

LETTER

Ecological release exposes genetically based niche variation

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Abstract

The evolutionary trajectories of ecological niches have profound impacts on community, population and speciation dynamics, yet the underlying causes of niche lability vs. stasis are poorly understood. Here, we conducted a field experiment to quantify the effects of competition and, conversely, competitive release on the microevolutionary processes driving microhabitat niche evolution in an annual plant population restricted to California vernal pool wetlands. Removing competitors generated a strong increase in mean fitness, the exposure of genetically based niche variation and directional selection for niche evolution in the experimental population. In contrast, genetic variation in the microhabitat niche and directional selection for niche evolution were not detected in individuals growing with competitors. These results indicate that ecological opportunity (here, the removal of competitors) can trigger the immediate expression of latent, heritable niche variation that is necessary for rapid evolutionary responses; conversely, competitors may restrict niche evolution, contributing to niche conservatism in saturated communities.

Keywords

Competition, ecological opportunity, ecological release, genetic variation, *Lasthenia fremontii*, niche conservatism, niche evolution, vernal pools.

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INTRODUCTION

The concept of the ecological niche plays a central role in explanations of the origin, maintenance and distribution of biodiversity. The potential for a species' niche—the set of conditions and resources required for a population to persist without immigration (*sensu* Hutchinson 1957)—to be moulded by natural selection influences its ability to coexist with competitors (Brown & Wilson 1956; Schluter 2000; Pfennig & Pfennig 2009), persist with natural enemies (Jeffries & Lawton 1984; Berdegue *et al.* 1996) and diversify in novel environments (Schluter 1996b; Losos *et al.* 2003). Conversely, the tendency for a species' niche to remain relatively constant over evolutionary time (hereafter niche conservatism) can have substantial consequences for community assembly processes (Ackerly 2003), the stability of distribution patterns (Kirkpatrick & Barton 1997; Holt 2003) and speciation (Wiens 2004). While empirical studies of ecological diversification demonstrate that species' niches can be remarkably labile over short evolutionary timescales (Schluter 1996a; Losos *et al.* 2003), comparative analyses have shown that ecological niches are often very conserved over macroevolutionary timescales (Simpson 1944; Bradshaw 1991). Given the evidence that patterns of niche evolution are diverse, with major consequences for a range of ecological and evolutionary processes, there is substantial interest in identifying the ecological, genetic and demographic mechanisms that facilitate or constrain niche evolution within populations and species.

A long-standing paradigm in evolutionary biology is that morphological evolution and adaptive divergence can be triggered by 'ecological opportunities' such as exposure to novel conditions, colonisation of new environments, the rise of a key innovation, or the elimination of natural enemies such as competitors, predators, or parasites (Simpson 1944; Losos

2010). The ecological theory of adaptive radiation predicts that niche diversification can be triggered in novel environments, when a colonising lineage gains access to habitats and resources that are pre-empted by competitors in its historical range (Schluter 2000; Losos 2010). The sudden availability of a broader resource base or unoccupied habitats leads to rapid population growth (i.e. ecological release), and, over time, opportunities for niche divergence. However, the precise mechanisms by which ecological release generates the expression of niche or trait variation – the fuel for adaptive evolution – remain unclear (Yoder *et al.* 2010).

In contrast to the conceptual framework explaining niche diversification, the processes that constrain niche evolution are poorly understood. Two primary hypotheses have been put forward for the drivers of niche conservatism: (1) stabilising selection actively maintains populations around the same optimum, restricting niche evolution and preventing ecological divergence; and (2) a lack of genetic variation in traits (which may be due to genetic constraints) limits adaptive evolution within and divergence among lineages (Ackerly 2003; Futuyma 2010; Haller & Hendry 2014). While stabilising selection has rarely been detected in nature, this could result from past selection eroding genetic variation on either side of a fitness peak, making it difficult to detect ongoing stabilising selection (e.g. Schluter 1988; Haller & Hendry 2014). Regardless, the abundant genetic variation frequently observed within populations, and the widespread documentation of local adaptation among populations, challenges the idea that low genetic variation in niche traits exists in most populations (Futuyma 2010).

Despite the purported significance of ecological release in facilitating niche evolution, the role of competitive interactions in promoting niche conservatism has received relatively little attention. It is somewhat intuitive that if the absence of

competitors promotes adaptive radiation and niche diversification, then the presence of competitors may play a key role in restricting it. Niche evolution may be inherently constrained in saturated communities, where competitive interactions cause species to sort into the habitats to which they are most adapted, rather than adapting to new ones (Ackerly 2003). In this scenario, selection favours specialisation on the most easily exploited resources in the presence of competitors, setting niche limits in both ecological and evolutionary time (Price & Kirkpatrick 2009). Competitive interactions can also promote niche conservatism by reducing population densities in regions where species overlap, enhancing the asymmetry in gene flow from favourable to marginal environments and restricting local adaptation in the area of sympatry (Case & Taper 2000). Collectively, these predictions resonate with ecological studies showing the influence of competitive interactions on population boundaries across environmental gradients (e.g. Connell 1972; Hairston 1980).

We conducted a field experiment (1) to test between the alternative hypotheses of stabilising selection vs. lack of genetic variation as causes of niche conservatism, and (2) to evaluate the effects of ecological release (by removal of competitors) on the microevolutionary processes underlying niche evolution and conservatism. We addressed these questions in a population of *Lasthenia fremontii* (Madieae, Asteraceae), an annual herb that is endemic to vernal pools of the Central Valley of California (Ornduff 1966). Vernal pools are geographically isolated ephemeral wetlands characterised by a perched water table during the fall and winter rains, a brief waterlogged phase during the spring, and a prolonged dry period during the summer (Holland & Jain 1981). *L. fremontii* is a winter annual, germinating in the fall and flowering in the spring, that is restricted to intermediate depths within pools (Barbour *et al.* 2003); as a result, seedlings experience several weeks to months of complete submergence in a growing season. Here, we consider the 'microhabitat niche' of *L. fremontii* to be the range of depths occupied by a population within a vernal pool. Both competition and abiotic factors influence plant distribution patterns across the inundation gradient (Emery *et al.* 2009), and comparative analyses have shown that the distribution of *Lasthenia* species across vernal pool inundation gradients is phylogenetically conserved relative to other niche axes (Emery *et al.* 2012). Here, we investigated the microevolutionary processes underlying microhabitat niche conservatism by planting paternal half-sib families across the vernal pool gradient at the centre, edges, and beyond the edges of their natural microhabitat range, in the presence and absence of competitors. Our experimental design allowed us to quantify the fundamental and realised niche of each family along the vernal pool gradient, test for additive genetic variation in the niche, and quantify patterns of selection for microhabitat niche evolution.

METHODS

Study site and population

This field experiment was conducted in a large vernal pool wetland at Mather Regional Park, Rancho Cordova, CA

(38.5336° latitude, −121.2649° longitude) that is approximately 550 m² in surface area and 1.5 m in maximum depth. *Lasthenia fremontii* grows at intermediate elevations along pool sideslopes (roughly 40–60 cm above the deepest point in the pool) and reaches maximum abundance approximately 50 cm above the pool bottom (Fig. 1a).

Seed collection and generation of paternal half-sib families

Seeds from 345 maternal families were collected from the source pool in the spring of 2006. Seeds were collected across the entire vertical and horizontal distribution of the population and on two different dates (June 5 and 11) to sample genotypes spanning the spatial and phenological distributions of the population. We assumed that genotypes represented a

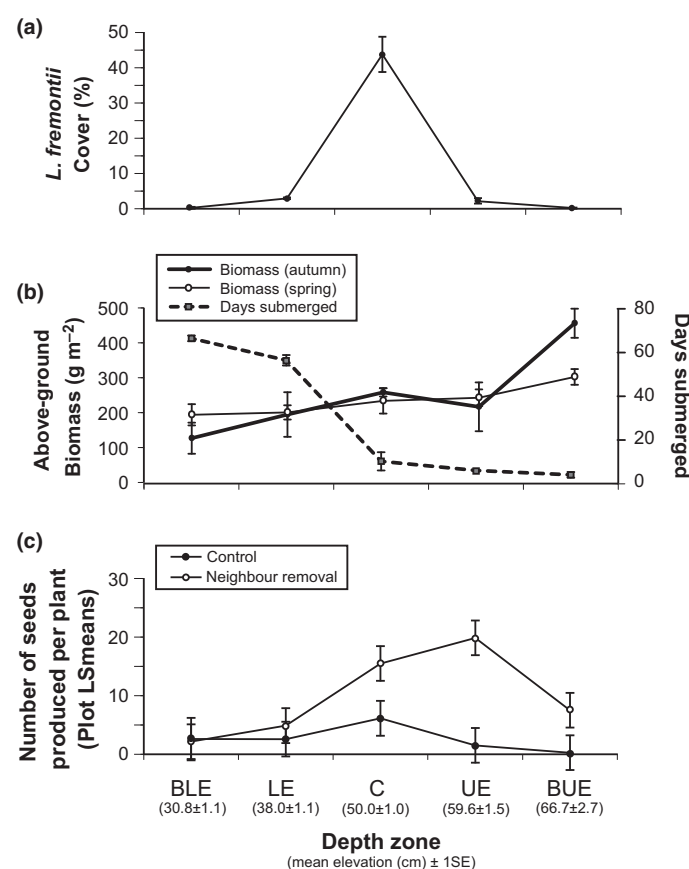


Figure 1 Environmental conditions and ecological responses of experimental plants across the vernal pool depth zones: Beyond Lower Edge (BLE), Lower Edge (LE), Centre (C), Upper Edge (UE) and Beyond Upper Edge (BUE). The mean elevation (cm, ± 1 SE) of experimental plots above the pool bottom is shown below the bottom x-axis. (a) Average percent cover (± 1 SE) of naturally occurring *L. fremontii* in each zone. (b) Flooding duration (dashed line, right y-axis) and above-ground productivity (solid lines, left y-axis) in each zone. Flooding duration is the average (± 1 SE) number of days that plots were submerged during the 2007–2008 growing season. Above-ground productivity was measured when seeds were planted in the autumn of 2007 (open circles) and at the end of the growing season in spring 2008 (filled circles). (c) Cumulative fitness (plot means ± 1 SE) of seed transplants in control (filled circles) and neighbour removal (open circles) plots.

single interbreeding population. Although phenological structure in flowering time across the inundation gradient can restrict gene flow by pollen movement (Emery 2009), our design did not investigate spatially structured niche variation at the subpopulation scale.

In January 2007, 10 seeds from each maternal family were planted together into 2.5×16 cm polypropylene tubes (Ray Leach Cone-tainers™, model RLC4; Stuewe & Sons, Tangent, OR, USA) containing a soil mixture of 50% potting soil and 50% sandy loam. Cone-tainers were positioned in racks, and racks were placed in plastic tubs that contained enough water to keep the soil column saturated. Tubs were initially placed in a lath house on the UC Davis campus to expose seeds (and eventually seedlings) to ambient winter temperatures, and then moved to the greenhouse immediately prior to flowering.

The goal of the greenhouse generation was to produce a minimum of 30 paternal half-sib families, with three dams/family and a minimum of 30 seeds/dam, to provide a family-structured population for the field experiment (we use 'dam' and 'sire' following conventions of quantitative genetics breeding designs). In anticipation of variable seed production among the greenhouse-raised plants, our crossing design contained an extra 20 families and one additional dam per group. Dams that failed to produce 30 seeds, and families that failed to yield three dams with 30 seeds apiece, were dropped from the experiment. Low fecundity of some dams appeared to be associated with low initial seed quality or sexual incompatibility with the randomly assigned sire. However, we cannot rule out the possibility that some unintentional selection for fecund genotypes occurred during the greenhouse generation.

At least one seed germinated from 96% of the maternal families from which seeds were collected and planted. When more than one seed germinated in a single cone-tainer, seedlings were thinned so that each maternal family was represented by a single plant. Prior to initiating crosses, individuals were randomly assigned into groups, with five plants per group, and covered with bridal veil tents to prevent local pollinators from visiting plants. Within each group, four individuals were randomly assigned to be pollen recipients (dams), and one individual was randomly selected to serve as the pollen donor (sire). Dam inflorescences were not emasculated because *L. fremontii* is an obligate outcrosser and thus cannot self-pollinate. Repeated pollinations were performed on multiple inflorescences per dam until 30 viable seeds were produced or the plant senesced. The final experimental seed population consisted of 30 paternal half-sib families with three dams/family.

Field experiment

On November 4, 2007, the family-structured seed population was planted into 30 plots in the source pool. Plots were stratified across five depth zones, with six plots per zone, which collectively spanned and exceeded the natural distribution of the resident population (Fig. 1a; Fig. 1a in Appendix S1). Each plot was 70×25 cm in size, with the long edge placed perpendicular to the inundation gradient to minimise within-plot variation in the hydrological environment (e.g. flooding time and frequency). Seeds representing all 30 families, with

one seed/dam and thus three paternal half-sibs/family, were individually planted into randomised grid positions in each plot, for a total of 90 seeds/plot and 2700 seeds across the entire experiment. We removed all vegetation from three plots/zone immediately prior to planting and continued to remove any recruits (other than experimental seed transplants) by hand throughout the duration of the experiment (Appendix S2). We monitored emergence, survival and phenology of each experimental transplant over the entire growing season (November–June). Seeds were collected from all transplants as they matured and were counted to provide an estimate of reproductive output. After all experimental plants had senesced, the aboveground vegetation in each control plot was clipped, dried and weighed to provide an estimate of productivity. The microelevation (depth) of each plot, relative to the deepest point in the pool, was measured to the nearest centimetre using an autolevel.

Statistical analyses

Environmental conditions along pool sideslopes

We compared the duration of inundation, above-ground biomass of the background vegetation during the emergence period (collected from the neighbour removal plots), and above-ground biomass at the end of the growing season (collected from control plots), in one-way ANOVAS with transplant zone (beyond lower edge/lower edge/population centre/upper edge/beyond upper edge) as the single main effect.

Ecological analysis of seed transplants

We evaluated the ecological effects of zone and competition treatment on the fitness of experimental plants using mixed model ANOVAS. Transplant zone and competition treatment were treated as fixed effects, and plot nested within zone, sire and dam nested within sire, were defined as random effects. We evaluated the effects of zone, competition treatment and their interaction, on (1) the probability of emergence, and (2) the number of seeds produced by plants that emerged, to independently investigate the effects of experimental treatments on early and late life history stages. The emergence analysis included all seeds that were planted and their emergence response (0 or 1), while the analysis of seed production only included data from plants that had successfully emerged. We analysed emergence using a generalised linear model for a binomial response variable and logit link function (PROC GLIMMIX in SAS v. 9.1, SAS Institute Inc., Cary, NC, USA). Denominator degrees of freedom were calculated using the Satterthwaite approximation. Seed production of emerged plants was evaluated using a general linear mixed model ANOVA; seed count data were $\ln(x + 1)$ transformed prior to analysis to meet the assumptions of ANOVA.

The effects of competition treatment and transplant zone on the cumulative fitness of each experimental unit, i.e. the number of seeds produced per seed planted, were evaluated using aster models (Geyer *et al.* 2007; Shaw *et al.* 2008). Our analysis accounted for the multiplicative effects of the following fitness components: (1) emergence, modelled as a Bernoulli variable, (2) survival to flowering, given emergence, modelled as a Bernoulli variable, and (3) the number of seeds produced

by a plant that emerged and survived to flower, modelled as a zero-truncated Poisson variable. We tested if cumulative fitness differed among transplant zones, and between competition treatments, using log-likelihood tests (Geyer *et al.* 2007; Shaw *et al.* 2008). The complete model included zone, competition treatment and the interaction as fixed main effects, and sire and dam (nested within sire) as random covariates. We tested the effects of zone and treatment on cumulative fitness removing each factor (and the interaction) from the model, and we evaluated the interaction effect by removing it while leaving the main effects in the model.

Analysis of niche components

Our experimental design, and measures of depth (microelevation) of each experimental plot, made it possible to quantify the fundamental and realised niche of individual paternal half-sib families across the vernal pool depth gradient. To do this, we first estimated the mean cumulative fitness of each family in each plot as the average of the three half-sibs. Because we did not replicate full sibs within each plot, we could not estimate niche components for individual full-sib families. Next, we calculated three niche components for the fundamental (neighbours removed) and realised (control treatment) niche of each paternal half-sib family, using the mean family fitness and the microelevation measure of each plot (Appendix S2): the niche optimum (depth of the plot in which mean family fitness was highest), niche position (fitness-weighted mean depth of each family across all plots) and niche breadth (fitness-weighted variance in depth across all plots) (Roughgarden 1979). Here, niche position reflects the average value of the environment utilised by the population (e.g. Roughgarden 1979); this differs from a definition used in the biogeographical literature that refers to the mean location of a species along a gradient relative to the mean of the gradient (*sensu* Shugart & Patten 1973). The estimates of niche position and niche optimum both reflect the environments in which fitness is relatively high, but these estimates can differ depending on the shape of the fitness response across the gradient. We tested if mean niche components varied between the realised and fundamental niche in separate one-way ANOVAs with treatment as the single main effect.

Heterogeneous germination rates caused the sample size for family-level niche components to be lower in the control treatment ($n = 23$) compared to the neighbour removal treatment ($n = 26$) because niche components could not be estimated for families with zero germination rates across all plots in a treatment. We evaluated if differences in the sample size and identity of families influenced the results of niche component analyses (including those described below) by repeating all of the statistical tests using only families for which components could be estimated in both treatments. All results were highly consistent with those using the larger data set, so only the latter are presented below.

Analysis of genetic variation

We evaluated the effect of competition treatment on the expression of genetic variation in the niche using two different statistical approaches. First, we tested if the expression of differences among families in their responses to the depth gradient differed between the control and neighbour removal treatments by

comparing the likelihoods of two models with different variance structures (Shaw 1991). Specifically, a model with heterogeneous variance structure (where the family variance component was allowed to differ between control and neighbour removal treatments) was compared to a model where the variance components were constrained to be identical in the two treatments. The heterogeneous variance model included treatment as a random effect and the family \times zone interaction as the grouping factor. If the heterogeneous model (with unequal variance between treatments) provided a significantly better fit to the data than the constrained model (evaluated using chi-squared test of log-likelihood ratios), we concluded that genetic differences among families in their responses to planting depth depended on the presence or absence of competitors. Second, we used Levene's tests to determine if variation among families in niche components differed between control and neighbour removal treatments (i.e. realised vs. fundamental niche, respectively). Here, we generated the residuals of each niche component (optimum, position or breadth) from a one-way ANOVA with competition treatment as the only factor, and then ran an identical ANOVA on the absolute values of the residuals. We evaluated the statistical significance of the competition treatment effect to determine if the expression of genetic variation in niche components depended on the presence of neighbours. We did not evaluate within-family variation because full sibs were not replicated within plots, limiting the reliable estimation of within-family variance.

Selection on niche components

We conducted regressions using family-level estimates of niche components (Rausher 1992) to test for significant linear and nonlinear selection on niche components (Lande & Arnold 1983), and if the patterns of selection varied with competition treatment. Prior to analysis, niche components were standardised to a mean of zero and standard deviation of one. Family-level relative fitness was estimated as the mean cumulative fitness of each family across all transplant depths, divided by the grand mean fitness of all families and depths. The standardisation of niche components and calculation of relative fitness were both conducted within competition treatment. Simple regression was used to test for significant linear selection on each niche component. Quadratic selection gradients were estimated from multiple regressions that included both the linear and quadratic terms for each niche component.

RESULTS

The sloping sides of the vernal pool in this study span less than 2 m in vertical relief, but nonetheless represent steep ecological gradients in flooding and productivity: experimental plots at the deepest end of the gradient were submerged for an average of 66 days, and accumulated 193 g/m² of above-ground vegetative biomass over the growing season, compared to only 4 days of inundation and 302 g/m² of biomass in the experimental plots nearest the pool edge (Fig. 1b).

Seeds planted into neighbour removal plots exhibited substantially higher overall fitness than those growing in plots with background vegetation intact (Fig. 1c). This response was most evident at later life-history stages: the neighbour

removal treatment had no effect on the probability of seedling emergence (competition treatment effect: $F_{1,18.1} = 1.29$, $P = 0.27$), but led to significantly increased seed production in plants that emerged (competition treatment effect: $F_{1,16.8} = 41.27$, $P < 0.0001$). Overall, depth within the pool and competition treatment both had significant individual and interacting effects on the cumulative fitness of experimental plants (Table 1). Neighbour removal shifted peak seed production towards the terrestrial end of the gradient, and had no effect on fecundity at the deepest pool positions (Fig. 1c).

Family-level niche components were significantly influenced by the presence of neighbouring plants (Fig. 2, Table 2). Removing the surrounding vegetation caused the optimum for the fundamental niche (i.e. depth at which mean fitness was highest) for each family to shift an average of 12 cm (in elevation) towards the terrestrial edge of the inundation gradient (although four families shifted in the other direction) (Fig. 2b), and the average niche breadth to increase by 4-fold (Fig. 2c). In contrast, removing neighbours did not significantly change the mean niche position across families (Fig. 2a, Table 2).

Genetic variation in the within-pool niche was only expressed in the absence of neighbours (Fig. 3a, b). Specifically, the extent of additive genetic variation in the ecological niche (i.e. the family \times zone variance component) was 18-fold greater in the neighbour removal treatment than the control treatment, and was statistically different from zero only in the neighbour removal treatment ($Z = 2.01$, $Pr(Z) > 0 = 0.02$). Levene's tests indicated that this variation was driven by the expression of greater differences among families in their niche position and niche breadth: the among-family variance in niche position doubled (Fig. 2a), and variance in niche breadth increased by over 350% (Fig. 2c), in the neighbour removal treatment compared to controls (Table 2). Among-family variance in the niche optimum was not significantly different between control and neighbour removal plots (Fig. 2b, Table 2).

Selection on niche components was more frequently detected in neighbour removal plots than in control plots (Fig. 4; Appendix S3). We observed marginally significant

Table 1 The effects of competition treatment, transplant zone and family structure on the cumulative fitness of experimental transplants. Cumulative fitness was modelled as the integrated outcome of emergence, survival to flowering and the number of seeds produced

Term	Residual d.f.	Test d.f.	Dev	<i>P</i>
Full model	12			
Zone	4	8	118.77	$5.96e^{-22}$
Treatment	7	5	135.01	$2.05e^{-27}$
Treatment \times Zone	8	4	35.92	$3.01e^{-7}$

Analyses were conducted using aster models to account for dependence among fitness estimates (e.g. a plant could not produce seeds if it did not emerge or survive to flower) and the different probability distributions for different fitness components (Geyer *et al.* 2007; Shaw *et al.* 2008). The significance of each factor was evaluated using likelihood ratio tests of unconditional, nested aster models (see methods). Sire ID and Dam ID were included as random effects in all models, and were each significant when compared to the full model (Sire effect, $P < 0.002$; Dam effect, $P < 3.05e^{-12}$).

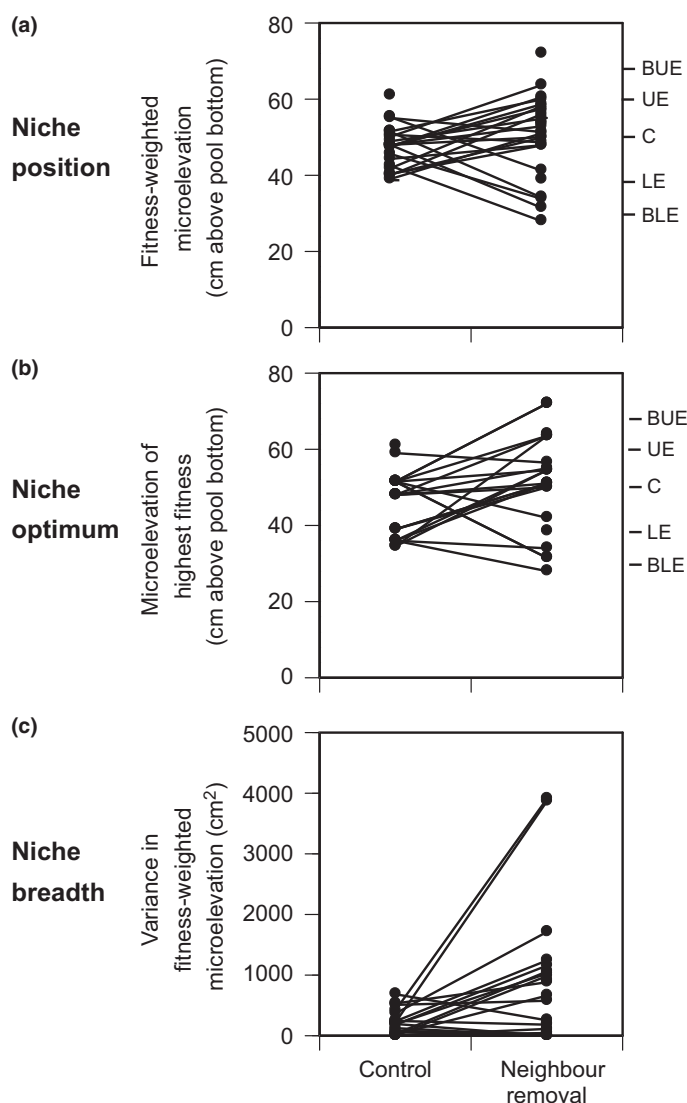


Figure 2 Family-level niche components of experimental *L. fremontii* transplants in control and neighbour removal plots, with respect to their location along the microelevation gradient: (a) niche position; (b) niche optimum; (c) niche breadth. See Appendix S1 for an explanation of the niche components. For reference, the mean microelevation of plots in each population zone are indicated on the right-hand axis of the graphs for niche optima and niche positions.

linear selection on niche position (Fig. 4d), and significant quadratic selection on the niche optimum (Fig. 4e), in neighbour removal plots, but found no evidence for significant selection on these components in control plots (Fig. 4a, b). Strong directional selection for increased niche breadth was observed in both treatments (Fig. 4c, f).

DISCUSSION

The results of our field experiment indicate that this *L. fremontii* population harbours substantial additive genetic variation in its fundamental niche, but not its realised niche. The removal of vegetation triggered the expression of differences among genotypes in the fundamental niche, primarily

Table 2 Statistical results for the effects of competition treatment on the niche position, niche optimum and niche breadth of *L. fremontii* families planted across an inundation gradient. (a) Analyses of overall shifts in family-level niche components in response to the neighbour treatment. In these models, family-level estimates of niche components are the response variable (see Fig. 2). (b) Levene's test on the residuals from the analyses presented in (a), where the response variable is the residual of each family's niche component from the mean estimate for its respective competition treatment category

	Mean square	F value	P value
(a) GLM using family-level niche components			
Niche position	0.01	1.50	>0.22
Niche optimum	0.06	5.43	<0.05
Niche breadth	0.04	6.04	<0.02
(b) Levene's test on residuals			
Niche position	0.02	6.29	<0.02
Niche optimum	0.007	1.93	>0.17
Niche breadth	0.04	12.39	<0.001

All analyses are one-way ANOVAS with competition treatment (neighbours removed vs. neighbours present, d.f. = 1) as the only factor. Significant *p*-values are highlighted in bold.

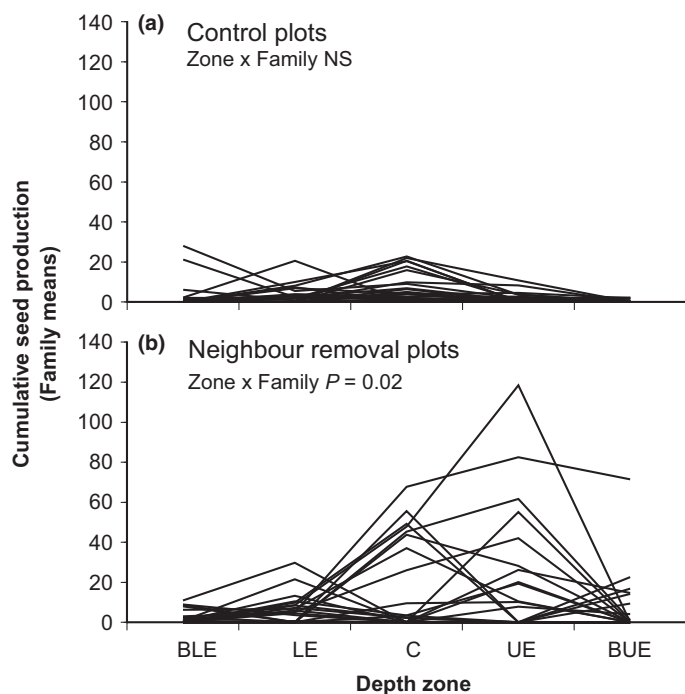


Figure 3 Genetic variation in the vernal pool niche of the experimental *L. fremontii* population. Each line represents the mean cumulative fitness of each family in each depth zone, averaged across three replicate plots/zone. (a) Family mean fitness in control plots with background vegetation present; (b) family mean fitness in plots where all neighbouring vegetation was removed (including background *L. fremontii* individuals when present). The family \times zone variance component was significant for neighbour removal plots only.

with respect to the niche position and the niche optimum, which are not evident when competitors are present. Furthermore, competitive release at the upper population boundary generated marginally significant directional selection for the niche position to shift towards the terrestrial edge of the

vernal pool inundation gradient, and significant stabilising selection on the niche optimum. Thus, ecological opportunity created a potential for selection on niche components that is largely absent when neighbouring vegetation is present. This result suggests a mechanism by which ecological opportunity can generate an increase in fitness variance and the potential for rapid evolution, as opposed to requiring a lag period during which potentially adaptive mutations accumulate *de novo* in a population (Raine & Travisano 1998). Conversely, it suggests an important role for competition in potentially restricting niche evolution and promoting niche conservatism: the expression of genetic variation in the microhabitat niche, and selection on microhabitat niche position, were only detected in the absence of neighbours.

The removal of neighbours produced a strong positive fitness response in our experimental plants, though the degree of ecological release varied across the inundation gradient (Fig. 1c). The strongest increase in fitness was observed at the terrestrial edge of the natural population boundary (UE zone), while no significant response to neighbour removal occurred in plots placed deeper in the pool. The variation in the extent of ecological release across the gradient can in part be attributed to the changing composition of the plant community: the centre zone is dominated by *L. fremontii*, while the edge and beyond-edge zones are dominated by other species. Thus, the fitness responses observed in the centre of the population reflects a release from mostly intraspecific competition, while the responses observed at the upper edge are due to a release from primarily interspecific competition (Fig. 2). These results indicate that interspecific competitive interactions play a significant role in setting the upper (terrestrial) boundary of *L. fremontii* in vernal pools, while physiological and abiotic factors limit the lower (deeper) population limit. These patterns are consistent with previous work in this system (Emery *et al.* 2009) and other plant communities distributed across wetland flood and soil moisture gradients (e.g. Wilson & Keddy 1985; Gurevitch 1986). Thus, the interacting roles of competition and hydrological stress may provide a general ecological explanation for plant distribution patterns in wetland systems across a diversity of wetland types (e.g. vernal pool, lakeshore, marsh) and plant life history (e.g. annual or perennial) and functional (e.g. monocot or dicot) strategies. These patterns also mirror those found in invertebrate (e.g. Connell 1972) and vertebrate communities (e.g. Hairston 1980) where competitive hierarchies interact with physiological tolerances to partition species across environmental gradients. In all of these systems, the conditions that are 'stressful' depend upon the underlying physiology of the organism, which may be understood in terms of the evolutionary history of the lineage. For example, the common ancestor of all *Lasthenia* species (and many other vernal pool endemic plants) was terrestrial, and thus it is perhaps not surprising that the flooded end of the vernal pool gradient imposes the stronger abiotic limits to growth and reproduction of our experimental transplants.

The population-level response of ecological release (Fig. 1c) was underlain by substantial changes in the niche components of individual families in response to the removal of neighbours (Fig. 2), revealing several differences between the fundamental and realised niche in this population. Most

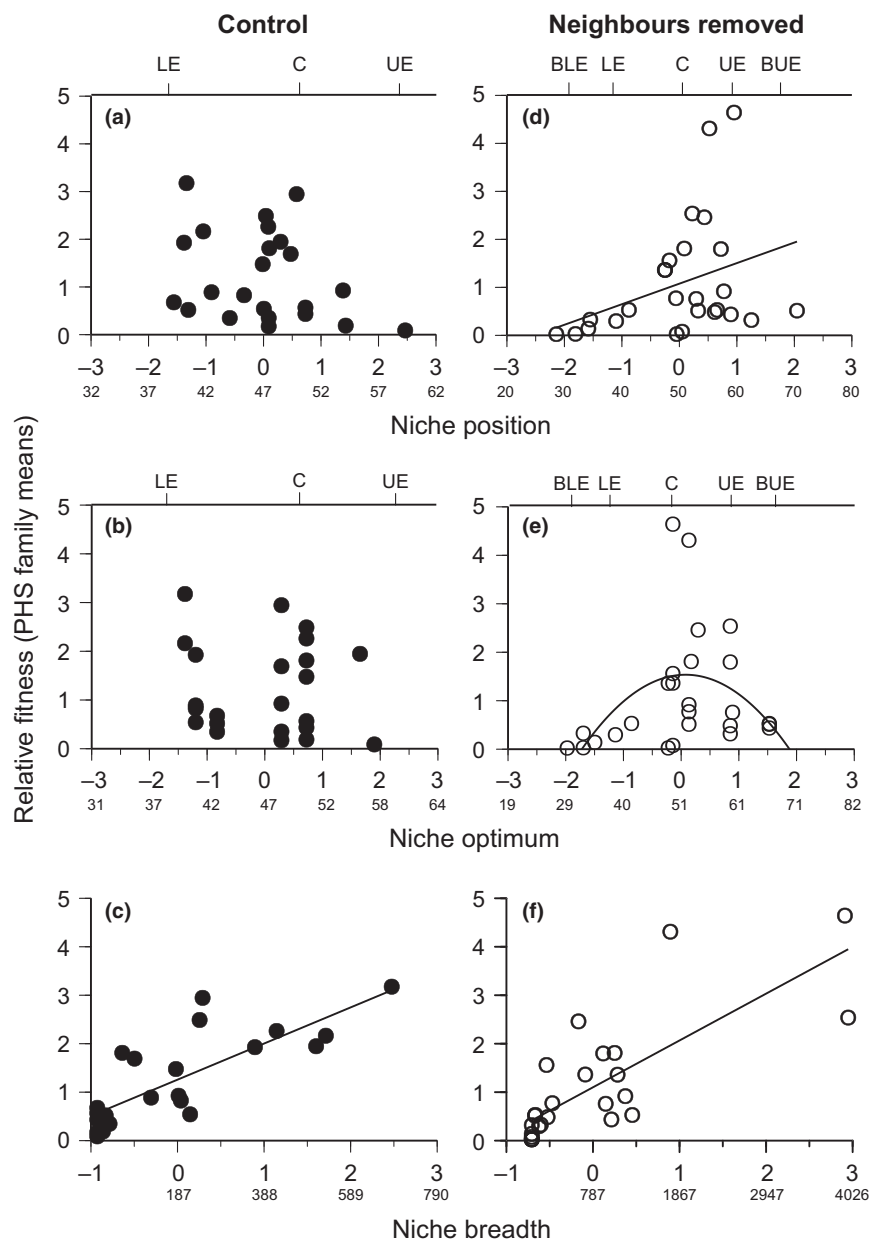


Figure 4 Results from a genotypic selection analysis on the family-level niche components in experimental *L. fremontii* in control (a–c; left column) and neighbour removal (d–f; right column) plots. The x-axis on each figure indicates range of the standardised niche component values used in the selection analyses (top, large text) and actual values of the unstandardised estimates (bottom, small text); units for unstandardised values are in centimetres for niche position and niche optimum, and cm^2 for niche breadth. For reference, the mean microelevation of plots in each population zone are indicated on the right-hand axis of the figures of niche positions (a, d) and niche optima (b, e). Lines are shown only for differentials and/or gradients were statistically significant ($P < 0.05$), in addition to the differential for niche position in the neighbour removal treatment (d) that was marginally significant ($P = 0.08$). The full statistical results for all selection analyses are available in Appendix S3.

families shifted their niche optimum towards the terrestrial edge of the pool (Fig. 2b) and exhibited less variable fitness across the hydrological gradient (i.e. increased niche breadth) in the neighbour removal treatment compared to the control (Fig. 2c). This ecological shift was mirrored by changes in the patterns of selection, with marginally significant linear selection favouring genotypes with niche positions near the terrestrial edge of the existing population boundary (Fig. 4d), and significant stabilising selection on the current niche optimum in the population (Fig. 4e). In addition, the *variability*

among families also increased in response to the removal of competitors: among-family variances in niche position and niche breadth were substantially higher when families grew in competitor-free conditions (Fig. 2a, c; Fig. 3a, b). In the paternal half-sib design, variance among families is due to additive genetic variation (Falconer & Mackay 1996; Lynch & Walsh 1998). Thus, the effect of ecological release on the extent of among-family variance indicates that removing competition reveals additive genetic variation in the fundamental niche that is concealed when neighbours are present (the

realised niche). These changes in the expression of genetic variation were accompanied by altered patterns of selection for niche evolution in neighbour removal plots (Fig. 4d, e; Appendix S3). While these results suggest that ecological release can influence the microevolutionary dynamics of niche evolution, the ultimate evolutionary response to selection will also depend on the effects of neighbour removal on *within-family* variance components (Falconer & Mackay 1996). An experimental design that allocates substantial replication to full-sib niche estimates would make it possible to precisely estimate variance components and heritability values, to ultimately predict the response to selection.

Previous field studies have demonstrated that estimates of quantitative genetic parameters can vary with the competitive environment (Mazer & Schick 1991; Knapp & Rice 2011), degree of environmental stress (Hoffmann & Schiffer 1998; Hoffmann & Merilä 1999) and exposure to novel environments (Schlichting & Smith 2002; Buckley *et al.* 2010). While the majority of this prior work has focused on the genetic basis of trait variation, our experimental results indicate that the expression of genetic variation in the niche *per se* is similarly context-dependent. There are at least two potential sources of this latent niche variation in a population's genome: residual ancestral variation (Barrett & Schluter 2008) or the accumulation of heritable variation in traits that affect fitness under conditions that are rarely (or never) encountered (Schmalhausen 1949). Both of these sources of genetic variation may contribute to the results we observed in this experiment for *L. fremontii*. The common ancestor of vernal pool *Lasthenia* taxa was a terrestrial species that subsequently diversified into (or within) vernal pool wetlands (Ornduff 1966; Emery *et al.* 2012), so genetic variation for tolerance to terrestrial conditions may still be present within and among the genomes of *L. fremontii* lineages. Alternatively, if *L. fremontii* has been competitively restricted to ecologically saturated vernal pool plant communities over its recent evolutionary history, heritable variation that influences fitness only in the absence of competitors would not have been exposed to selection and would accumulate in the genome over time (Schluter 1988; Haller & Hendry 2014). This could explain why we observed significant stabilising selection on the niche optimum only in the *absence* of competitors, which runs contrary to the hypothesis that competitors are the *cause* of stabilising selection on the ecological niche (Ackerly 2003; Price & Kirkpatrick 2009): past stabilising selection has eroded genetic variation in the realised niche, making it difficult to detect patterns of stabilising selection in our control plots (Schluter 1988; Haller & Hendry 2014). Interestingly, the significant quadratic gradient on the niche optimum in the absence of neighbours (Fig. 4e) suggests that competitors are not the only source of stabilising selection on this niche component, and that genetic variation in responses to other factors across the vernal pool inundation gradient also contribute to selection for stasis in this population.

The expression of genetic variation in the ecological niche is necessary for adaptive evolution and diversification to proceed in environments with reduced competition; conversely, the suppression of niche variation in the presence of competition may promote niche conservatism among lineages occupying

saturated communities. There is ongoing debate over the relative importance of low genetic variation vs. stabilising selection in maintaining ecological similarities among close relatives (Futuyma 2010), though this may be a false dichotomy since past selection influences subsequent levels of genetic variation (Schluter 1988; Haller & Hendry 2014). The two closest relatives to *L. fremontii*, *L. burkei* and *L. conjugens*, are also vernal pool endemics, and all three species are restricted to similar depths within vernal pools. Phylogenetic comparative analyses of habitat associations in *Lasthenia* have found that the microhabitat niche (depth position within pools) is phylogenetically conserved, whereas large-scale niche parameters (climatic associations) have evolved rapidly throughout the diversification of the clade (Emery *et al.* 2012). Thus, while our results provide a microevolutionary mechanism for rapid niche diversification in response to ecological release, a phylogenetic perspective suggests that the long-term presence of competitors in the vernal pool communities has restricted niche evolution and promoted niche conservatism among close relatives in *Lasthenia*. Together, these results indicate that interspecific competition may influence the rate of niche evolution through previously unrecognised effects on the expression of genetically based variation in the ecological niche.

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