pyšek, P., van Kleunen, M., Winter, M., Ansong, M., Arianoutsou, M., Bacher, S.,  
491 Blasius, B., Brockhoff, E., Brundu, G., Capinha, C., Causton, C., Celesti-Grapow,  
492 L., Dawson, W., Dullinger, S., Economo, E., Fuentes, N., Guénard, B., Jäger, H.,  
493 Kartesz, J., Kenis, M., Kühn, I., Lenzner, B., Liebhold, A., Mosena, A., Moser, D.,

494 Nentwig, W., Nishino, M., Pearman, D., Pergl, J., Rabitsch, W., Rojas-Sandoval, J.,  
495 Roques, A., Rorke, S., Rossinelli, S., Roy, H.E., Scalera, R., Schindler, S., Štajerová,  
496 K., Tokarska-Guzik, B., Walker, K., Ward, D.F., Yamanaka, T. & Essl, F. (2018)  
497 Global rise in emerging alien species results from increased accessibility of new  
498 source pools. *Proceedings of the National Academy of Sciences*, 201719429.

499 Stuessy, T.F., Crawford, D.J. & Marticorena, C. (1990) Patterns of phylogeny in the endemic  
500 vascular flora of the Juan Fernandez Islands, Chile. *Systematic Botany*, 15, 338-346.

501 Sturtz, S., Ligges, U. & Gelman, A. (2005) R2WinBUGS: A Package for Running WinBUGS  
502 from R. *Journal of Statistical Software*, 12, 1-16.

503 Vallejo-Marín, M. & O'Brien, H.E. (2007) Correlated evolution of self-incompatibility and  
504 clonal reproduction in *Solanum* (Solanaceae). *New Phytologist*, 173, 415-421.

505 Vamosi, J.C., Zhang, Y. & Wilson, W.G. (2007) Animal dispersal dynamics promoting  
506 dioecy over hermaphroditism. *The American Naturalist*, 170, 485-491.

507 van Kleunen, M., Dawson, W., Bossdorf, O. & Fischer, M. (2014) The more the merrier:  
508 Multi-species experiments in ecology. *Basic and Applied Ecology*, 15, 1-9.

509 van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt,  
510 P., Kartesz, J., Nishino, M., Antonova, L.A., Barcelona, J.F., Cabezas, F.J., Cardenas,  
511 D., Cardenas-Toro, J., Castano, N., Chacon, E., Chatelain, C., Ebel, A.L., Figueiredo,  
512 E., Fuentes, N., Groom, Q.J., Henderson, L., Inderjit, Kupriyanov, A., Masciadri, S.,  
513 Meerman, J., Morozova, O., Moser, D., Nickrent, D.L., Patzelt, A., Pelsner, P.B.,  
514 Baptiste, M.P., Poopath, M., Schulze, M., Seebens, H., Shu, W.-s., Thomas, J.,  
515 Velayos, M., Wieringa, J.J. & Pysek, P. (2015) Global exchange and accumulation of  
516 non-native plants. *Nature*, 525, 100-103.

517 Weigelt, P., König, C. & Kreft, H. (2017) The Global Inventory of Floras and Traits (GIFT)  
518 database. Available at: <http://gift.uni-goettingen.de>

519 Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution,*  
520 *and conservation*. Oxford University Press, New York.

521 Zuur, A., Ieno, E., Walker, N., Saveliev, A. & Smith, G. (2009) *Mixed effects models and*  
522 *extensions in ecology with R*. Springer, New York.

### 523 **Data accessibility**

524 The data supporting the results are available online from Dryad

525 doi:10.5061/dryad.89pd54f.

526 **Table 1** Association of island and mainland occurrence of species with selfing ability based  
527 on the non-conservative dataset. Logistic regression coefficients of four multinomial logistic  
528 regressions testing how the likelihood of being island colonists and island endemics compared  
529 to mainland species depends on the self-compatibility or the autofertility index of species,  
530 scaled to a mean of zero and a standard deviation of one, their life history (annual/biennial or  
531 perennial), and the interaction between self-compatibility or autofertility and life history.  
532 Shown are the mean, the 2.5 % and the 97.5 % percentiles (95 % credible intervals) of a  
533 sample of 29,400 posterior distributions of each model parameter.

Multicategorical response variable with mainland species as a reference	Island colonist vs. mainland species	Island endemic vs. 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 x 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 = 1297.600)†		
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 x 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)

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Selfing-ability indices based on seed production

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Analysis with self-compatibility (DIC = 711.157)<sup>‡</sup>

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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 x 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)

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Analysis with autofertility (DIC = 487.485)<sup>§</sup>

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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 x 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)

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534 \*  $n_{\text{mainland species}} = 700$ ;  $n_{\text{island colonists}} = 440$ ;  $n_{\text{island endemics}} = 44$

535 †  $n_{\text{mainland species}} = 517$ ;  $n_{\text{island colonists}} = 315$ ;  $n_{\text{island endemics}} = 36$

536 ‡  $n_{\text{mainland species}} = 207$ ;  $n_{\text{island colonists}} = 199$ ;  $n_{\text{island endemics}} = 13$

537 §  $n_{\text{mainland species}} = 141$ ;  $n_{\text{island colonists}} = 133$ ;  $n_{\text{island endemics}} = 10$

538 **Table 2** Association of the occurrence of species on oceanic or continental islands with  
539 selfing ability. Results of four logistic regressions testing how the occurrence of island  
540 colonist species on oceanic islands depends on self-compatibility or the autofertility index of  
541 species, scaled to a mean of zero and a standard deviation of one, their life history  
542 (annual/biennial or perennial), and the interaction between self-compatibility or autofertility  
543 and life history. Shown are the degrees of freedom (df),  $\chi^2$  values and  $p$  values from log-  
544 likelihood ratio tests.

	Analysis with self-compatibility			Analysis with autofertility		
Selfing-ability indices based on fruit set						
Explanatory variables	df	$\chi^2$	$p$	df	$\chi^2$	$p$
Selfing ability index	1	0.849	0.357	1	0.002	0.964
Annual/biennial	1	6.884	0.009	1	4.792	0.029
Selfing ability x Annual/biennial	1	4.153	0.041	1	1.497	0.221
Random effect	sd	sd <sub>residuals</sub>	$n$	sd	sd <sub>residuals</sub>	$n$
Family	1.182	1.028	388	1.128	1.005	274
Selfing-ability indices based on seed production						
Explanatory variables	df	$\chi^2$	$p$	df	$\chi^2$	$p$
Selfing ability index	1	1.248	0.264	1	1.367	0.242
Annual/biennial	1	6.053	0.014	1	3.963	0.046
Selfing ability x Annual/biennial	1	3.833	0.050	1	2.014	0.156
Random effect	sd	sd <sub>residuals</sub>	$n$	sd	sd <sub>residuals</sub>	$n$

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Family	0.725	1.055	171	1.138	0.953	113
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545

546 **Table 3** Association of the occurrence of native vs. naturalized species on islands with selfing  
547 ability. Results of four logistic regressions testing how the naturalization status of island  
548 colonist species depends on the self-compatibility or the autofertility index of species, scaled  
549 to a mean of zero and a standard deviation of one, their life history (annual/biennial or  
550 perennial), and the interaction between self-compatibility or autofertility and life history.  
551 Shown are the degrees of freedom (df),  $\chi^2$  values and  $p$  values from log-likelihood ratio tests.

	Analysis with self-compatibility			Analysis with autofertility		
Selfing-ability indices based on fruit set						
Explanatory variables	df	$\chi^2$	$p$	df	$\chi^2$	$p$
Selfing ability index	1	0.462	0.497	1	0.146	0.703
Annual/biennial	1	10.123	0.001	1	14.039	<0.001
Selfing ability x Annual/biennial	1	0.028	0.867	1	1.254	0.262
Random effect	sd	sd <sub>residuals</sub>	$n$	sd	sd <sub>residuals</sub>	$n$
Family	0.707	1.049	440	0.887	0.989	315
Selfing-ability indices based on seed production						
Explanatory variables	df	$\chi^2$	$p$	df	$\chi^2$	$p$
Selfing ability index	1	0.710	0.399	1	0.342	0.559
Annual/biennial	1	8.735	0.003	1	11.980	<0.001
Selfing ability x Annual/biennial	1	0.044	0.833	1	1.746	0.186
Random effect	sd	sd <sub>residuals</sub>	$n$	sd	sd <sub>residuals</sub>	$n$

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Family	0.856	1.023	199	0.874	1.010	133
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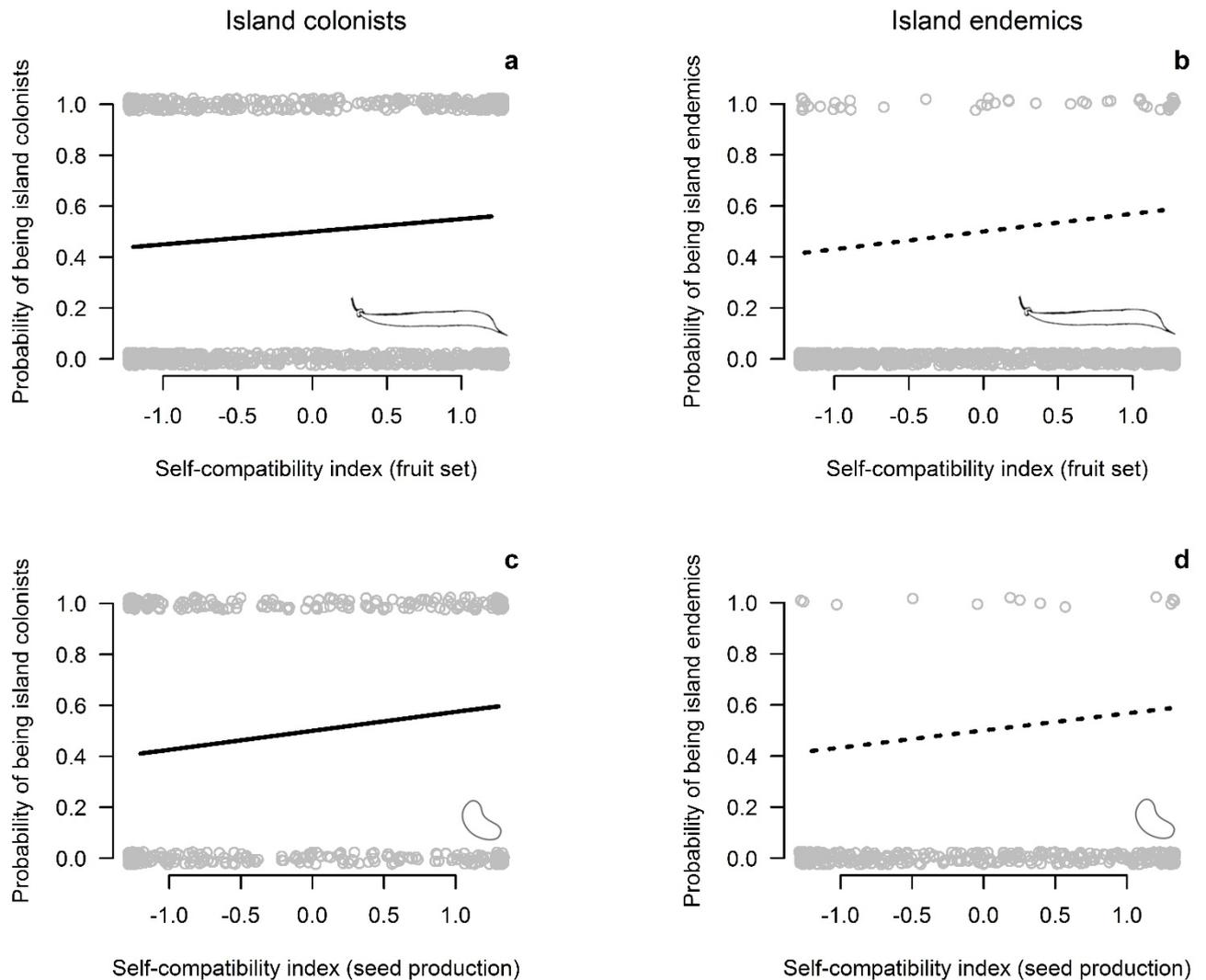
552

553 **Figure legends**

554 **Figure 1** Island and mainland occurrence of plant species in relation to self-compatibility  
555 based on the non-conservative dataset. (a-d) Results of four multinomial logistic regressions  
556 testing how the occurrence of native and naturalized plant species on both the mainland and  
557 islands (island colonists) and only on islands (island endemics) compared to only on the  
558 mainland depends on self-compatibility of species. Each row corresponds to a model. Selfing  
559 ability of species was measured as (a-b) a self-compatibility index calculated based on fruit  
560 set (n=1184); (c-d) a self-compatibility index calculated based on seed production (n=419).  
561 Self-compatibility indices were standardized to a mean of zero and a standard deviation of  
562 one. Sample sizes refer to the total number of species from individual studies in the breeding  
563 system database. Solid curves and dotted curves indicate that the posterior distribution of the  
564 model parameter overlaps with zero and do not overlap with zero, respectively.

565 **Figure 2** Island and mainland occurrence of plant species in relation to autofertility based on  
566 the non-conservative dataset. (a-d) Results of four multinomial logistic regressions testing  
567 how the occurrence of native and naturalized plant species on both the mainland and islands  
568 (island colonists) and only on islands (island endemics) compared to only on the mainland  
569 depends on autofertility of species. Each row corresponds to a model. Selfing ability of  
570 species was measured as (a-b) an autofertility index calculated based on fruit set (n=868); (c-  
571 d) an autofertility index calculated based on seed production (n=284). Autofertility indices  
572 were standardized to a mean of zero and a standard deviation of one. Sample sizes refer to the  
573 total number of species from individual studies in the breeding system database. Solid curves  
574 and dotted curves indicate that the posterior distribution of the model parameter overlaps with  
575 zero and do not overlap with zero, respectively.

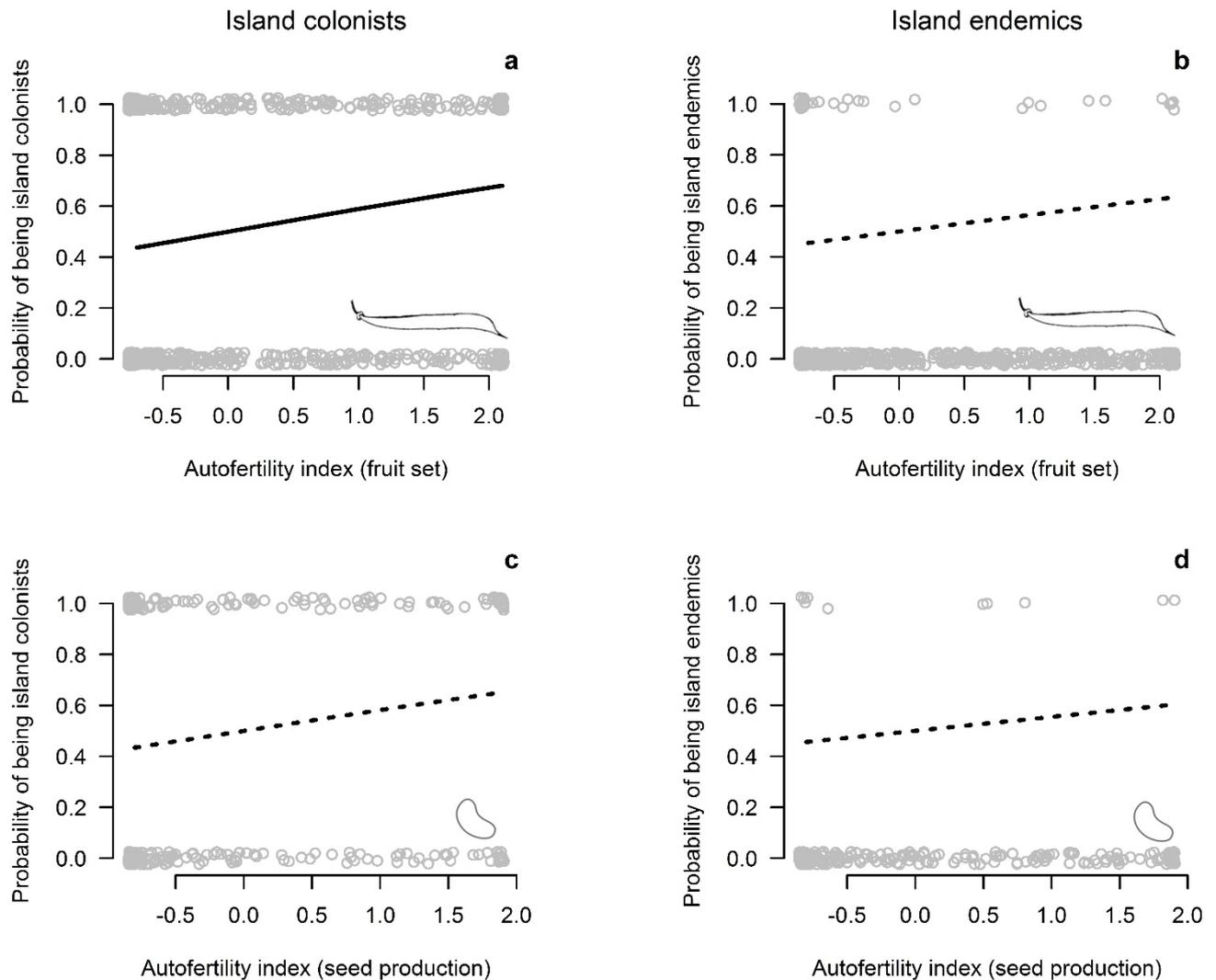
576 **Figure 3** Association of island and mainland occurrence of species with selfing ability based  
577 on the non-conservative dataset. (a-d) Posterior distribution of the logistic regression  
578 coefficients of four multinomial logistic regressions testing how the occurrence of native and  
579 naturalized plant species on both the mainland and islands (island colonists) and only on  
580 islands (island endemics) compared to only on the mainland (mainland species) depends on  
581 selfing ability of species. Selfing ability of species was measured (a) as an index of self-  
582 compatibility calculated based on fruit set (n=1184); (b) an index of autofertility calculated  
583 based on fruit set (n=868); (c) a self-compatibility index calculated based on seed production  
584 (n=419); (d) an autofertility index calculated based on seed production (n=284). Sample sizes,  
585 given in brackets, refer to the total number of species from individual studies in the breeding-  
586 system database.



587

588 **Figure 1** Island and mainland occurrence of plant species in relation to self-compatibility  
 589 based on the non-conservative dataset. (a-d) Results of four multinomial logistic regressions  
 590 testing how the occurrence of native and naturalized plant species on both the mainland and  
 591 islands (island colonists) and only on islands (island endemics) compared to only on the  
 592 mainland depends on self-compatibility of species. Each row corresponds to a model. Selfing  
 593 ability of species was measured as (a-b) a self-compatibility index calculated based on fruit  
 594 set (n=1184); (c-d) a self-compatibility index calculated based on seed production (n=419).  
 595 Self-compatibility indices were standardized to a mean of zero and a standard deviation of  
 596 one. Sample sizes refer to the total number of species from individual studies in the breeding

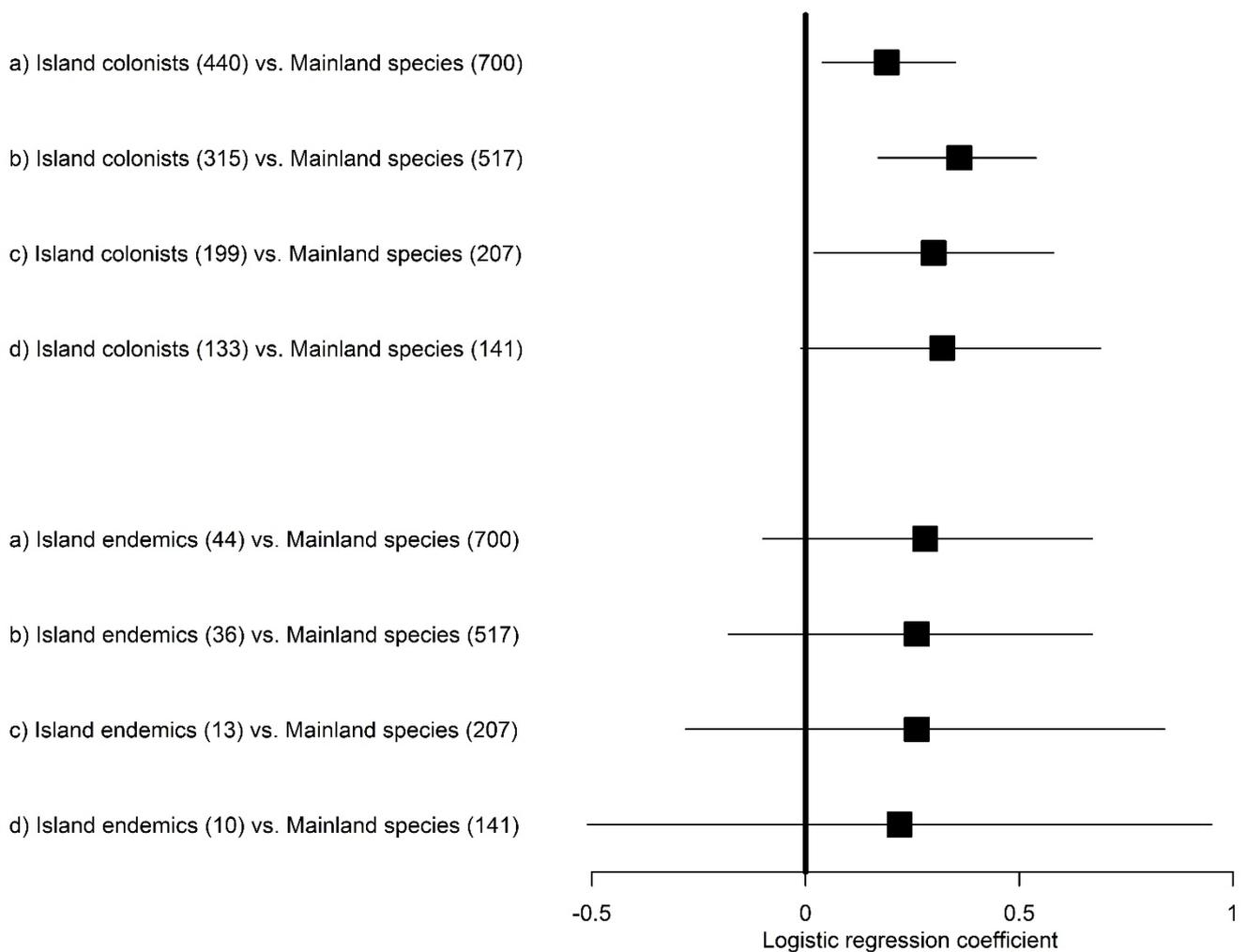
597 system database. Solid curves and dotted curves indicate that the posterior distribution of the  
598 model parameter overlaps with zero and do not overlap with zero, respectively.



599

600 **Figure 2** Island and mainland occurrence of plant species in relation to autofertility based on  
 601 the non-conservative dataset. (a-d) Results of four multinomial logistic regressions testing  
 602 how the occurrence of native and naturalized plant species on both the mainland and islands  
 603 (island colonists) and only on islands (island endemics) compared to only on the mainland  
 604 depends on autofertility of species. Each row corresponds to a model. Selfing ability of  
 605 species was measured as (a-b) an autofertility index calculated based on fruit set (n=868); (c-  
 606 d) an autofertility index calculated based on seed production (n=284). Autofertility indices  
 607 were standardized to a mean of zero and a standard deviation of one. Sample sizes refer to the  
 608 total number of species from individual studies in the breeding system database. Solid curves

609 and dotted curves indicate that the posterior distribution of the model parameter overlaps with  
610 zero and do not overlap with zero, respectively.



612

613 **Figure 3** Association of island and mainland occurrence of species with selfing ability based

614 on the non-conservative dataset. (a-d) Posterior distribution of the logistic regression

615 coefficients of four multinomial logistic regressions testing how the occurrence of native and

616 naturalized plant species on both the mainland and islands (island colonists) and only on

617 islands (island endemics) compared to only on the mainland (mainland species) depends on

618 selfing ability of species. Selfing ability of species was measured (a) as an index of self-

619 compatibility calculated based on fruit set (n=1184); (b) an index of autofertility calculated

620 based on fruit set (n=868); (c) a self-compatibility index calculated based on seed production

621 (n=419); (d) an autofertility index calculated based on seed production (n=284). Sample sizes,

622 given in brackets, refer to the total number of species from individual studies in the breeding-  
623 system database.