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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Abstract

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

Introduction

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

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

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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

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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 km^2

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

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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

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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

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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

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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

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265   among closely-related annual plant species (Andreasen & Baldwin 2001), the differences in branch

266   lengths (*i.e*., substitutions) we observed between sefling 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 (Foxe *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.*

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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

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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.

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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
Response: ln-transformed niche breadth							
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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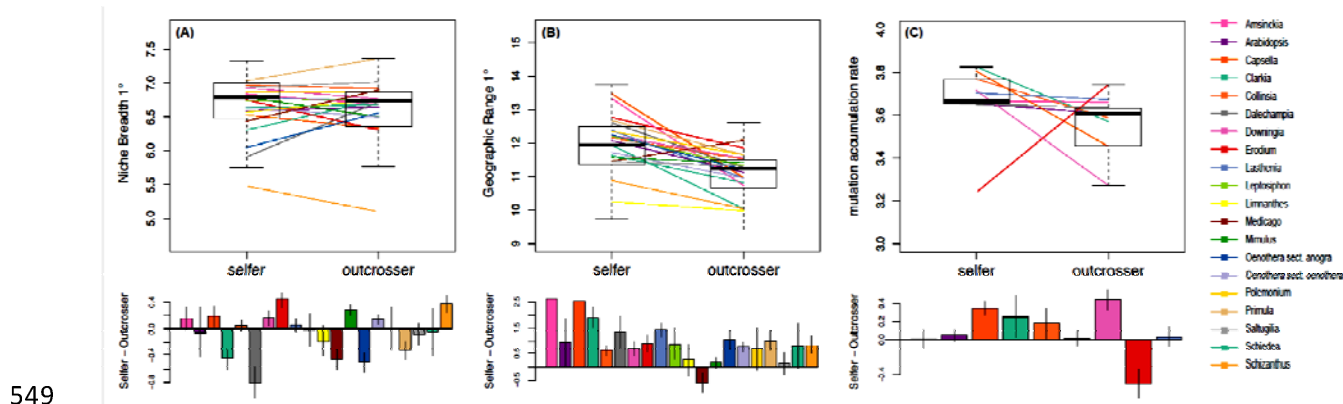
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Figures:


Figure 1. Comparisons of niche breadth, geographic range, and mutation accumulation rates among selfers and outcrossers. (A) Top panel: Box plots of predicted (fitted) niche breadth of selfing and outcrossing sister species assessed in 19 dimensional climate space and at 1° resolution. Colored line segments indicate predicted slopes for each of 20 clades and the vertical axis is natural logarithmic scale. Bottom bar charts: average sister species log difference in niche breadth for each of 20 clades, with vertical lines representing standard errors. (B) Top panel: Box plots of predicted range size of selfing and outcrossing sister species assessed at 1° resolution. Bottom bar charts: average sister-species log difference in range size, with vertical lines representing standard errors. (C) Top panel: Box plots of predicted rate of mutation accumulation of annual selfing and outcrossing sister species. Bottom bar charts: average sister-species log difference in rate, with vertical lines representing standard errors. Clade averages are only used for illustration purposes, and statistical analyses were performed with individual species-pair estimates.
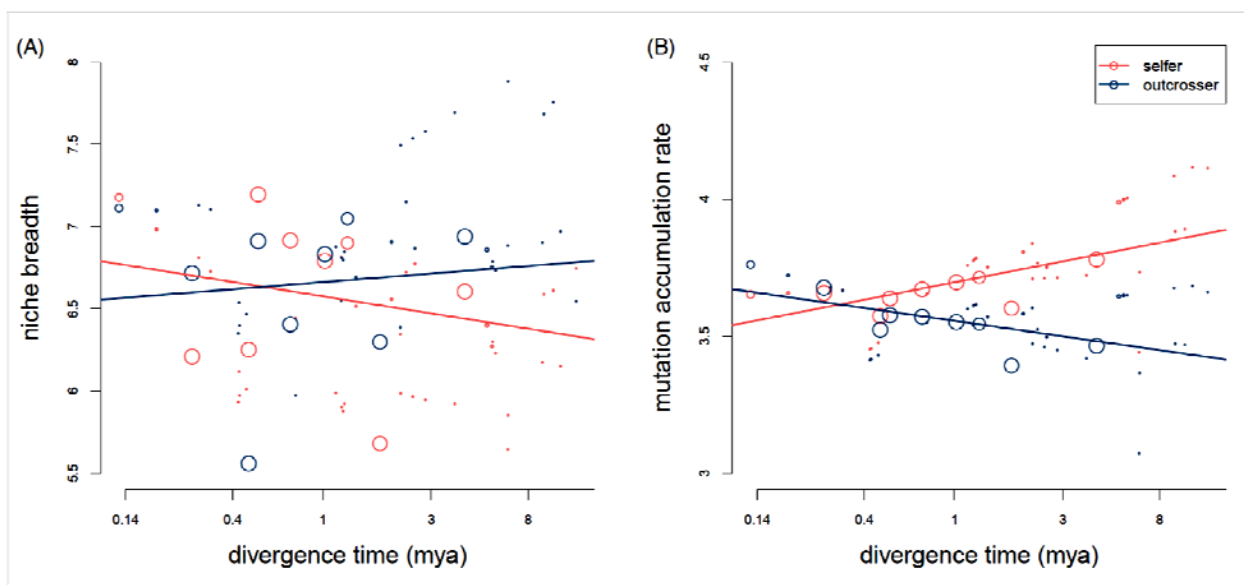
Figure 2. Niche breadth (A) and mutation accumulation rate (B) as a function of divergence time for selfing and outcrossing sister species at 1° resolution. The size of the circles represent the posterior probability of which the focal species pair were each other's sister taxon. The line segments represent the linear regression results for selfers (pink) and outcrossers (blue). Niche breadth is log-transformed and divergence time is on a back-transformed natural logarithmic scale.
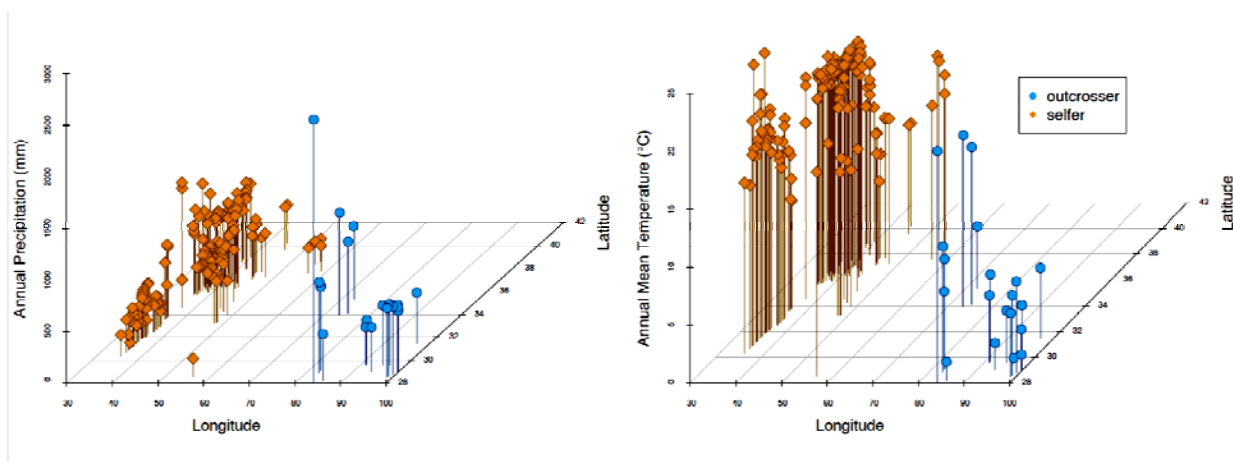
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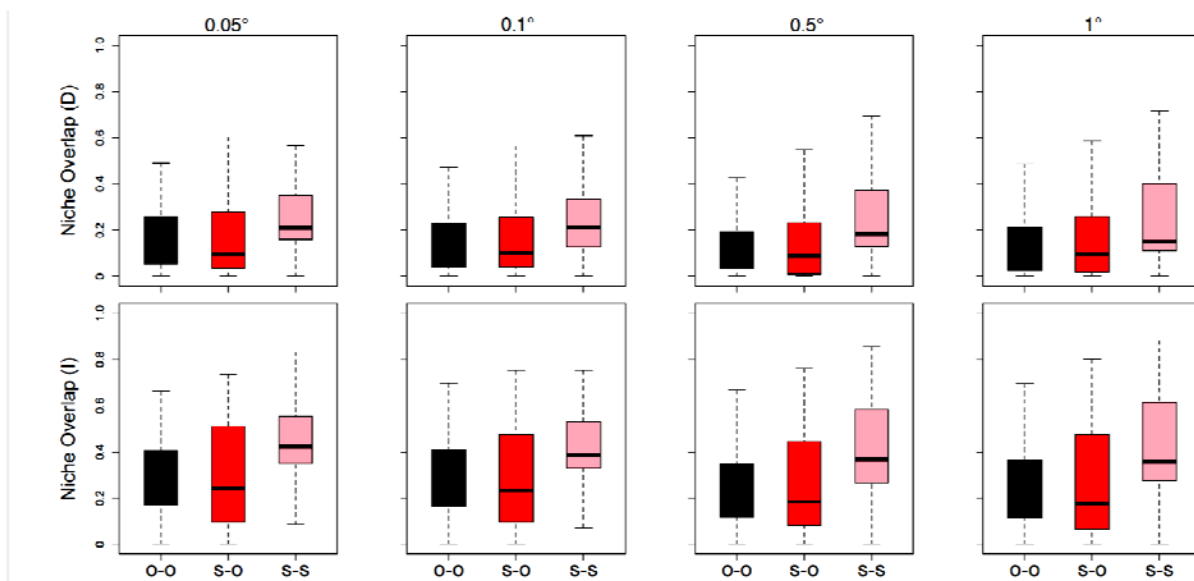
Figure 3. Boxplots of two metrics of sister pair niche overlap by mating system category at four spatial resolutions; outcrosser–outcrosser (s-s, dark grey), selfer–outcrosser (o-o, red), selfer–selfer (s-o, pink).
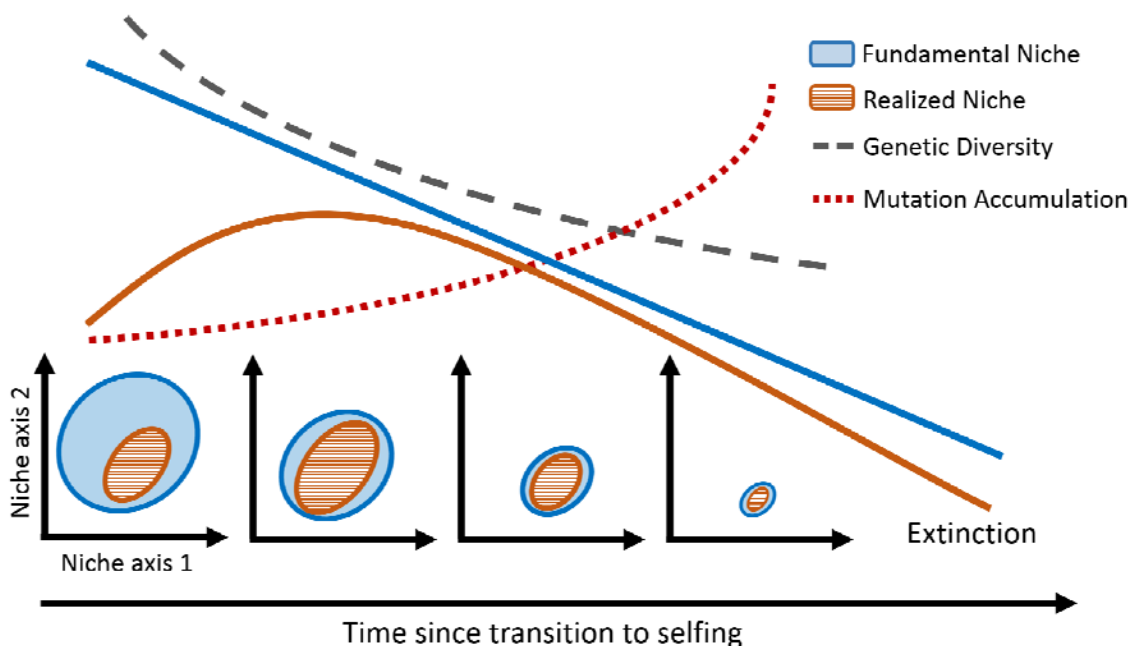
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Figure 4. Geographic range and climatic range inhabited by *Medicago edgeworthii* (outcrosser) and *Medicago radiata* (selfer). Points represent the geographic locations of each species.

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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.