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Research

Extreme environments select for reproductive assurance: evidence from evening primroses (*Oenothera*)

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Summary

- Competing evolutionary forces shape plant breeding systems (e.g. inbreeding depression, reproductive assurance). Which of these forces prevails in a given population or species is predicted to depend upon such factors as life history, ecological conditions, and geographical context. Here, we examined two such predictions: that self-compatibility should be associated with the annual life history or extreme climatic conditions.
- We analyzed data from a clade of plants remarkable for variation in breeding system, life history and climatic conditions (*Oenothera*, sections *Anogra* and *Kleinia*, Onagraceae). We used a phylogenetic comparative approach and Bayesian or hybrid Bayesian tests to account for phylogenetic uncertainty. Geographic information system (GIS)-based climate data and ecological niche modeling allowed us to quantify climatic conditions.
- Breeding system and reproductive life span are not correlated in *Anogra* and *Kleinia*. Instead, self-compatibility is associated with the extremes of temperature in the coldest part of the year and precipitation in the driest part of the year.
- In the 60 yr since this pattern was anticipated, this is the first demonstration of a relationship between the evolution of self-compatibility and climatic extremes. We discuss possible explanations for this pattern and possible implications with respect to anthropogenic climate change.

Introduction

Puzzling over variation and evolution of plant breeding systems has occupied some of the greatest thinkers in the area of evolutionary biology (Darwin, 1876; Fisher, 1941; Dobzhansky, 1950; Stebbins, 1950, 1957). A central pattern of interest is variation in inbreeding vs outbreeding, which is thought to arise from competing evolutionary forces. On one hand, the negative fitness consequences of inbreeding (known as inbreeding depression) favor outbreeding (Nagylaki, 1976; Lande & Schemske, 1985; Charlesworth & Charlesworth, 1987). In many plants, self-incompatibility enforces outcrossing, so that self-fertilization, the most extreme form of inbreeding, is impossible. Phylogenetic analyses suggest that there have been relatively few origins of self-incompatibility in seed plants (Weller *et al.*, 1995; Igic & Kohn, 2001; Steinbachs & Holsinger, 2002; Igic *et al.*, 2008), whereas change to self-compatibility is described as the most common evolutionary transition experienced by flowering plant lineages (Stebbins, 1974). On the other hand, self-compatibility can be advantageous if it provides 'reproductive assurance': a plant that finds itself without mates or pollinators may still be able to reproduce (Darwin, 1876; Lloyd, 1979, 1992; Fausto *et al.*, 2001; Weber & Goodwillie, 2009). These two selective factors, inbreeding depression and reproductive assurance, are thought to be among the most important acting on plant breeding systems (Lloyd, 1979; Holsinger, 1996, 2000; Eckert *et al.*, 2006).

Which of these competing forces wins out in shaping the breeding system of a particular species or population is context-dependent, including factors such as life history, ecological conditions, and geographical context. For example, it is thought that selection for reproductive assurance should be stronger in plants that have just one opportunity to reproduce in their lifetime (annuals, monocarpic perennials) compared with plants that have several chances to reproduce (polycarpic perennials; Morgan *et al.*, 1997; Morgan, 2001). Thus annuals should be more likely than perennials to evolve self-compatibility, whereas perennials should be more likely to retain self-incompatibility (Stebbins, 1950; pp. 176–181). This prediction has been borne out in some surveys of plant breeding systems (Barrett *et al.*, 1996) but not in others (Raven, 1979).

Ecological conditions are also thought to modify selection on plant breeding systems. Insect pollinator abundance can be low under cold conditions (i.e. at high elevations and latitudes), which might increase selection for reproductive assurance in the plants found there (Moldenke, 1979; Kalin Arroyo *et al.*, 1985; Korner, 1999; but see Garcia-Camacho & Totland, 2009). Extremely arid conditions are associated with variation in reproductive success (Beatley, 1974; Kadmon & Schmida, 1990; Philippi, 1993; Clauss & Venable, 2000; Schemske & Bierzychudek, 2001), which may generate selection for reproductive assurance. Stebbins (1950) generalized this by suggesting that extreme conditions should favor the evolution of selfing: 'selection in favor of self-fertilization is very likely to occur in all annuals and other short-lived plants living in deserts, alpine or arctic regions, or other extreme environments'. Lloyd (1992) made a similar association between environmental conditions (extreme temperatures, high latitudes and altitudes) and selfing.

Here we evaluate patterns of covariation and coevolution of reproductive life span (annual vs iteroparous perennial), breeding system, and climatic conditions in a clade of plants found in western North America: *Oenothera* sections *Anogra* and *Kleinia* (Onagraceae). This group of 19 taxa is remarkable for variation in climatic conditions, life history, and breeding system (Table 1). Some of the *Anogra* and *Kleinia* taxa are found in low-elevation deserts of the southwestern USA, others in semiarid grasslands, and others in alpine meadows in the Rocky Mountain region (Wagner *et al.*, 2007; Evans *et al.*, 2009). Ten of the *Anogra* and *Kleinia* taxa are self-incompatible, four are polymorphic in breeding system (either among or within populations), and five are self-compatible (Klein, 1970; Raven, 1979; Theiss *et al.*, 2010). In this same group, 10 are perennial, two are variable in life history, and seven are annual (Klein, 1970; Evans *et al.*, 2005; Wagner *et al.*, 2007). This variation makes the *Anogra* + *Kleinia* clade an excellent group in which to evaluate coevolution of: breeding system and reproductive life span; and breeding system and climate. We use a molecular phylogenetic comparative approach to account for nonindependence of taxa. Because of the young age of the *Anogra* + *Kleinia* radiation (crown date within the last 1 million yr; Evans *et al.*, 2009), there is considerable phylogenetic uncertainty (Fig. 1a), which we account for using a sample from the posterior distribution of Bayesian phylogenetic trees. We use geographic information system (GIS)-based climate data and ecological niche

Table 1 Life history (LH), breeding system (BS), and climate data for all taxa in sections *Anogra* and *Kleinia*, *Oenothera*, Onagraceae

Taxon	Abbreviaton	LH	BS	P_{dry} (cm)	$P_{\text{dry¼}}$ (cm)	$T_{\text{cold¼}}$ (°C)	T_{min} (°C)
Oenothera wigginsii	WIG	A	SC	0	0.23	13.28	5.31
O. deltoides ssp. *cognata*	COG	A/P	SC	0.05	0.42	8.58	1.74
O. deltoides ssp. *howellii*	HOW	P	SI	0.06	0.47	8.15	2.34
O. deltoides ssp. *deltoides*	DELT	A	SI/SC	0.07	0.57	12.17	4.07
O. californica ssp. *californica*	CAL	P	SI/SC	0.17	1.25	8.55	1.63
O. arizonica	AZ	A	SC	0.26	1.26	12.45	4.14
O. californica ssp. *eurekensis*	EUR	P	SI	0.52	2.10	4.03	−4.35
O. deltoides ssp. *ambigua*	AMB	A	SI	0.62	2.98	4.52	−3.07
O. deltoides ssp. *piperi*	PIP	A	SI	0.83	3.37	0.16	−7.09
O. californica ssp. *avita*	AV	P	SI	0.84	3.48	2.51	−5.08
O. pallida ssp. *runcinata*	RUNC	P	SI	0.89	3.41	1.96	−6.86
O. albicaulis	ALB	A	SI	0.98	3.65	0.82	−7.80
O. pallida ssp. *pallida*	PAL	P	SI/SC	1.08	4.16	−0.82	−7.87
O. pallida ssp. *latifolia*	LAT	P	SI	1.11	3.85	−2.74	−11.46
O. engelmannii	ENG	A	SI	1.13	4.07	5.24	−3.96
O. neomexicana	NEO	P	SC	1.15	4.55	2.12	−6.66
O. nuttallii	NUT	P	SC	1.19	4.07	−5.91	−13.98
O. pallida ssp. *trichocalyx*	TRI	P/B/A	SI	1.22	4.16	−5.03	−13.26
O. coronopifolia	COR	P	SI/SC	1.30	4.65	−2.64	−11.16

Life history states are annual (A), biennial (B), and perennial (P). Breeding system states are self-incompatible (SI) and self-compatible (SC). Climate variables are precipitation in the driest month (P_{dry}), precipitation in the driest quarter ($P_{\text{dry¼}}$), mean temperature in the coldest quarter ($T_{\text{cold¼}}$), and minimum temperature in the coldest month (T_{min}).

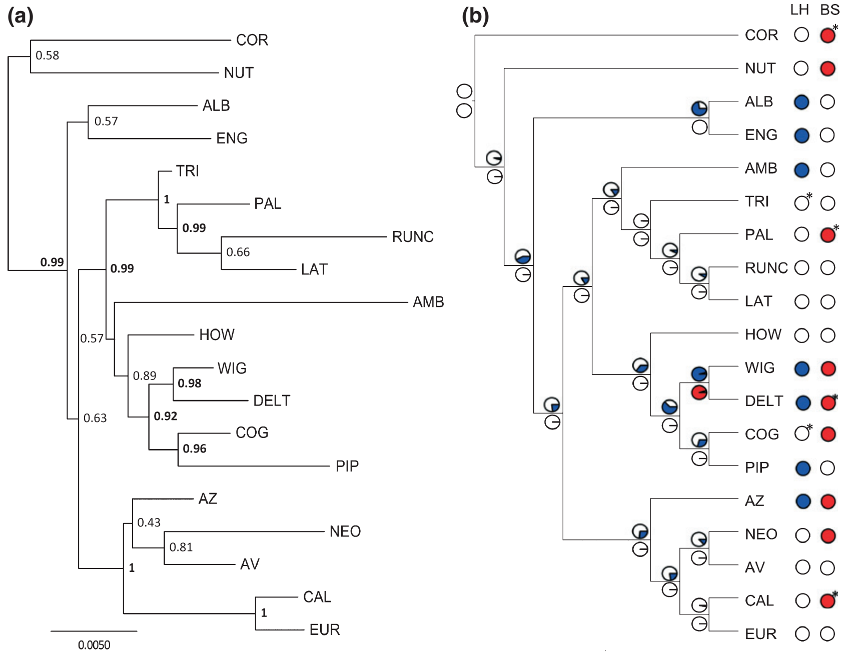

Fig. 1 (a) Bayesian majority-rule consensus tree for *Oenothera*, sections *Anogra* and *Kleinia* (from the all-compat command in MrBayes). Posterior probabilities indicate the support for each node. Branch lengths are proportional to sequence change, in units of expected sequence change per site. (b) Maximum *a posteriori* tree with character mapping of life history (white, perennial; blue, annual) and breeding system (white, self-incompatible; red, self-compatible). The character states at the root node were set to perennial, self-incompatible, and the backwards transition for breeding system was set at 0.001. At interior nodes, we show the posterior mean probability of each trait state for the most recent common ancestor that includes the descendent taxa below that node, thus summarizing across phylogenetic uncertainty (from simulations in BayesTraits). Asterisks indicate taxa that are variable in life history or breeding system (see Table 1). Bold values indicate strongly supported nodes in the phylogeny.

modeling to quantify the climatic conditions where the *Anogra* + *Kleinia* taxa are found. Using the combination of phylogenetic hypotheses, trait data, and climatic niche estimates, we evaluate the predictions that: the perennial habit should be associated with self-incompatibility and the annual habit with self-compatibility; and self-compatibility should be associated with ecologically marginal conditions.

Materials and Methods

Study system and trait data

Sections *Anogra* and *Kleinia* (*Oenothera*) form a well-supported clade (Levin *et al.*, 2004; Evans *et al.*, 2005). All 19 taxa have large, white flowers that are visited by widely distributed hawkmoths (particularly *Hyles lineata*) during crepuscular hours and by specialist pollen-collecting bees in the morning (Linsley *et al.*, 1963a,b; Klein, 1970).

We compiled data on breeding system and life history for all taxa in sections *Anogra* and *Kleinia* from the literature, including our own previous research (Klein, 1970; Raven, 1979; Evans *et al.*, 2005; Wagner *et al.*, 2007; Theiss *et al.*, 2010; see Table 1). Of the two taxa that are variable in life history, *O. californica* ssp. *cognata* and *O. pallida* ssp. *trichocalyx*, the former is reportedly variable among years (Klein, 1970; Hickman, 1993) and the latter is variable among populations (Martins & Hutchins, 1980). Of the taxa variable in breeding system, two are variable among populations (*O. deltoides* ssp. *deltoides* and *O. coronopifolia*; Klein, 1970; Raven, 1979; Theiss *et al.*, 2010), and two are variable within populations (*O. californica* ssp. *californica* and *O. pallida* ssp. *pallida*; Theiss *et al.*, 2010).

Climatic conditions were characterized as described in Evans *et al.* (2009), using ecological niche or bioclimatic niche modeling as implemented by Maxent (Phillips *et al.*, 2006). We created predictions of each taxon's geographic range based on locality and climate data. These predictions, which take the form of probability distributions (when using Maxent), were integrated with respect to each climate variable (see Fig. 3f in Evans *et al.*, 2009). This takes into account variation in climatic conditions across the entire (predicted) geographic range of each taxon. Here we use the weighted mean (across each geographic range) per climate variable for further analyses.

Comparative analyses

We used aligned DNA sequence data from Evans *et al.* (2009) to generate phylogenetic hypotheses for *Anogra* + *Kleinia*. This included sequences for six gene regions: one nuclear (*ITS*) and five chloroplast spacer regions (*trnH-trnK*, *trnL-trnF*, *rpoB-trnC*, *trnD-trnT*, and *trnS-trnG*), for a total of 6491 base pairs. These six regions were analyzed as a combined data set, based on a partition homogeneity test (Evans *et al.*, 2009). Substitution models were as in Evans *et al.* (2009). *Oenothera xylocarpa* was used as the outgroup for rooting purposes. We estimated the posterior distribution of trees using the MC^3 algorithm in MrBayes (version 3.1.2; Ronquist & Huelsenbeck, 2003). Four chains were run for 10^7 generations. We examined convergence by plotting the likelihood values and removed the first 2×10^6 generations as burn-in. The post-burn-in sample included every 1000th generation. This was replicated twice, yielding a posterior sample of 16 000 trees. The consensus tree has considerable phylogenetic uncertainty, as well as three strongly supported groupings (posterior probabilities > 0.99): *O. nuttallii* and *O. coronopifolia*, the four subspecies of *O. pallida*, and the three subspecies of *O. californica* plus *O. arizonica* and *O. neomexicana* (Fig. 1a). The five subspecies of *O. deltoides* plus *O. wigginsii* may or may not form a clade (compare the placement of *O. deltoides* ssp. *ambigua* in Fig. 1a and b). *Oenothera albicaulis* and *O. engelmannii* form a clade or grade outside the *pallida*, *californica*, and *deltoides* groups.

We used BayesTraits (version 1.0; Pagel & Meade, 2006) to test the fit (marginal likelihood) of the data to two alternative models of the evolution of breeding system and life history: the two traits evolve independently or they depend upon one another (Pagel, 1994). BayesTraits compares the two models using Bayes factor, that is, the ratio of the marginal likelihood of the independent model to the dependent model. The marginal likelihoods are estimated by the harmonic mean of the likelihoods over a large number of (post burn-in) iterations of a Markov chain Monte Carlo (MCMC) simulation, thus integrating over phylogenetic and parameter uncertainty. The transition rates were assigned exponential priors, with a uniform hyperprior (0, 30) for the parameters governing these exponential distributions. The MCMC simulation was run for 10^6 generations, sampling every 10^3 generations. The first 5×10^4 generations were discarded as burn-in. Life history and breeding system were each assigned a binary coding scheme. We considered two coding schemes for each trait, but because the results changed little with coding scheme, we present only the results from grouping the two taxa that are variable in life history with perennials. The five taxa that are variable in breeding system were either grouped with the self-compatible taxa (coding scheme 'BS1') or grouped with the self-incompatible taxa ('BS2'). For breeding system, we constrained the rate of the 'backwards' transition (evolution of self-incompatibility from self-compatibility) to 0.001, because it is unlikely for a second mutation to repair the self-incompatibility system after it has been disabled (Igic *et al.*, 2008; Goldberg *et al.*, 2010), and we set the state at the root node to be self-incompatible (Goldberg & Igic, 2008). Because there is not a similar strong argument for constraining the model of life history evolution, we conducted simulations under the possible alternatives: the backwards transition (from annual back to perennial) constrained or unconstrained, and the root state constrained to perennial or annual.

We also conducted stochastic mapping (*sensu* Nielsen, 2002; Huelsenbeck *et al.*, 2003) of breeding system and life history using Mesquite (version 2.74; Maddison & Maddison, 2010), to evaluate their evolutionary lability. Evolutionary parameters were estimated using maximum likelihood inference on a posterior sample of 16 000 trees. Specifically, transition rates among breeding systems were estimated under an asymmetrical two-parameter Markov model, with the rate of the 'backwards' transition (evolution of self-incompatibility from self-compatibility) set at 0.001. For life history, we considered both an asymmetrical two-parameter model (constraining the transition from annual to perennial to 0.001) and a symmetrical one-parameter model.

To evaluate the correlated evolution of breeding system and climate, we calculated phylogenetically independent contrasts on the same posterior sample of 16 000 trees. If there is no association between breeding system and climate, the sum of the contrasts (on any given tree) should be zero or close to zero. The significance of any deviation from zero is evaluated using a *t*-test. However, an association between changes to self-compatibility and extreme environments cannot be detected with a straightforward implementation of this method, because positive contrasts towards one extreme of a climate variable would be cancelled out by negative contrasts towards the other extreme, summing to zero, leading to the inference of no association. Thus we rescaled climate data: the center of the range of variation for a climate variable was set to zero, and deviations in both directions were given positive values. For example, if the original climate data were 1, 2, 3, 4, 5, 6, 7, 8, 9, the rescaled climate data were 4, 3, 2, 1, 0, 1, 2, 3, 4. We used a one-sided *t*-test of the deviation of phylogenetically independent contrasts from zero since we had a specific hypothesis about the direction of change in climate (towards the extremes) that should be associated with the evolution of self-compatibility. In addition, we report the results of tests that do not correct for relatedness: logistic regressions relating breeding system to climate, with a quadratic term to fit the nonlinear response.

Results

Both breeding system and life history have been evolutionarily labile in *Anogra* and *Kleinia*, but they have not evolved in a correlated fashion (Fig. 1b). Stochastic mapping suggests that self-compatibility evolved from self-incompatibility 8.7

times in the *Anogra* + *Kleinia* clade (on average, across the posterior sample of phylogenetic trees). With the backwards life history transition constrained, stochastic mapping produced an average of 5.9 changes to the annual habit (compared with an average of 18.5 changes in life history when the backwards transition is unconstrained). We found only weak support for correlated evolution of breeding system and life history: with the root states set to self-incompatible and perennial, and both backwards transitions set at 0.001 (thus constraining the evolution of the two characters towards the predicted combination of self-incompatible and perennial), Bayes factor favoring the dependent model was only 2.90 (a Bayes factor > 3 is necessary for the evidence in favor of the preferred model to be regarded as substantial; Jeffreys, 1961). When the backwards transition for life history is unconstrained (which is a more likely model for life history evolution; Young & Augspurger, 1991; Lesica & Young, 2005; Good-Avila *et al.*, 2006; Tank & Olmstead, 2008), the Bayes factor is −2.40 against the dependent model (see Fig. 1b). Across all coding schemes for breeding system and life history, different states at the root node (for life history), and constrained vs unconstrained models of the backwards transition (for life history), Bayes factor for the dependent vs independent model ranged from −17.08 to 3.04.

By contrast, we found that changes to self-compatibility were strongly associated with evolution towards the extremes of certain climate variables (Table 1, Fig. 2).

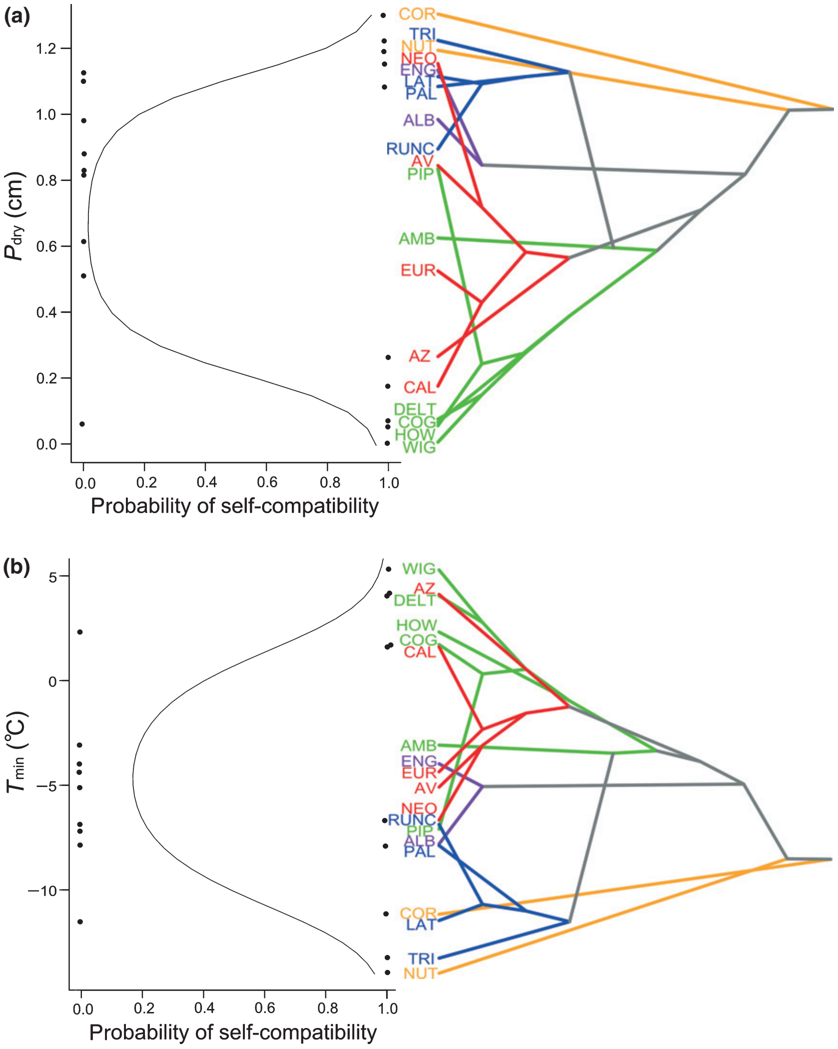

Fig. 2 Relationship between climate and self-compatibility and inferred evolutionary history of climate in *Oenothera*, sections *Anogra* and *Kleinia*, with respect to (a) precipitation in the driest month and (b) minimum temperature (T) in the coldest month. In the panels on the left, breeding systems of the extant taxa are shown as points (see Table 1), with variable taxa grouped with self-compatible taxa (BS1 coding scheme). Curves show the relationship between climate and self-compatibility predicted by quadratic logistic regression. On the right is the maximum *a posteriori* phylogeny (with equal branch lengths) drawn in climate space. Colors indicate strongly supported phylogenetic groups described in the Results section; climate values for interior nodes were reconstructed using least-squares parsimony.

Contrasts of climate with respect to breeding system that were significantly different from zero on the maximum *a posteriori* (MAP) tree include minimum temperature in the coldest month ($P = 0.025$), mean temperature in the coldest quarter ($P = 0.016$), precipitation in the driest month ($P = 0.022$), and precipitation in the driest quarter ($P = 0.029$; Supporting Information, Table S1). This was in spite of low power: just seven contrasts on the MAP tree. Contrasts of these four variables were significant on 707 of 1000 probable trees (minimum temperature in the coldest month), 797 of 1000 trees (mean temperature in the coldest quarter), 956 of 1000 trees (precipitation in the driest month), and 854 of 1000 trees (precipitation in the driest quarter; Table S1). Changes to self-compatibility were associated with evolution towards the extremes of these same four climate variables under a more restrictive coding scheme for breeding system (BS2; Table S1). Thus this result is quite robust to coding scheme and phylogenetic uncertainty, especially considering the small number of contrasts. Logistic regressions of the relationship between breeding system and climate (that do not correct for relatedness) showed similar patterns, with the exception that mean temperature in the coldest quarter was not significantly related to breeding system (though minimum temperature in the coldest month was related; Table S1).

Since minimum temperature in the coldest month and mean temperature in the coldest quarter are correlated, and precipitation in the driest month and precipitation in the driest quarter are correlated, we can speak of essentially two climate variables that correlate with breeding system: winter minimum temperatures and precipitation in the driest part of the year.

Discussion

This study affirms the notion that breeding system evolution is context-dependent, though not always in the classic manner expected. It has long been predicted that annuals are more likely than perennials to be self-compatible (Stebbins, 1950; Barrett *et al.*, 1996), but in the *Anogra* + *Kleinia* clade, breeding system does not correlate with reproductive life span in this manner. Four of seven annuals are self-incompatible, and two of 10 perennials are self-compatible (with another three variable in compatibility; Table 1, Fig. 1b). While the *Anogra* + *Kleinia* clade is small, Raven (1979) made the same conclusion for the Onagraceae as a whole: among the 581 species for which data were available, an approximately equal fraction were modally outcrossing vs selfing. Many of the annuals in the *Anogra* + *Kleinia* clade are desert annuals (Evans *et al.*, 2005; Wagner *et al.*, 2007), which often have seed banks (Venable & Pake, 1999; Evans *et al.*, 2007). Seed banks buffer environmental variation in reproductive success (Philippi & Seger, 1989; Pake & Venable, 1996; Evans & Dennehy, 2005; Meyer *et al.*, 2006), which should reduce selection for reproductive assurance and modify the prediction for self-compatibility in annuals. While life history should be expected to affect selection on the breeding system, many life history traits can affect reproductive success, so we should expect more than one to be important, for example, reproductive life span *and* seed banking.

Instead of reproductive life span, climate correlates with breeding system in the *Anogra* + *Kleinia* clade. The extremes of temperature in the coldest part of the year and precipitation in the driest part of the year are associated with the evolution of self-compatibility. Note that Stebbins (1950) predicted extreme environments should select for self-fertilization, whereas we found an association with self-compatibility. We take self-compatibility as a mark of selection for reproductive assurance (as a working hypothesis for our 19 study taxa; though see the detailed work of Herlihy & Eckert, 2002 on *Aquilegia canadensis*). We discuss two sources of selection for reproductive assurance, pollinator limitation and mate limitation, and their relationship to climate. Pollinator limitation seems likely in the evolutionary history of *O. neomexicana*, which is reported to self-fertilize (autonomously set seed; Theiss *et al.*, 2010), and thus has been freed from dependence on insects for pollination. *Oenothera neomexicana* is a perennial found from 1800 to 2700 m in mountains ('sky islands') of New Mexico and Arizona, where pollinator activity may be limited or variable because of cold temperatures (Moldenke, 1979; Kalin Arroyo *et al.*, 1985; Korner, 1999; Carlson *et al.*, 2008). At the other end of the temperature spectrum, *O. wigginsii* in the Sonoran desert is the only other *Anogra* + *Kleinia* taxon reported to set 'abundant' seed via spontaneous selfing (Klein, 1970). It is not clear why *O. wigginsii* would experience poorer pollinator service than neighboring *Anogra* + *Kleinia* taxa (*O. arizonica* and *O. deltoides* ssp. *deltoides* in the Sonoran desert, *O. californica* ssp. *californica* in southern California), though, interestingly, the first is self-compatible and the latter two polymorphic in breeding system. While self-compatibility alone (as opposed to self-fertilization) is not expected to provide reproductive assurance against pollinator limitation, low amounts of spontaneous selfing may occasionally prevent total reproductive failure, which may be relevant in the arid southwestern USA.

The alternative is that selection for reproductive assurance (and the evolution of self-compatibility) could be related to mate limitation, specifically, extinction–colonization dynamics. Baker (1955, 1967) and Stebbins (1957) argued that self-compatibility is favored during colonization (known as 'Baker's law'). Baker's law was originally framed in terms of colonization of islands, and plants in the *Anogra* + *Kleinia* clade are found on loose, coarse-grained soils (Klein, 1970; Wagner *et al.*, 2007) that are distributed on the landscape in patches, much like islands. The evolution of self-compatibility can also occur with post-glacial colonization (Dobzhansky, 1950; Shimizu *et al.*, 2004; Ansell *et al.*, 2008; Guo *et al.*, 2009; Winkler *et al.*, 2010). Within *Oenothera*, Johnson *et al.* (2010) found that asexual species are more northerly-distributed than sexual species, which they attributed to the superior colonization ability associated with asexuality. The hypothesis of post-glacial range expansion (to explain the evolution of self-compatibility) could be relevant for three northerly-distributed perennials: *O. coronopifolia*, *O. nuttallii*, and *O. pallida* ssp. *pallida*. Cold winter temperatures are associated with their northern distribution.

Extinction–colonization dynamics on a much shorter timescale may occur in the arid southwestern USA (where winters are mild and there is little precipitation). There, the *Anogra* + *Kleinia* taxa are associated with washes, which periodically flood, potentially burying or displacing patches of plants. Combined with the wild fluctuations in abundance for which short-lived plants in the arid southwestern USA are known (Beatley, 1974; Schemske & Bierzychudek, 2001; Bowers, 2005; Evans *et al.*, 2007; Venable, 2007), extinction–colonization dynamics are possibile. Self-compatibility is selected for in a metapopulation (Pannell & Barrett, 1998; Busch, 2005). This explanation for self-compatibility could apply to *O. arizonica*, *O. californica* ssp. *californica*, *O. deltoides* ssp. *cognata*, and *O. deltoides* ssp. *deltoides*.

Though the mechanism(s) remains uncertain at this point, the data from *Anogra* and *Kleinia* are consistent with the idea that short-lived plants under extreme conditions should experience selection for reproductive assurance (Stebbins, 1950). This is the first time, in the 60 yr since the idea was articulated, that a relationship has been demonstrated between the evolution of self-compatibility and climatic extremes. Integrating GIS-based environmental data into the comparative framework of evolutionary biology makes it possible to evaluate climatic and geographic predictions about trait evolution (Kozak *et al.*, 2008; Swenson, 2008). In the *Anogra* + *Kleinia* clade, this pattern deserves further investigation: breeding systems are known from few populations per taxon, and some taxa have geographic ranges that cover large latitudinal or elevational gradients. Further, we do not yet know whether the currently delineated taxonomy of this group corresponds with independently evolving lineages (phylogenetic work thus far has relied on sampling from a single individual per taxon). The extreme environments pattern deserves investigation outside the *Anogra* + *Kleinia* clade as well. Many other groups of short-lived plants that have diversified across elevational or latitudinal gradients would be good candidates for testing the scope of Stebbins (1950) prediction.

What implications can be drawn from this study, with respect to plant diversity facing climate change? Anthropogenic climate change may favor leading-edge evolution of self-compatibility as appears to have been the case in the Pleistocene (Ansell *et al.*, 2008; Guo *et al.*, 2009; Winkler *et al.*, 2010). In addition, climate change is expected to generate more extreme weather, and can produce phenological mismatches between plants and pollinators (Memmott *et al.*, 2007; Hegland *et al.*, 2009; Yang & Rudolf, 2010), both of which can lead to reproductive failure and hence increased selection for reproductive assurance. The evolution of self-compatibility may not be detrimental in the short-term (if selfing is limited, inbreeding depression is not strong, or it is quickly purged); selfing may even be associated with larger ranges at the timescale of sister taxa comparisons (Randle *et al.*, 2009). But in the longer term, selfing is considered disadvantageous (Dobzhansky, 1950; Stebbins, 1950, 1957, 1974; Holsinger, 2000; Takebayashi & Morrell, 2001; Igic *et al.* 2008; Goldberg *et al.*, 2010). Though the relationship is not inevitable, it is possible for climate change to favor the evolution of a mating system that reduces long-term evolutionary potential (in the extreme, known as 'evolutionary suicide'; Dieckmann & Ferriere, 2004).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Test statistics of the relationship between breeding system and 19 climate variables in the *Anogra* + *Kleinia* clade (*Oenothera*, Onagraceae)