

1 **-Title Page-**

2 Title: Selfing species exhibit diminished niche breadth over time.

3 Running Title: Selfing leads to diminished niche breadth

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21 **Abstract**

22 Self-pollinating plants (“selfers”) have larger geographic ranges and inhabit higher latitudes than their
23 outcrossing relatives. This finding has led to the hypothesis that selfers also have broader climatic niches.
24 It is possible that the increased likelihood of successful colonization into new areas and the initial purging
25 of deleterious mutations may offset selfers’ inability to adapt to new environments due to low
26 heterozygosity. Here, for the first time, we examine the climatic niches and mutation accumulation rates
27 of hundreds of closely related selfing and outcrossing species. Contrary to expectations, selfers do not
28 have wider climatic niche breadths than their outcrossing sister taxa despite selfers’ greatly expanded
29 geographic ranges. Selfing sister pairs also exhibit greater niche overlap than outcrossing sisters, implying
30 that climatic niche expansion becomes limited following the transition to selfing. Further, the niche
31 breadth of selfers is predicted to decrease significantly faster than that of closely-related outcrossers. In
32 support of these findings, selfers also display significantly higher mutation accumulation rates than their
33 outcrossing sisters, implying decreased heterozygosity, effective population size, and adaptive potential.
34 These results collectively suggest that while the release from mate limitation among selfing species may
35 result in initial range expansion, range size and niche breadth are decoupled, and the limitations of an
36 increasingly homogeneous genome will constrict selfers’ climatic niches and over time reduce their
37 geographic ranges.

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44 **Introduction**

45 Species ranges are influenced by various life-history traits (Sexton *et al.* 2009), including the
46 evolution of autonomous reproduction (Igic & Busch 2013). “Baker’s Law” posits that the ability of a
47 species to self-fertilize increases colonization and establishment success by bypassing mate limitation and
48 pollinator requirements (Baker 1955; Stebbins 1957; Pannell & Barrett 1998). Along these lines, self-
49 pollinating plant species (“selfers”) consistently display larger geographic ranges and occupy higher
50 maximum latitudes than closely related outcrossing species (Grossenbacher *et al.* 2015). Based on these
51 results, it has been hypothesized that selfing species may have greater climatic tolerances and climatic
52 niche breadths (hereafter “niche breadths”) than outcrossing sister taxa (Randle *et al.* 2009;
53 Grossenbacher *et al.* 2015). In support of this argument, ecologists and evolutionary biologists have
54 established that the distribution and range size of plant species are influenced strongly by climate (Parker
55 1963; Stephenson 1990; Park & Potter 2015), and large geographic range size is thought to be associated
56 with wider niche breadths (Brown 1984; Slatyer *et al.* 2013). Species occurring at higher latitudes have
57 also been hypothesized to have broader environmental tolerances due to larger seasonal fluctuations
58 (Stevens, 1989; but see Šizling *et al.*, 2015). Additionally, selfing has been hypothesized to promote local
59 adaptation and niche divergence by converting non-additive genetic variance to additive variance for
60 tolerance to new habitats, thus facilitating expansion into novel climatic conditions (Lande 1977;
61 Kirkpatrick 2000; Levin 2010).

62 An alternative interpretation is that the switch to self-fertilization is an evolutionary “dead-end”
63 (Dobzhansky 1950; Stebbins 1957). Selfing is associated with increased homozygosity, reduced effective
64 population sizes (Pollak 1987; Schoen & Brown 1991), increased accumulation of mutations (Heller &
65 Smith 1978; Morran *et al.* 2009), and reduced genetic diversity (Jarne & Städler 1995; Hamrick & Godt
66 1996; Nybom 2004; Glemin *et al.* 2006). These effects are hypothesized to limit the ability of selfers to
67 adapt to different environments and extend their ranges relative to their outcrossing relatives (Crawford &
68 Whitney 2010). If selfing is an evolutionary dead-end, then selfers should not have greater niche breadths

69 than their outcrossing sister taxa. Moreover, it is possible that geographic range and niche breadth are
70 decoupled over short evolutionary times (Randle *et al.* 2009). Under this scenario, we would hypothesize
71 that selfers may inhabit larger geographic ranges that exhibit relatively little climatic variation relative to
72 their outcrossing sisters. Furthermore, we would also expect that the lack of genetic heterozygosity and
73 adaptive potential limit the degree to which climatic niches of selfers species can diverge from each other,
74 resulting in greater niche overlap between selfing sister species than between outcrossing sisters.

75 Here, we test this hypothesis by examining whether selfers with larger geographic ranges than
76 their outcrossing relatives also have greater niche breadths, and how the relationship between range size
77 and niche breadth changes over time. We also examine niche overlap between pairs of selfing sister taxa
78 and between pairs of outcrossing sister taxa to determine whether niches are less likely to change after the
79 shift to selfing . Niche overlap is negatively proportionate to the amount of niche change since divergence,
80 and thus may reflect the potential of species to expand their niches (Broennimann *et al.* 2007; Turner *et al.*
81 2015). Finally, as the accumulation of deleterious mutations is thought to limit long-term adaptive
82 potential and fitness in selfing lineages (Heller & Smith 1978), we explore whether rates of mutation
83 accumulation differ significantly between selfers and outcrossers. We hypothesize that freedom from
84 mate limitation initially allows selfers to expand their geographic ranges and niche breadth. However, as
85 homozygosity and the accumulation of mildly deleterious mutations increase due to inbreeding, the
86 adaptive potential of selfers should decrease more rapidly than that of outcrossers, resulting in more
87 constrained niches.

88

89 **Materials and Methods**

90 All analyses described below were done in R (R Core Team 2013); detailed information on the packages
91 used are provided in Table S1.

92 *Dataset*

93 To estimate and compare the niche breadth of selfing and outcrossing species, we used a
94 previously published dataset that collated 54 studies describing plant species' mating systems from 20
95 well supported, phylogenetically divergent clades representing 15 families (Grossenbacher *et al.* 2015).
96 All taxa were included in previously published species-level phylogenies containing at least one
97 predominantly selfing species and one predominantly outcrossing species. Species were classified as
98 predominantly selfing when outcrossing rates were below 0.2 and predominantly outcrossing when above
99 0.8 (see Table S3 in Grossenbacher *et al.*, 2015). Species with outcrossing rates in between, or those
100 exhibiting extensive among-population variation in outcrossing rates and traits associated with
101 outcrossing were treated as having a variable mating system and not used in this study. We also used
102 previously published time-calibrated phylogenies for all 20 clades based on internal transcribed spacer
103 (*nrITS*) sequences (Grossenbacher *et al.* 2015, 2016). Sister species were identified in a subset of 9000
104 trees from the posterior distribution for each clade. The posterior probability of each sister pair, *i.e.*, the
105 proportion of trees in which the two species were sister, was used as a measure of phylogenetic
106 uncertainty. A total of 498 sister species pairs were identified, of which 194 differed in mating system.

107 *Estimating climatic niche breadth and overlap*

108 We used curated geographic records (excluding those with coordinate accuracy > 100 km,
109 coordinates failing to match the locality description, or those with taxonomic misidentifications), from the
110 Global Biodiversity Information Facility (<http://www.gbif.org>) to infer the environmental conditions each
111 species occupies (Grossenbacher *et al.* 2015, 2016). Among abiotic environmental variables, temperature
112 (Parker 1963) and moisture (Stephenson 1990; Pigott & Pigott 1993) have been shown to strongly
113 influence plant ranges (Holdridge 1947). We thus examined global data on 19 bioclimatic variables at 2.5
114 arc-minute resolution derived from monthly temperature and rainfall values (Nix 1986; Busby 1991;
115 Hijmans *et al.* 2005). To maximize comparability with previous examinations of geographic range
116 (Grossenbacher *et al.* 2015, 2016), we recorded the minimum, maximum, and standard deviations (SD) of
117 each bioclimatic variable in species' climatic ranges, which together define univariate climatic niche

118 breadth (May & MacArthur 1972). We also examined each species' niche breadth by calculating the
119 average Euclidian distance between all points in each species' range and the center of their distribution in
120 in 19-dimensional climatic space (*i.e.*, multivariate standard deviation). As Euclidian distance measures
121 can be sensitive to covariance among variables, we repeated this process on a subset of seven bioclimatic
122 variables likely associated with the distribution of plant species, and whose pairwise Pearson's correlation
123 coefficient $r < 0.75$: isothermality (BIO2), minimum temperature of the coldest month (BIO6), mean
124 temperature of the wettest quarter (BIO8), precipitation of wettest month (BIO13), precipitation
125 seasonality (BIO15), precipitation of the warmest quarter (BIO18), and precipitation of the coldest quarter
126 (BIO19). We also used PCA to summarize all the bioclimatic variables, and calculated niche breadth as
127 the area of the convex hull surrounding each species' points of occurrence in climate space defined by the
128 first two principal axes. Species ranges were defined as the summed area of occupied grid cells across cell
129 sizes of 0.05, 0.1, 0.5, or 1 decimal degree, corresponding roughly to 25, 100, 2500, and 10,000 km²
130 respectively (Grossenbacher *et al.* 2015, 2016). All subsequent analyses were done using niches derived
131 from each of these cell sizes to assess whether the results were sensitive to the spatial grain of estimation.

132 To examine the degree of niche overlap between sister species, we used the approach developed
133 by Broennimann *et al.* (2012), which has been shown to be robust to errors and biases associated with the
134 estimation of niche overlap. This method compares the environmental conditions available for a species
135 within a defined study extent with its observed occurrences and calculates the available environmental
136 space defined by the first two principal axes. These extents again were delimited as occupied cells of 0.05,
137 0.1, 0.5, and 1 decimal degrees to account for different spatial grains. The same 19 bioclimatic variables
138 used above were used for the multivariate PCA. Sampling bias was corrected by employing a Gaussian
139 kernel density smoothing approach. The degree of niche overlap between each sister species pair was
140 calculated using Schoener's D (Schoener 1968) and modified Hellinger distance (I) (Warren *et al.* 2008),
141 which vary from 0 (no niche overlap) to 1 (identical niche).

142 *Statistical analyses*

143 Linear mixed effects models were used to test differences in \ln -transformed niche breadth
144 between outcrossing and selfing sister species. Mating system was treated as a fixed effect. Genus (or
145 section, in the case of *Oenothera*) and sister-pair identity entered the model as random factors, and we
146 estimated slopes for each genus. The posterior probability of each sister species pair was included as a
147 weighting factor in our models to account for phylogenetic uncertainty. We included the interaction of
148 divergence time (\ln -transformed) with mating system as a fixed effect in the model to test whether the
149 effect of divergence time on niche breadth co-varied with mating system. This test also included a random
150 effect for genus-specific mating system. As niche breadth may be affected by ploidy and lifespan
151 (Morishima *et al.* 1984; Thompson *et al.* 2014), we also ran these analyses including only sister pairs that
152 did not differ in by these potentially correlated traits.

153 Niche overlap values range from 0 to 1. These bounds, and the right-skewed distributions of these
154 measures, violate the assumptions of standard linear models (Ramalho *et al.* 2011). Hence, we used
155 fractional logit regression models (Papke & Wooldridge 1996) to test whether the mating systems of
156 sister-species pairs (s-s, s-o, o-o) influenced niche overlap, with sister-pair mating system as a categorical
157 predictor and niche overlap (Schoener's D or Hellinger's I) as the response variable. The posterior
158 probability of each sister-species pair again was included as a weighting factor to account for
159 phylogenetic uncertainty, and models were fit using maximum likelihood. We similarly used fractional
160 logit models to test whether time since divergence (\ln -transformed) influenced niche overlap. All analyses
161 were replicated across the four spatial scales defined above to examine whether our results were robust to
162 the spatial scale at which species niche was estimated. Finally, to address the possibility that certain
163 clades may heavily influence the overall results, we ran these analyses dropping each individual genus
164 alternatively. Only those cases for which dropping a genus (or section in *Oenothera*) affected the
165 statistical significance of the analyses are reported.

166 Last, we used linear mixed models to test whether the rate at which lineages accumulate
167 mutations was influenced by mating system, and how this relationship changes over time. The interaction

168 of divergence time (*ln*-transformed) with mating system entered the model as a fixed effect, and we
169 estimated a genus-specific random slope for divergence time. We restricted these analyses to the 42 sister
170 pairs with annual life histories and identical ploidy levels because both of these factors can influence
171 mutation fixation rates. Annuals have higher rates of molecular evolution than perennials, and unlike
172 perennials display rates similar to other closely-related annuals (Andreasen & Baldwin 2001). Mutation
173 accumulation rates were calculated by dividing the number of nucleotide substitutions since divergence
174 by divergence time for each selfer-outcrosser sister-species pair across all phylogenies (Smith &
175 Donoghue 2008). In all cases, we report pseudo-R-squared values as measures of the variation explained
176 by fixed and random effects.

177

178 **Results**

179 Mating system did not significantly influence niche breadth measured as multivariate climate
180 space (Fig. 1A, Table 1) or based on individual bioclimatic variables ($p > 0.05$ all cases; Table S2). The
181 relationship between mating system and niche breadth was inconsistent, in contrast to that between
182 mating system and geographic range size. Comparisons of niche breadth for the uncorrelated subset of
183 bioclimatic variables yielded similar results, as did comparisons based on the first two principal axes of
184 climate space occupied by species (PCA; $p > 0.05$; Fig. S1, Table S3). These results were consistent
185 across all spatial grains and when excluding sister pairs that differed in ploidy and life history (Table S4,
186 S5). However, the niche breadth of selfing species tended to decrease more over evolutionary time than
187 the niche breadth of their outcrossing sisters (divergence time \times mating system: $p < 0.05$; Fig. 2A, Table
188 S6).

189 To compare niche expansion ability between selfers and outcrossers, we assessed the proportion
190 of shared niche space (overlap) among sister taxa of different mating system combinations: selfing-selfing
191 (s-s), selfing-outcrossing (s-o), and outcrossing-outcrossing (o-o). Patterns of niche overlap were

192 significantly influenced by mating system. In particular, selfing sister pairs (s-s) had significantly greater
193 degrees of niche overlap (e.g., Schoener's $D = 0.23$) than sister pairs with at least one outcrossing species
194 (e.g., s-o: $D=0.15$; o-o: $D=0.17$) regardless of the metric examined ($p < 0.05$; Fig. 3; Table S7). These
195 patterns were robust to the removal of all genera except *Medicago* ($p > 0.05$; Table S8). Although the
196 distribution of divergence times differed among the three mating system pairs (Grossenbacher *et al.* 2016),
197 niche overlap was not influenced by divergence time (Table S9).

198 Finally, to investigate whether genetic degradation might limit selfers' niche expansion and
199 differentiation over time, we examined mutation accumulation rates across sister taxa with different
200 mating systems. Wide variation was observed in the mutation accumulation rates among the taxa we
201 examined. Selfers had higher mutation accumulation rates than their outcrossing sisters in general (Fig.
202 1C). Together with time since divergence, the shift to selfing explained a significant proportion of this
203 variation ($R^2 > 0.27$; Table S10). The rate of mutation accumulation was predicted to increase through
204 time for selfers while concomitantly decreasing for their outcrossing sisters (Fig. 2B).

205

206 **Discussion**

207 Even though selfers occupy larger geographic ranges and higher latitudes than their outcrossing sisters
208 (Grossenbacher *et al.* 2015), we find that this does not necessarily translate into greater climatic niche
209 breadth. Our results indicate that niche breadth and range size are decoupled, potentially leading to
210 species with large geographic ranges but narrow climatic niches. For three reasons discussed below, we
211 argue that the large range sizes currently observed for selfing plant species are an evolutionarily transient
212 phenomenon.

213 *Mating system does not consistently predict niche breadth*

214 Our niche breadth analyses do not support a tight association between range size and niche
215 breadth. Neither do our results support the hypothesis that selfers should have wider niche breadth than

216 their outcrossing sisters due to their higher latitude ranges. This suggests that although the reproductive
217 assurance offered by self-fertilization may allow selfers to expand their geographic range (Grossenbacher
218 *et al.* 2015), this expansion does not always occur into novel climates. Because the vagaries of geography
219 can result in certain climates occurring more frequently than others, species adapted to common climatic
220 conditions may exhibit larger geographic distributions than their climatic niches would suggest (Burgman
221 1989; Hanski *et al.* 1993; Gaston & Spicer 2001; Thompson & Ceriani 2003). For instance, the
222 outcrossing *Medicago edgeworthii* Sirj. grows in a wider range of climates than its close selfing relative
223 *M. radiata* L. despite having a much more restricted geographic range centered at a lower latitude (Fig. 4).
224 Furthermore, given the penchant of selfers to exist in comparative low abundance at small fragmented
225 habitats, their geographic ranges; and the climatic space they occupy; may have been overestimated
226 relative to their outcrossing relatives.

227 *Niche divergence is negatively impacted by selfing*

228 It has been suggested that selfing species have a reduced capacity to adapt to different
229 environments (Crow 1992; Morran *et al.* 2009). This lack of adaptability was supported by our finding
230 that the degree of niche overlap was higher among selfing sister-species pairs than outcrossing pairs. This
231 result suggests that species' niches are slow to diverge following the transition to selfing. As there are no
232 known instances of outcrossing revolving from selfing lineages, we can reasonably assume that selfing
233 sister species diverged post-transition (i.e., their most recent common ancestor is likely a selfer).
234 Assuming a degree of spatial autocorrelation among environmental conditions, this result seemingly
235 supports the long-held theory that autonomous self-fertilization facilitates range overlap of closely-related
236 species (Antonovics & Bradshaw 1970). Numerous mechanisms can promote the coexistence of selfers
237 and their close relatives, including minor range shifts following peri- or parapatric speciation that promote
238 early secondary range overlap, reproductive isolation from ancestral or sister species, and reduced
239 competition for pollinators (Grossenbacher *et al.* 2016). However, the higher level of niche overlap that
240 we observed for selfing sister-species pairs did not result from geographic proximity, as there was no

241 association between mating system and co-occurrence among sister species (Grossenbacher *et al.* 2016).
242 This suggests that once species have transitioned to selfing, they may be unable to establish in new
243 climates as readily as their outcrossing relatives, and thus expand their geographic range by colonizing
244 familiar environments.

245 Finally, although the effect of selfing pairs was no longer significant when the genus *Medicago*
246 was removed from our analysis (Table S8; see also ref. 25), this result is likely a consequence of a
247 substantial reduction in sample size. *Medicago* includes 39 selfing sister pairs: over 43% of the weighted
248 sample of selfing sister pairs and more than any other genus included in our study. Nonetheless, these
249 results suggest that climatic niche divergence is not facilitated by selfing. Indeed, in Gallagher *et al.*'s
250 (2010) examination of niche shifts in 26 plant species introduced to Australia, the six species that do not
251 exhibit evidence of niche shifts are all primarily self-pollinating. Furthermore, a number of recent studies
252 have illustrated the greater potential for niche expansion by outcrossing species (Broennimann *et al.* 2007;
253 Petitpierre *et al.* 2012; Gallien *et al.* 2016).

254 *Selfing leads to decreased niche breadth over time*

255 Among the species we examined, selfers did not uniformly have smaller niches than their
256 outcrossing sisters, but the climatic ranges of the former were predicted to decrease significantly more
257 rapidly over time. Thus, the climatic niches of selfing species eventually will become narrower than the
258 niches of related outcrossing species, irrespective of their initial niche breadth. It is possible that the
259 decrease of a selfer's niche over time can be attributed to genetic impoverishment caused by inbreeding.
260 The reduction in effective population size that accompanies selfing limits both positive and purifying
261 selection, increases the fixation of deleterious mutations, and impairs the ability of a species to adapt to
262 novel conditions over time (Bachtrog & Charlesworth 2002; Wright & Andolfatto 2008).

263 Along these lines, significantly higher amounts of nucleotide substitutions were fixed in selfing
264 species following divergence from their outcrossing sisters. As molecular evolutionary rates are similar

265 among closely-related annual plant species (Andreasen & Baldwin 2001), the differences in branch
266 lengths (*i.e.*, substitutions) we observed between selfing and outcrossing sisters reflect the faster rates at
267 which mutations were **fixed** in selfing lineages. Although a non-coding region was used to build the
268 phylogenetic trees in our dataset, our results demonstrate that selfers accumulate non-lethal mutations
269 more rapidly. This reflects the lack of heterozygosity present in selfer genomes, and small effective
270 population sizes. As with selectively neutral mutations, mildly deleterious, non-lethal mutations can also
271 escape purifying selection, and thus are likely to more rapidly accumulate in selfing lineages (Slotte *et al.*
272 2013). The comparatively small sizes of selfing species' genomes increases the chance of deleterious
273 mutations being fixed via linked (background) selection as well (Hudson & Kaplan 1995; Albach &
274 Greilhuber 2004; Charlesworth 2012). Our results further suggest that mutation accumulation rates of
275 selfers will only increase through time. As each generation of selfing reduces heterozygosity by 50%, the
276 genomes of primarily selfing species will rapidly reach near clonal status. Similarly, selfing is expected to
277 reduce effective population size by a factor of two, or more due to a high probability of experiencing
278 bottlenecks through founding effects and a more pronounced effects of linked selection (Jarne 1995;
279 Charlesworth & Wright 2001; Hartfield 2016). In this case, non-lethal deleterious mutations will become
280 fixed almost as soon as they arise (Glémin & Ronfort 2013). Thus, lineages of selfing species may persist
281 for less time than outcrossing lineages, and extant selfing lineages have accordingly been found to be
282 evolutionarily recent (Foxye *et al.* 2009; Escobar *et al.* 2010; Ness *et al.* 2010; Busch *et al.* 2011; Pettengill
283 & Moeller 2012).

284 Additional factors may influence the rate at which mutations are fixed or niche breadth changes,
285 but we minimized the potential effects of unaccounted variables by comparing closely-related sister
286 species. Although our analyses are limited in scope and do not enable us to make a direct or causal
287 connection between the predicted decrease in niche breadth of selfing species and long-term costs of
288 reduced genetic diversity, previous studies have shown them to be linked (Noy *et al.* 1987; Morran *et al.*

289 2009), and selfing lineages have been shown to experience considerable accumulation of deleterious
290 mutations over relatively short timescales (Hu *et al.* 2011; Slotte *et al.* 2013).

291 *Reconciling geographic range and climatic niche breadth*

292 In general, species with higher levels of genetic diversity should maintain populations across
293 greater environmental heterogeneity, thus facilitating larger geographic ranges than species with narrow
294 ecological niches (Brown 1984). However, it is possible that the realized niche of selfing species is closer
295 to their fundamental niche than it is for their outcrossing sisters. The fundamental niche refers to the
296 environmental requirements of a species to maintain a population indefinitely, independent of species
297 interactions and immigration (Hutchinson 1957; Holt 2009). The realized niche is the proportion of a
298 species' fundamental niche that remains after accounting for interspecific interactions (e.g., competition),
299 dispersal limitation, and the lack of suitable contemporary environments (Colwell & Rangel 2009). The
300 release from mate limitation allows selfers to colonize small or fragmented habitats, enabling them to
301 explore a larger extent of their fundamental niche (i.e., increase of realized niche). The initial purging of
302 recessive deleterious alleles could also contribute to the expansion of selfers' realized niche (Peterson &
303 Kay 2015). Such a scenario could translate to a transiently larger species range for selfers, but the
304 limitations of an increasingly homogeneous genome should become apparent over time. Mutations
305 accumulate as heterozygosity decreases, the fundamental niche contracts, and eventually the geographic
306 range shrinks (Fig. 5).

307 Like previous studies (Grossenbacher *et al.* 2015, 2016), our analyses are correlative and we
308 cannot demonstrate a causal relationship between niche breadth and mating system. We restricted our
309 analysis to definitively selfing or outcrossing species, but multiple mechanisms affect intermediate levels
310 of self-fertilization, even within populations (Goodwillie *et al.* 2005). Despite the inclusion of the largely
311 tropical genera *Dalechampia* and *Schiedea*, most of the clades we analyzed have primarily temperate
312 distributions, and different patterns might have been observed if more tropical taxa had been included. As

313 more data become available, we can examine further the relationships between the degree of selfing,
314 range size, and niche breadth that account for additional factors, including biotic interactions.

315 Nonetheless, our observations that, relative to outcrossing sister taxa, the climatic niches of
316 selfing species are slower to differentiate (Fig. 3) and stand to become narrower over time with genetic
317 degradation (Fig 2) are consistent with the well-established idea that selfing is an evolutionary dead-end
318 (Dobzhansky 1950; Stebbins 1957). Despite high transition rates to selfing, < 15% of extant seed plants
319 are predominantly selfing (Goodwillie *et al.* 2005; Igic & Kohn 2006) and transitions from selfing to
320 outcrossing occur rarely, if ever (Igic & Busch 2013). Furthermore, selfing lineages have been shown to
321 be younger than outcrossing ones, implying that they are more short-lived (Holsinger 2000). Genetic
322 impoverishment and accumulation of mildly deleterious alleles may not manifest as short-term losses of
323 fitness or geographic range in all selfing species, but it likely will affect their potential for evolutionary
324 adaptation (Honnay & Jacquemyn 2007) and eventually outweigh any (initial) advantages of self-
325 fertilization (Fig. 5). Indeed, simulations have demonstrated that the greater genetic load in self-
326 compatible lineages results in overall increases in time to adaptation and extinction risks regardless of
327 self-fertilization rates (Peterson & Kay 2015). Given rapid rates of recent climatic change, this may have
328 severe consequences in the near future, especially since many plant species lack sufficient ability to track
329 the shifting climate northward or upward (Honnay *et al.* 2002). The larger geographic range and
330 comparable niche breadth of many selfers most likely is a temporary phenomenon caused by an expanded
331 realized niche, and may be a snapshot of the early stages of a temporal spiral towards extinction.

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526 **Data Accessibility:** Phylogenetic trees, occurrence data, and mating system data are available at: Dryad
527 doi:10.5061/dryad.hv117

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529 **Author Contributions:** D.S.P conceived the study idea and performed all analyses; A.M.E. advised
530 statistical analyses; D.S.P., A.M.E., and C.C.D. interpreted the results; and D.S.P and C.C.D. wrote the
531 manuscript. All authors contributed significantly to revisions.

532

533 **Tables:**

534 Table 1. Results of five separate linear mixed models analyzing the effect of mating system on species'
535 niche breadth in 19 dimensional climate space estimated at four different spatial resolutions. The
536 categorical coefficient estimates are log-odds ratios and represent departures from the “outcrosser” mating
537 category. Marg. R^2 represents the proportion of variance in explained by mating system and Cond. R^2
538 values are the variance explained by the entire model.

Resolution	Estimate	Std. Error	df	t	p-value	Marg. R^2	Cond. R^2
<i>Response: ln-transformed niche breadth</i>							
0.05°	-0.11	0.24	18.28	-0.49	0.63	0.00	0.97
0.1°	-0.17	0.19	16.28	-0.88	0.39	0.01	0.95
0.5°	-0.06	0.14	16.63	-0.41	0.69	0.00	0.95
1°	-0.05	0.10	14.50	-0.53	0.60	0.00	0.95

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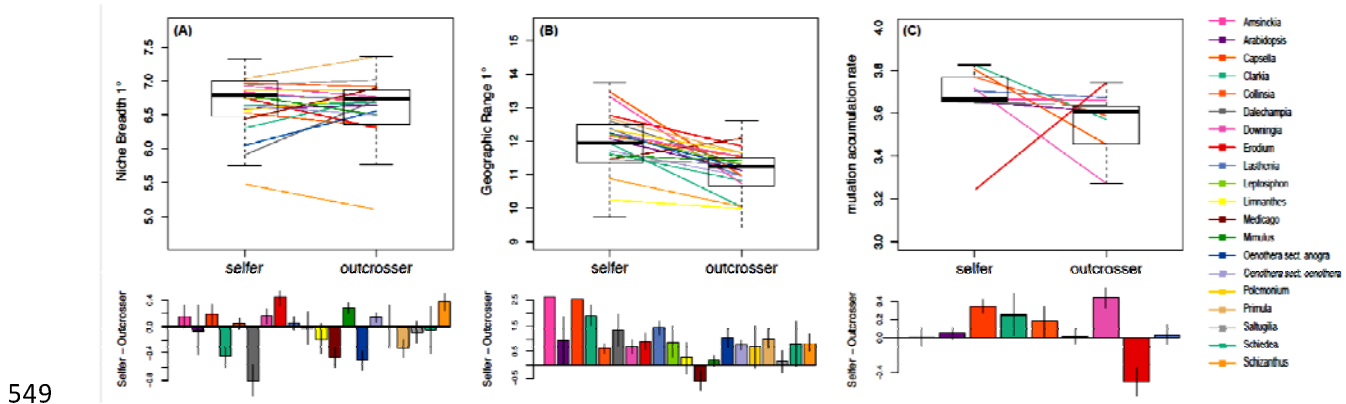
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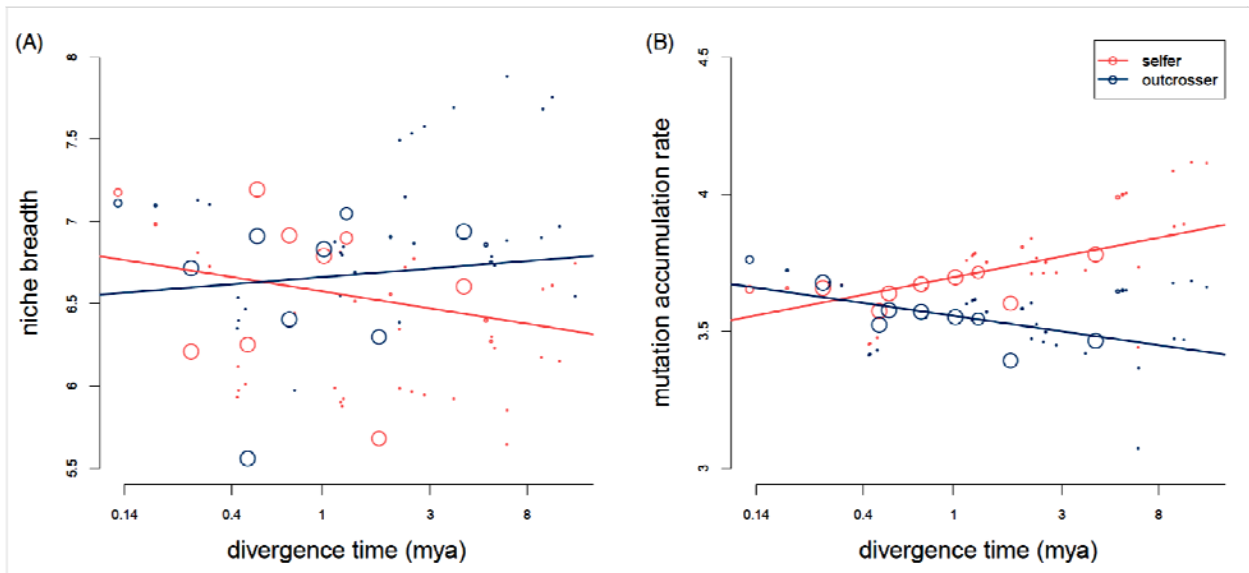
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548 **Figures:**



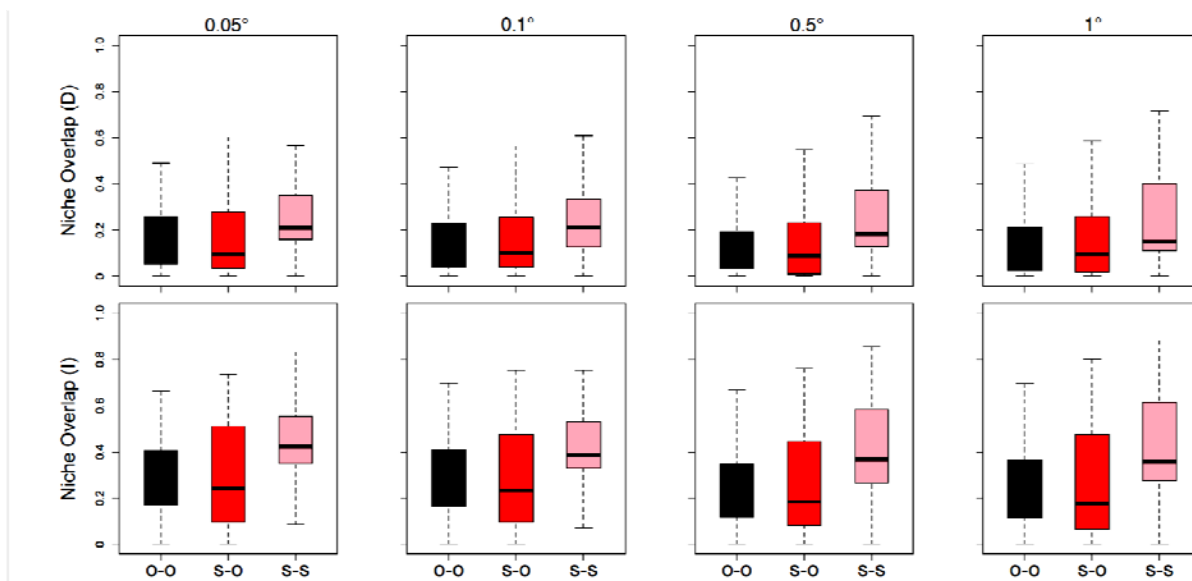
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 550 Figure 1. Comparisons of niche breadth, geographic range, and mutation accumulation rates among
 551 selfers and outcrossers. (A) Top panel: Box plots of predicted (fitted) niche breadth of selfing and
 552 outcrossing sister species assessed in 19 dimensional climate space and at 1° resolution. Colored line
 553 segments indicate predicted slopes for each of 20 clades and the vertical axis is natural logarithmic scale.
 554 Bottom bar charts: average sister species log difference in niche breadth for each of 20 clades, with
 555 vertical lines representing standard errors. (B) Top panel: Box plots of predicted range size of selfing and
 556 outcrossing sister species assessed at 1° resolution. Bottom bar charts: average sister-species log
 557 difference in range size, with vertical lines representing standard errors. (C) Top panel: Box plots of
 558 predicted rate of mutation accumulation of annual selfing and outcrossing sister species. Bottom bar
 559 charts: average sister-species log difference in rate, with vertical lines representing standard errors. Clade
 560 averages are only used for illustration purposes, and statistical analyses were performed with individual
 561 species-pair estimates.

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 564 Figure 2. Niche breadth (A) and mutation accumulation rate (B) as a function of divergence time for
 565 selfing and outcrossing sister species at 1° resolution. The size of the circles represent the posterior
 566 probability of which the focal species pair were each other's sister taxon. The line segments represent the
 567 linear regression results for selfers (pink) and outcrossers (blue). Niche breadth is log-transformed and
 568 divergence time is on a back-transformed natural logarithmic scale.

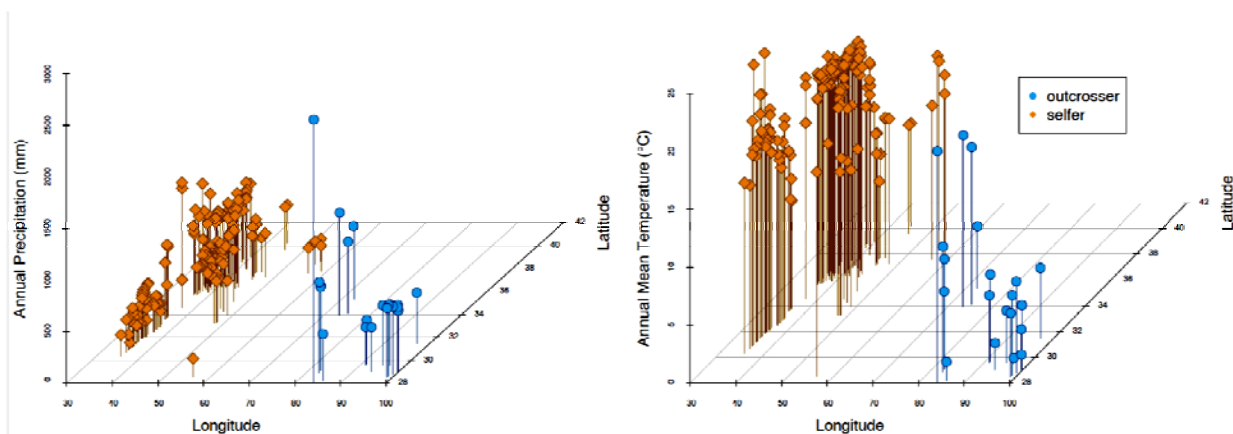
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571 Figure 3. Boxplots of two metrics of sister pair niche overlap by mating system category at four spatial
572 resolutions; outcrosser-outcrosser (s-s, dark grey), selfer-outcrosser (o-o, red), selfer-selfer (s-o, pink).

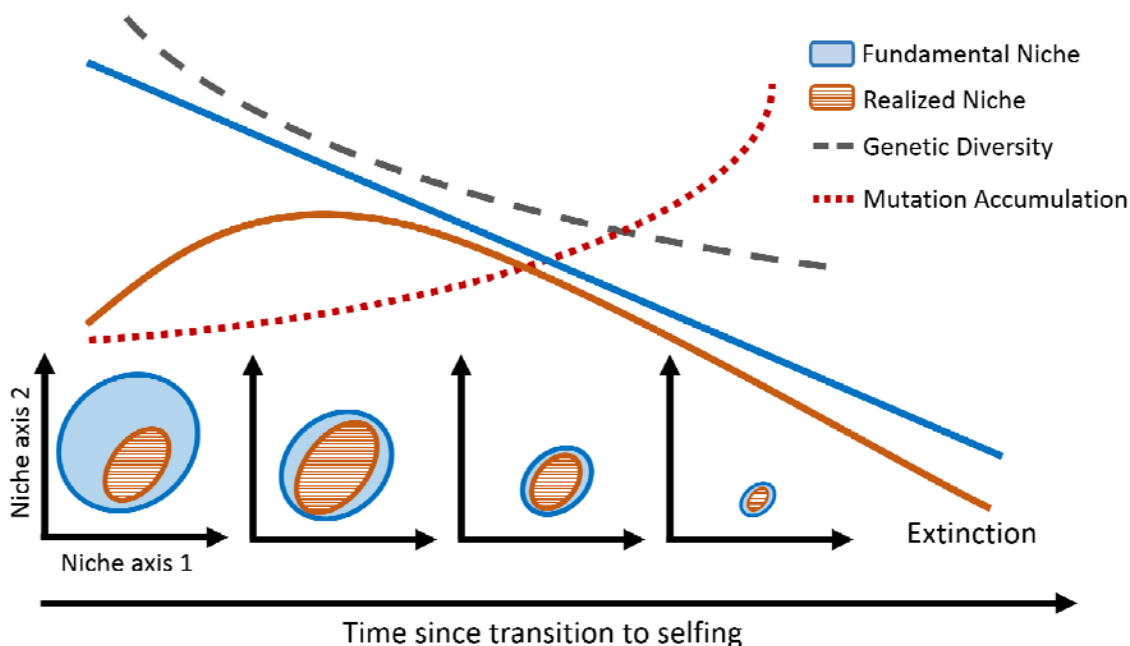
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575 Figure 4. Geographic range and climatic range inhabited by *Medicago edgeworthii* (outcrosser) and
576 *Medicago radiata* (selfer). Points represent the geographic locations of each species.

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579 Figure 5. Expected changes in genetic diversity, mutation accumulation, fundamental niche, and realized
580 niche following transition to selfing.

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582 **Supporting information**

583 Figure S1: Comparisons of niche breadth and geographic range among selfers and outcrossers.

584 Table S1: R Packages used in analyses.

585 Table S2: Results of linear mixed models analyzing the effect of mating system on species' range (max –
586 min) and standard deviation (SD) across 19 bioclimatic variables estimated at four different spatial
587 resolutions.

588 Table S3: Results of five separate linear mixed models analyzing the effect of mating system on species'
589 niche breadth in 7 dimensional climate space estimated at four different spatial resolutions.

590 Table S4: Results of ten separate linear mixed models analyzing the effect of mating system on species'
591 niche breadth in 19 dimensional climate space estimated at four different spatial resolutions.

592 Table S5: Results of linear mixed models analyzing the effect of mating system on species' range (max –
593 min) and standard deviation (SD) across 19 bioclimatic variables estimated at four different spatial
594 resolutions.

595 Table S6: Results of four separate linear mixed models examining the effect of mating system, divergence
596 time, and their interaction on species' niche breadth assessed across four spatial resolutions.

597 Table S7: Results of fractional logit regression models assessing the effect of sister pair mating system on
598 niche overlap at four spatial scales.

599 Table S8: Results of fractional logit regression models assessing the effect of sister pair mating system on
600 niche overlap at four spatial scales, sequentially removing each genus.

601 Table S9: Results of fractional logit regression models assessing the effect of sister pair divergence time
602 on niche overlap four spatial scales. The coefficient estimates are log-odds ratios.

603 Table S10: Results of a linear mixed model examining the effect of mating system, divergence time, and
604 their interaction on species' rates of molecular evolution.