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RESEARCH PAPER

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Mating system does not predict niche breath*

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Abstract

Aim: Self-pollinating plants ('selfers') have larger geographical ranges and inhabit higher latitudes than their outcrossing relatives. This finding has led to the hypothesis that selfers also have broader climatic niches ('niches') because the increased likelihood of successful colonization into new areas and the initial purging of deleterious mutations could offset the inability of selfers to adapt to new environments owing to low heterozygosity. Here, we examine the niches of hundreds of closely related selfing and outcrossing species to determine whether selfers do indeed have larger niche breadths.

Location: Global.

Time period: Current.

Major taxa studied: Twenty clades of flowering plants comprising 424 species.

Methods: We estimated and compared the climatic niches of 194 pairs of sister species across 15 families, which differed in mating system. We incorporated these results into models predicting niche breadth and its change over time to estimate the effects of mating system on niche breadth. Furthermore, we compared the degree of niche divergence between sister-species pairs of various mating system combinations.

Results: Selfers did not have wider niche breadths than their outcrossing sister taxa. Sister pairs of selfers also exhibited greater niche overlap than outcrossing sisters, implying that niche expansion becomes limited after the transition to selfing. Furthermore, the niche breadth of selfers was predicted to decrease significantly faster than that of closely related outcrossers.

Main conclusions: Our results demonstrate a decoupling in the range size and niche breadth of selfers. The larger geographical range and comparable niche breadths of many selfers is most likely to be a temporary phenomenon caused by a transiently expanded realized niche, and both will become constricted over time in comparison to outcrossers.

KEYWORDS

Baker's law, geographical range, mating system, niche breadth, outcrossing, selfing

1 | INTRODUCTION

Species ranges are influenced by various life-history traits (Sexton, McIntyre, Angert, & Rice, 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; Pannell & Barrett, 1998; Stebbins, 1957). Along these lines, self-pollinating plant species (hereafter, 'selfers') consistently display larger geographical ranges and occupy higher maximal latitudes than closely related outcrossing species (hereafter, 'outcrossers'; Grossenbacher, Briscoe Runquist, Goldberg, & Brandvain, 2015; but see Lowry & Lester, 2006). Based on these results, it has been hypothesized that selfing species may also have greater climatic tolerances and climatic niche (hereafter, 'niche') breadths than outcrossing sister taxa (Grossenbacher et al., 2015; Randle, Slyder, & Kalisz, 2009). In support of this argument, ecologists and evolutionary biologists have established that the distribution

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*This research was uploaded to a preprint server (bioRxiv): https://doi.org/10.1101/157974 and range size of plant species are influenced strongly by climate (Park & Potter, 2015; Parker, 1963; Stephenson, 1990), and large geographical range size is thought to be associated with wider niche breadths (Brown, 1984; Sheth & Angert, 2014; Slatyer, Hirst, & Sexton, 2013). Species occurring at higher latitudes have also been hypothesized to have broader environmental tolerances because of larger seasonal fluctuations (Stevens, 1989; but see Šizling, Storch, & Keil, 2015). Additionally, selfing has been hypothesized to promote local adaptation and niche divergence by converting non-additive genetic variance resulting from elements such as epistasis or dominance into additive variance for tolerance to new habitats, thus facilitating expansion into new climates (Kirkpatrick, 2000; Lande, 1977; Levin, 2010).

It is challenging to reconcile the observation that selfers have larger geographical ranges (and possibly wider niches) with the widely supported hypothesis that the switch to self-fertilization is an evolutionary 'dead end' (Dobzhansky, 1950; Stebbins, 1957; Takebayashi & Morrell, 2001). Selection usually favours outcrossing over selfing (Goldberg et al., 2010); the latter has been associated with increased homozygosity and reduced effective population sizes (Pollak, 1987; Schoen & Brown, 1991), increased accumulation of mutations (Heller & Smith, 1978; Morran, Parmenter, & Phillips, 2009) and reduced genetic diversity (Glemin, Bazin, & Charlesworth, 2006; Hamrick & Godt, 1996; Jarne & Städler, 1995; Nybom, 2004). These effects are hypothesized to limit the ability of selfers to colonize and adapt to different environments successfully (Crawford & Whitney, 2010; Hamrick & Godt, 1996). Moreover, it is possible that geographical range and niche breadth are decoupled over short evolutionary times (Randle et al., 2009). In this case, we hypothesize that relative to their outcrossing sisters, selfers might inhabit larger geographical ranges that exhibit relatively little climatic variation. Furthermore, we would also expect that the lack of genetic heterozygosity and adaptive potential could limit the degree to which niches of selfers can diverge from each other, manifesting as greater niche overlap between sister selfers than between sister outcrossers.

Here, we test whether selfers with larger geographical ranges than their outcrossing relatives also have greater niche breadths. We also test whether niches are less likely to change after evolutionary shifts from outcrossing to selfing by examining niche overlap between pairs of selfing sister taxa and between pairs of outcrossing sister taxa. Given that niche overlap is negatively proportional to the amount of niche change since divergence, it may reflect the potential of species to expand their niches (Broennimann et al., 2007; Turner, Fréville, & Rieseberg, 2015). We hypothesize that freedom from mate or pollen limitation initially allows selfers to expand their geographical ranges and realized niche breadth. However, as homozygosity and the accumulation of mildly deleterious mutations increase because of inbreeding, the adaptive potential of selfers should decrease more rapidly than that of outcrossers, resulting in more constrained niches.

2 | MATERIALS AND METHODS

All analyses described below were done in R (R Core Team, 2013); detailed information on the packages used is provided in Supporting Information Table S1. Source data and R code are freely available from Dryad: doi:10.5061/dryad.hv117.

2.1 | Dataset

To estimate and compare the niche breadth of selfing and outcrossing species, we used a previously published dataset compiled from literature by Grossenbacher et al. (2015) that collated 54 studies describing mating systems of plant 424 species from 20 well-supported, phylogenetically divergent clades representing 15 families. All clades had previously published species-level phylogenies, contained at least one predominantly selfing species and one predominantly outcrossing species, and had DNA sequence data for $\geq$ 50% of the species available from GenBank (http://www.ncbi.nlm.nih.gov/genbank). Overall, clades comprised 35 ± 7 ($\pm$ 1 *SE*) species, 80 ± 4.6% of which had sequence data. Grossenbacher et al. (2015) classified species as 'variable mating' when outcrossing rates were between .2 and .8, or when there was extensive among-population variation in outcrossing rates and traits associated with outcrossing. Such species were not considered in our study. An exception to this classification were the species in *Oenothera* sect. *Oenothera*, which were classified as either sexually reproducing or functionally asexual because individuals can self-fertilize but do not undergo segregation and recombination owing to permanent translocations (Johnson, Smith, & Rausher, 2010). Thus, sexual *Oenothera* sect. *Oenothera* species are partly or wholly self-incompatible and were assumed to be outcrossing. The mating systems of different taxa have different indicators; hence, the methods and criteria varied to some degree among clades but were consistent within them (see table S3 of Grossenbacher et al., 2015).

We also used previously published time-calibrated phylogenies for all 20 clades based on internal transcribed spacer (*nrITS*) sequences (Grossenbacher et al., 2015, 2016). Grossenbacher et al. (2015) estimated phylogenetic relationships and divergence times in a Bayesian framework with an uncorrelated log-normal relaxed clock model and a Yule process of speciation. Sister species, which are exclusively one another's closest relative, were identified by searching for monophyletic groups composed of two species in a subset of 9,000 trees from the posterior distribution for each clade. The posterior probability of each sister pair (i.e., the proportion of trees in which the two species were sister to one another) was used as a measure of phylogenetic uncertainty. A total of 498 sister-species pairs were identified, of which 194 differed in mating system. Among clades, the number of selfer–outcrosser sister pairs ranged from one to 68, with posterior probabilities ranging from $< .01$ to 1.0. As these phylogenies may not comprise all extant taxa, these sister pairs may not represent true extant sisters, but are nonetheless recently diverged species and represent independent evolutionary replicates (Grossenbacher et al., 2015).

2.2 | Estimating niche breadth and overlap

We used curated geographical records (excluding those with coordinate accuracy $>$ 100 km, coordinates failing to match the locality description or those with taxonomic misidentifications), from the Global Biodiversity

Information Facility (http://www.gbif.org) to infer the environmental conditions occupied by each species (Grossenbacher et al., 2015, 2016). Only coordinates from species' native ranges were used. Among abiotic environmental variables, temperature (Parker, 1963) and moisture (Pigott & Pigott, 1993; Stephenson, 1990) strongly influence plant ranges (Holdridge, 1947). We thus used global data on 19 bioclimatic variables at 2.5 arc-min resolution derived from monthly temperature and rainfall values (Busby, 1991; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Nix, 1986). We recorded the range (maximum–minimum) and standard deviation (*SD*) of each bioclimatic variable in species' distributions, which each represent different facets of univariate climatic niche breadth (May & MacArthur, 1972). We also estimated the niche breadth of each species by calculating the average Euclidian distance between all points in each species' range and the centre of their distribution in 19-dimensional climatic space (i.e., multivariate standard deviation). As Euclidian distance measures can be sensitive to covariance among variables, we repeated this process on a subset of seven bioclimatic variables likely to be associated with the distribution of plant species, and whose pairwise Pearson's correlation coefficient was $|r| < .7$ to avoid multicollinearity (Dormann et al., 2013): isothermality (BIO2), minimal temperature of the coldest month (BIO6), mean temperature of the wettest quarter (BIO8), precipitation of wettest month (BIO13), precipitation seasonality (BIO15), precipitation of the warmest quarter (BIO18) and precipitation of the coldest quarter (BIO19). We also used principal component analyses (PCAs) to summarize all the bioclimatic variables, and estimated niche breadth as the area of the convex hull surrounding each species' points of occurrence in climate space defined by the first two principal axes. Species ranges were defined as the summed area of occupied grid cells across cell sizes of .05, .1, .5 or 1 decimal degree, corresponding roughly to 25, 100, 2,500 and 10,000 km^2 respectively (Grossenbacher et al., 2015, 2016). All subsequent analyses were done using niches derived from each of these cell sizes to assess whether the results were sensitive to the spatial grain of estimation.

To compare niche-expansion ability between selfers and outcrossers, we assessed the proportion of shared niche space (overlap) among sister taxa whose mating systems differed: sister pairs in which each taxa is a selfer (s-s: 'selfing–selfing'); sister pairs in which one of the taxa is a selfer and the other is an outcrosser (s-o: 'selfing–outcrossing'); and sister pairs in which both are outcrossers (o-o: 'outcrossing–outcrossing'). To examine the degree of niche overlap between sister species, we used the approach developed by Broennimann et al. (2012), which has been shown to be robust to errors and biases associated with the estimation of niche overlap. This method compares environmental conditions available for a species within a defined study extent with their observed occurrences and calculates the available environmental space defined by the first two principal axes (PCA-env). These extents again were delimited as occupied cells of .05, .1, .5 and 1 decimal degrees to account for different spatial grains. The same 19 bioclimatic variables used above were used for the multivariate PCA. Sampling bias was corrected by using a Gaussian kernel-density smoothing approach (Broennimann et al., 2012; Silverman, 1986). The degree of niche overlap between each sister-species pair was calculated using Schoener's *D* (Schoener, 1968) and modified Hellinger distance (*I*) (Warren, Glor, Turelli, & Funk, 2008), both of which vary from zero (no niche overlap) to one (identical niche).

2.3 | Statistical analyses

The following analyses were done separately for all three calculations of niche breadth. Linear mixed-effects models were used to test differences in ln-transformed niche breadth between outcrossing and selfing sister species. Mating system was treated as a fixed effect. Genus (or section, in the case of *Oenothera*) and sister-pair identity entered the model as random factors, and we estimated slopes for each genus. The posterior probability of each sister-species pair was included as a weighting factor in our models to account for phylogenetic uncertainty. We included the interaction of divergence time (ln-transformed) with mating system as a fixed effect in the model to test whether the effect of divergence time on niche breadth covaried with mating system. This test also included a random effect for genus-specific mating system. As niche breadth may be affected by ploidy and life history (Morishima, Sano, & Oka, 1984; Thompson, Husband, & Maherali, 2014), we also ran these analyses including only sister pairs that did not differ in these potentially correlated traits. Ploidy and life history for our focal taxa were classified based on previously published literature (see table S4 of Grossenbacher et al., 2015).

Niche overlap values (Schoener's *D*, modified Hellinger's distance *I*) range from zero to one. These bounds, and the right-skewed distributions of these measures, violate the assumptions of standard linear models (Ramalho, Ramalho, & Murteira, 2011). Hence, we used fractional logit regression models (Papke & Wooldridge, 1996) to test whether the mating systems of sister-species pairs (s-s, s-o and o-o) influenced niche overlap, with sister-pair mating system as a categorical predictor and niche overlap (Schoener's *D* or Hellinger's *I*) as the response variable. The posterior probability of each sister-species pair was again included as a weighting factor to account for phylogenetic uncertainty, and models were fitted using maximum likelihood. Likewise, we used fractional logit models to test whether the time since divergence (ln-transformed) influenced niche overlap. All analyses were replicated across the four spatial scales defined above to examine whether our results were robust to the spatial scale at which species niche was estimated. Finally, to address the possibility that certain clades might have heavily influenced the overall results, we ran these analyses while sequentially dropping individual genera (i.e., a statistical jackknife). That is, we repeated our analyses on 20 subsets of 19 clades, and in each case examined whether the time since divergence had a significant effect on the degree of niche overlap. In all cases, we report pseudo-R^2 values as measures of the variation explained by fixed and random effects.

3 | RESULTS

Mating system did not significantly influence niche breadth measured either as multivariate climate space (Figure 1, Table 1) or based on individual bioclimatic variables ($p > .05$ all cases; Supporting Information Table S2). The relationship between mating system and niche breadth was inconsistent across clades and sister pairs. Comparisons of niche

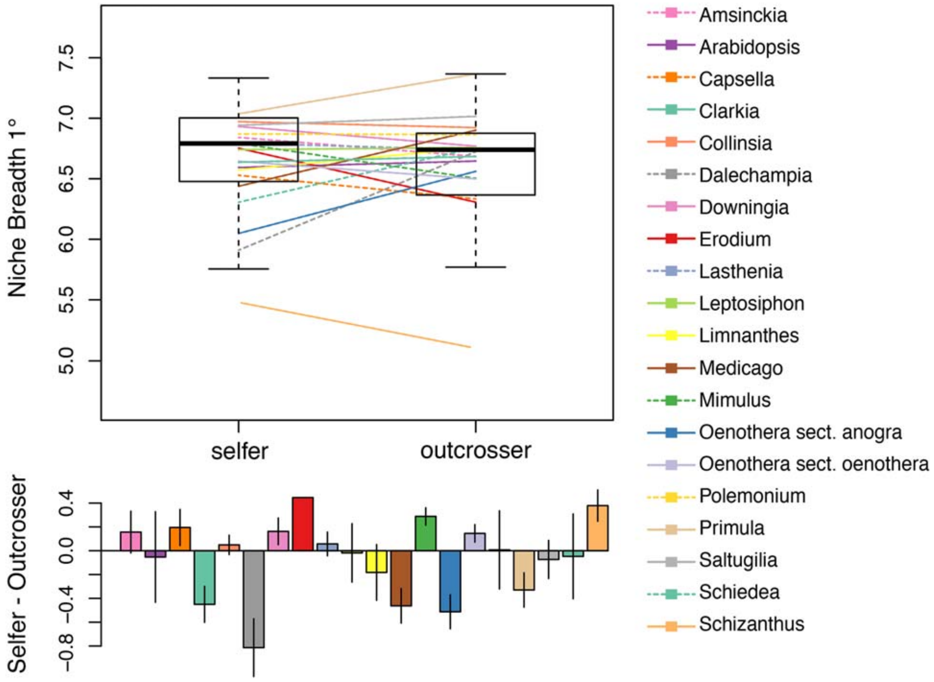

FIGURE 1 Comparisons of niche breadth among selfers and outcrossers. Top panel: Box plots of predicted (fitted) niche breadth of selfing and outcrossing sister species assessed in 19-dimensional climate space and at 1° resolution. Coloured line segments indicate predicted slopes for each of 20 clades, and the vertical axis is a 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. Clade averages are used for only for purposes of illustration, and statistical analyses were performed with individual species-pair estimates. Dotted lines were added to increase visibility

breadth for the uncorrelated subset of bioclimatic variables yielded similar results, as did comparisons based on the first two principal axes of climate space occupied by species (PCA; $p > .05$; Supporting Information Figure S1, Table S3). These results were consistent across all spatial grains and when excluding sister pairs that differed in ploidy and life history (Supporting Information Tables S4 and S5). However, the niche breadth of selfing species tended to decrease over evolutionary time compared with the niche breadth of their outcrossing sisters, which tended to increase over evolutionary time (divergence time × mating system: $p < .05$; Figure 2; Supporting Information Table S6).

Selfing sister pairs (s-s) had significantly greater degrees of niche overlap than sister pairs with at least one outcrossing species (s-o and o-o; Figure 3; Supporting Information Table S7). These patterns were robust to the removal of all genera except *Medicago*, which comprised the largest number (39) of s-s pairs (Supporting Information Table S8). Although the distribution of divergence times differed among the three pairs of mating systems (s-s, s-o and o-s) (Grossenbacher, Briscoe Runquist, Goldberg, & Brandvain, 2016), niche overlap was not significantly influenced by divergence time (Supporting Information Table S9).

4 | DISCUSSION

Despite the fact that selfers occupy larger geographical ranges and higher latitudes than their outcrossing sisters (Grossenbacher et al., 2015), we found that this did not necessarily translate into greater climatic niche breadth. Instead, our results indicate that niche breadth and range size have been decoupled, potentially leading to species with large geographical ranges but narrow climatic niches. For three reasons

TABLE 1 Results of five separate linear mixed models analysing the effect of mating system on species niche breadth in 19-dimensional climate space estimated at four different spatial resolutions

Resolution (°)	Estimate	*SE*	d.f.	*t*	*p*-value	Marginal R^2	Conditional R^2
Response: ln-transformed niche breadth							
0.05	−.11	.24	18.28	−.49	.63	.00	.97
0.1	−.17	.19	16.28	−.88	.39	.01	.95
0.5	−.06	.14	16.63	−.41	.69	.00	.95
1	−.05	.10	14.50	−.53	.60	.00	.95

Note. The categorical coefficient estimates are log-odds ratios and represent departures from the 'outcrosser' mating category. Marginal R^2 represents the proportion of variance explained by mating system, and conditional R^2 values are the variance explained by the entire model.

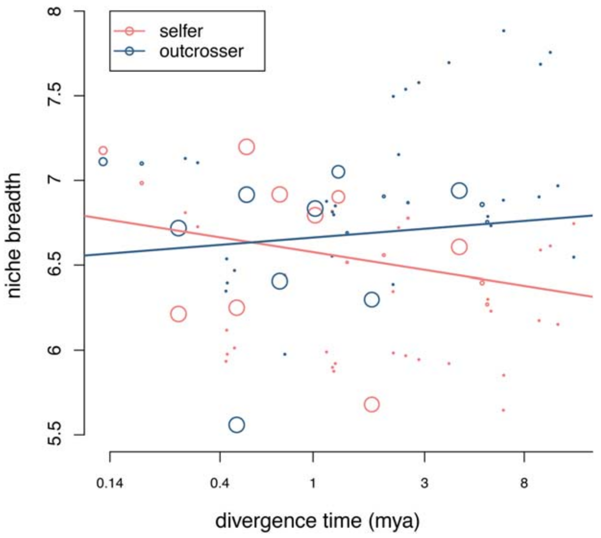

FIGURE 2 Niche breadth as a function of divergence time for selfing and outcrossing sister species at 1° resolution. The size of the circles represents the posterior probability of the focal species pair being each other's sister taxon. The line segments represent the linear regression of niche breadth and log divergence time for selfers (pink) and outcrossers (blue). The transition from outcrossing to selfing had a significant negative effect with increasing time since divergence ($p < .05$). Niche breadth is log-transformed, and divergence time is on a back-transformed natural logarithmic scale

discussed below, we argue that the large range sizes currently observed for selfing plant species are an evolutionarily transient phenomenon.

4.1 | Mating system does not consistently predict niche breadth

No effect of mating system was detected, regardless of the method used to quantify niche breadth or spatial scale examined, even across individual climatic variables. Our niche-breadth analyses did not support a tight association between range size and niche breadth. Our results also did not support the hypothesis that selfers should have wider niche breadths than their outcrossing sisters because of the higher latitude ranges of the selfers (Grossenbacher et al., 2015). These results together suggest that although the reproductive assurance offered by self-fertilization may allow selfers to expand their geographical range (Baker, 1955), such expansion does not always occur into new climates. As the vagaries of geography can result in certain climates occurring more frequently than others, species adapted to common climatic conditions may exhibit larger geographical distributions than their niches would suggest (Burgman, 1989; Gaston & Spicer, 2001; Hanski, Kouki, & Halkka, 1993; Thompson & Ceriani, 2003). For instance, the outcrossing *Medicago edgeworthii* Sirj. grows in a wider range of climatic conditions than its close selfing relative *Medicago radiata* L., despite the former having a much smaller geographical range centred at a lower latitude (Figure 4). Furthermore, given the penchant of selfers to exist in comparative low abundance in small fragmented habitats, their geographical ranges, and the climatic space they occupy, may have been overestimated relative to their outcrossing relatives. Along these lines, it has been suggested that the range size of outcrossers can be underestimated because of their frequent ability to hybridize with close relatives, which can lead to their misclassification as different species or subspecies (Lowry & Lester, 2006).

4.2 | Niche divergence is negatively impacted by selfing

It has been suggested that selfing species have a reduced capacity to adapt to different climates (Crow, 1992; Morran et al., 2009). This lack of adaptability was supported by our finding that the degree of niche overlap was higher among selfing sister-species pairs than it was among outcrossing sister-species pairs. This result suggests that species

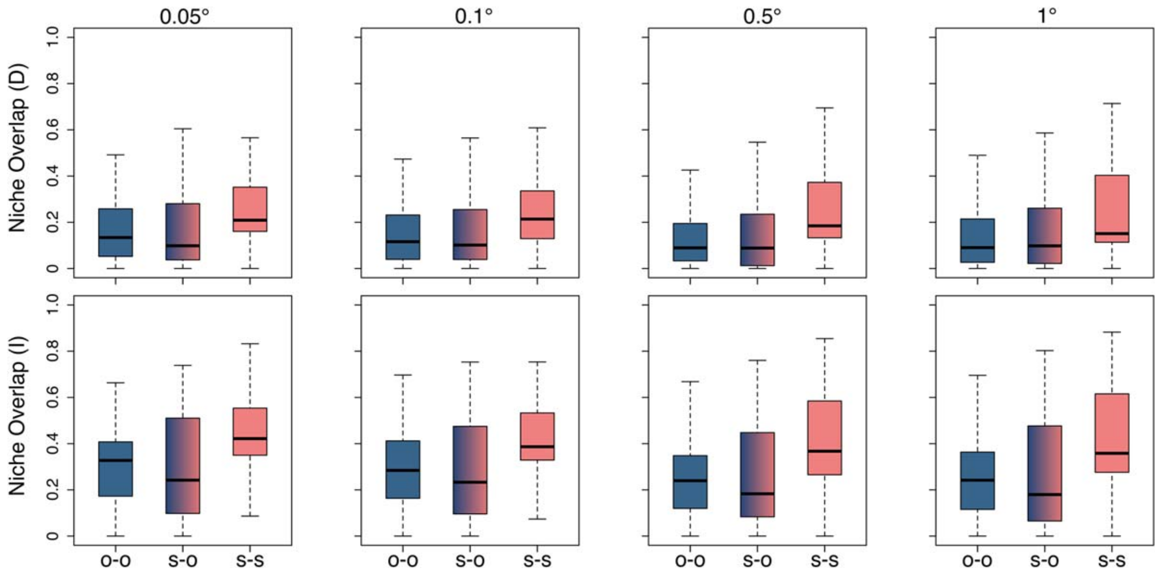

FIGURE 3 Boxplots of two metrics of sister-pair niche overlap by mating system category [outcrosser-outcrosser (o-o, blue), selfer-outcrosser (s-o, mixed) or selfer-selfer (s-s, pink)] at four spatial resolutions

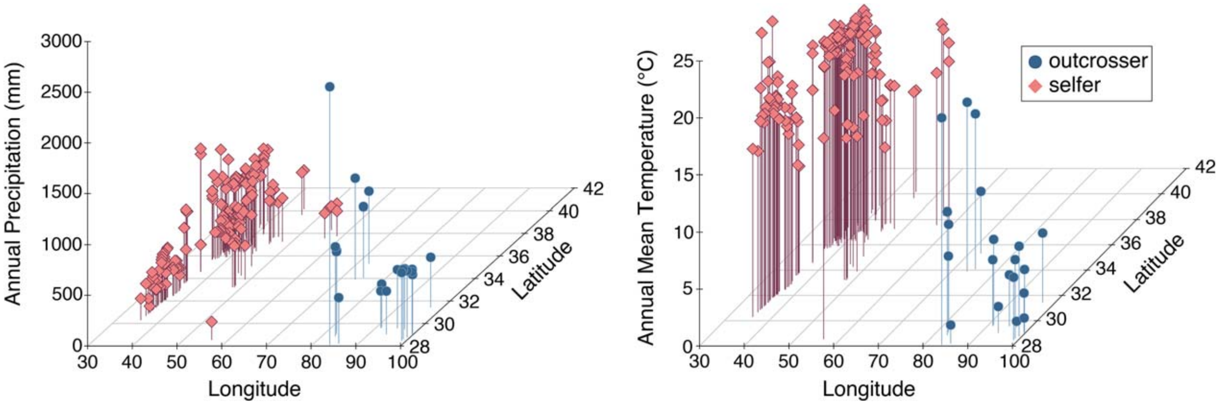

FIGURE 4 Geographical range and climatic range inhabited by *Medicago edgeworthii* (outcrosser) and *Medicago radiata* (selfer). Points represent the geographical locations of each species

niches may be slow to diverge after the transition to selfing. Given that environmental conditions are likely to be autocorrelated spatially, this result seemingly supports the long-held theory that selfing facilitates range overlap of closely related species (Antonovics & Bradshaw, 1970). However, the higher level of niche overlap that we observed for selfing sister-species pairs did not result from geographical proximity, because there was no association between mating system and geographical co-occurrence among sister species (Grossenbacher et al., 2016). These results suggest that once species have transitioned to selfing, they may be unable to establish in new climates as readily as their outcrossing relatives; rather, selfers may expand their geographical range by colonizing familiar environments. Indeed, selfing is more prominent at higher latitudes (Grossenbacher et al., 2015; Moeller et al., 2017), which constitute larger landmasses where climates tend to be more geographically uniform than across similar spatial extents at low latitudes (Janzen, 1967).

The effect of selfing pairs on niche divergence was no longer significant when the genus *Medicago* was removed from our analysis (Supporting Information Table S8; see also Grossenbacher et al., 2016). This result is likely to be a consequence of the substantial reduction in sample size after removal of *Medicago*, which in our dataset includes 39 selfing sister pairs [$>$ 43% of the weighted sample of selfing sister pairs (s-s) and more than any other genus included in our study]. Although the apparent effect of mating system on niche divergence may have been driven by the large proportion of *Medicago* species pairs, this result nonetheless suggests that climatic niche divergence is not facilitated by selfing. Indeed, in Gallagher et al.'s (2010) examination of niche shifts in 26 plant species introduced to Australia, the six species that did not exhibit evidence of niche shifts were all primarily self-pollinating. A number of other recent studies have also illustrated the greater potential for niche expansion by outcrossing species (Broennimann et al., 2007; Gallien et al., 2016; Petitpierre et al., 2012).

4.3 | Selfing leads to decreased niche breadth over time

Among the species we examined, selfers did not always have smaller niches than their outcrossing sisters, but the climatic ranges of the former were predicted to decrease significantly more rapidly over time. Thus, the climatic niches of selfing species eventually should become narrower than the niches of related outcrossing species, irrespective of their initial niche breadth. The temporal decline in the niche breadth of selfers could be attributed to genetic impoverishment caused by inbreeding. The reduction in effective population size that accompanies selfing limits both positive and purifying selection, increases the fixation of deleterious mutations, and impairs the ability of a species to adapt to new conditions (Bachtrog & Charlesworth, 2002; Wright & Andolfatto, 2008). Although we cannot make a direct or causal connection between the predicted decrease in niche breadth of selfing species and long-term costs of reduced genetic diversity, previous studies have shown them to be linked (Morran et al., 2009; Noy, Lavie, & Nevo, 1987), and selfing lineages have been shown to experience considerable accumulation of deleterious mutations over relatively short time scales (Hu et al., 2011; Slotte et al., 2013). Further investigations along these lines with larger, more robust ecological datasets are needed.

4.4 | Reconciling geographical range and climatic niche breadth

All else being equal, species with higher levels of genetic diversity should be able to maintain populations across a larger number of climates, thus leading to larger geographical ranges than species with generally low genetic diversity (e.g., selfers). However, it is possible that the realized niches of selfing species are closer to their fundamental niches than they are in their outcrossing sisters. The release from mate limitation allows selfers to colonize small or fragmented habitats and enables them to explore a larger extent of their fundamental niche (i.e., increase in realized niche breadth). The initial purging of recessive deleterious alleles after the evolution of selfing also could contribute to expansion of the realized niche breadth of selfers (Peterson & Kay, 2015). Such a scenario could translate to transiently larger species ranges for selfers, but the limitations of an increasingly homogeneous genome should become apparent over time. With prolonged selfing, heterozygosity should decrease, mutations should accumulate, and the fundamental niche should contract, eventually leading to constriction of the geographical range (Figure 5).

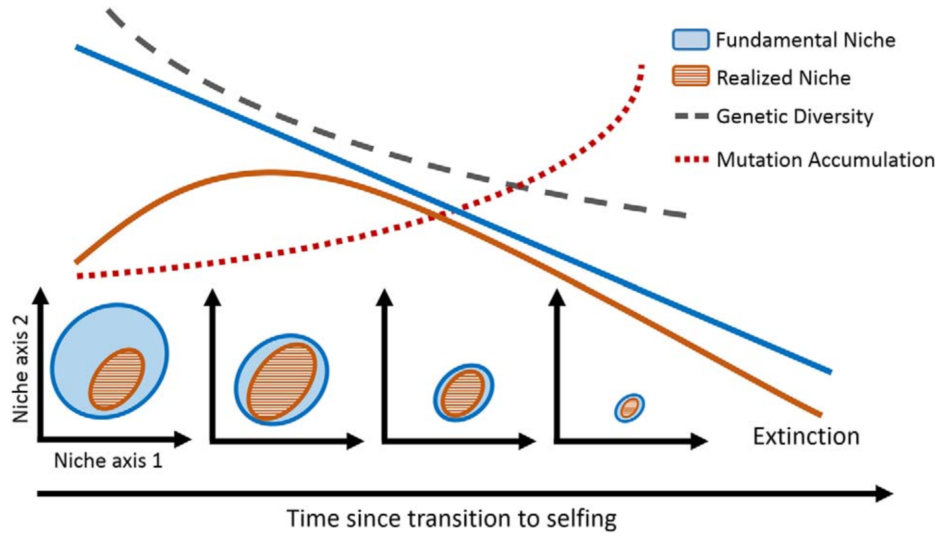

FIGURE 5 Expected changes in genetic diversity, mutation accumulation, fundamental niche and realized niche after transition to selfing

Like previous studies (Grossenbacher et al., 2015, 2016), our analyses are correlative, and we cannot demonstrate a causal relationship between niche breadth and mating system. We restricted our analysis to definitively selfing or outcrossing species, but multiple mechanisms affect intermediate levels of self-fertilization, even within populations (Goodwillie, Kalisz, & Eckert, 2005). Despite the inclusion of the largely tropical genera *Dalechampia* and *Schiedea*, most of the clades we analysed have primarily temperate distributions, and different patterns might have been observed if more tropical taxa had been included. Although we minimized the potential effects of unaccounted variables by comparing closely related sister species, additional factors may still influence niche breadth. Also, our knowledge of species' distributions, and thus the climatic space they inhabit, may be biased and/or incomplete (Daru et al., 2018; Park & Davis, 2017). As more data become available, we can examine in more detail the relationships between the degree of selfing, range size and niche breadths that account for additional factors, including biotic interactions.

Nonetheless, our results that the climatic niches of selfing species are slower to differentiate (Figure 3) than niches of outcrossing sister taxa and stand to become narrower over time with genetic degradation (Figure 2) are consistent with the well-established hypothesis that selfing is an evolutionary dead-end (Dobzhansky, 1950; Stebbins, 1957). Despite high transition rates to selfing, $<$ 15% of extant seed plants are predominantly selfing (Goodwillie et al., 2005; Igic & Kohn, 2006), and transitions from selfing to outcrossing occur rarely, if ever (Igic & Busch, 2013). Furthermore, selfing lineages have been shown to be younger than outcrossing ones, implying that they are more short lived (Busch, Joly, & Schoen, 2011; Escobar et al., 2010; Foxe et al., 2009; Holsinger, 2000; Ness, Wright, & Barrett, 2010; Pettengill & Moeller, 2012). Genetic impoverishment and accumulation of mildly deleterious alleles may not manifest as short-term losses of fitness or geographical range in all selfing species, but they are likely to affect selfers' potential for evolutionary adaptation (Honnay & Jacquemyn, 2007) and eventually outweigh any (initial) advantages of selfing (Figure 5). Indeed, simulations have demonstrated that the greater genetic load observed in self-compatible lineages results in overall increases in time to adaptation and extinction risks regardless of self-fertilization rates (Peterson & Kay, 2015). Given the rapid rates of recent climatic change, this may have severe consequences in the near future, especially because many plant species lack sufficient ability to track the shifting climate northward or upward (Honnay et al., 2002). The larger geographical range and comparable niche breadths of many selfers is most probably a temporary phenomenon caused by a transiently expanded realized niche, and may be a snapshot of the early stages of an eventual reduction in both niche and geographical range.

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DATA ACCESSIBILITY

Phylogenetic trees, occurrence data and mating system data are available at: Dryad doi:10.5061/dryad.hv117

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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