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Research

The scale of local adaptation in *Mimulus guttatus*: comparing life history races, ecotypes, and populations

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Summary

• Fitness trade-offs between environments are central to the evolution of biodiversity. Although transplant studies often document fitness trade-offs consistent with local adaptation (LA), many have also found an advantage of foreign genotypes (foreign advantage (FA)). Understanding the mechanisms driving the magnitude and distribution of fitness variation requires comparative approaches that test the ecological scales at which these different patterns emerge.

• We used a common garden transplant experiment to compare the relative fitnesses of native vs foreign genotypes at three nested ecological scales within *Mimulus guttatus*: annual vs perennial life history races, perennial ecotypes across an elevational range, and populations within perennial elevational ecotypes. We integrated fitness across the life-cycle and decomposed LA vs FA into contributions from different fitness components.

• We found LA, measured as home-site advantage, between annual and perennial races and a trend towards LA among populations within montane habitats. Conversely, we found strong FA of low-elevation perennials in a montane environment.

• LA between life history races reflects the fitness advantages of adult survival and vegetative growth in a mesic environment. Within the perennial race, recent climate conditions or nonselective processes, such as dispersal limitation or mutational load, could explain FA of low-elevation perennials in a montane environment.

Introduction

Plants encounter diverse selective environments throughout their ranges. The consequences of this variation for the evolution of biodiversity will depend on the ability of plant populations to respond to local selective pressures as well as the effect of adaptation on fitness in other environments. When adaptation to a local environment confers a fitness cost in foreign environments, environmental variation can generate and maintain biodiversity (Kawecki & Ebert, 2004). Alternatively, plant populations may fail to respond to local selective pressures (e.g. Anderson & Geber, 2010), or fitness trade-offs can be weak or absent (e.g. Lowry *et al.*, 2009). In these cases, nonselective processes such as genetic drift or gene flow will structure the distribution of trait and fitness variation within species.

Meta-analyses of the transplant literature suggest that local adaptation (LA, defined here as the fitness advantage of native compared with foreign genotypes) is both common and strong (Leimu & Fischer, 2008; Hereford, 2009). Yet, this generalization masks substantial variation in the frequency and magnitude of LA among studies. Many comparisons, in fact, find that a foreign genotype has the highest relative fitness in a specific environment (Leimu & Fischer, 2008; Hereford, 2009) – a pattern that we refer to as 'foreign advantage' (FA). Further, this is almost certainly an underestimate of the strength and frequency of FA among natural plant populations, because the transplant literature is subject to both publication and experimental design biases that favor the detection of LA (Hereford, 2009). Alternatively, FA could reflect inadequate fitness measures, such as single fitness proxies, that fail to capture the true pattern of fitness trade-offs (Hereford, 2009; Anderson *et al.*, 2014). Approaches that integrate multiple components of fitness across the life-cycle, such as the intrinsic rate of increase or the lifetime reproductive rate, are necessary to accurately estimate local vs foreign fitness differences. Finally, fitness differences within species are determined by a balance of selective and nonselective forces, including gene flow, inbreeding depression, and genetic drift (Kawecki & Ebert, 2004). Thus, understanding the evolution of FA is a necessary counterpoint to the study of LA.

Among plant populations, LA is most likely to evolve when divergent selection is strong and consistent, genetic variation is high, and gene flow is restricted (Kawecki & Ebert, 2004). Alternatively, FA is most likely when divergent selection is weak or inconsistent and genetic drift, inbreeding depression, or maternal effects limit the fitness of local genotypes (e.g. Heschel & Paige, 1995; Stanton & Galen, 1997; Leimu & Fischer, 2008). Correspondingly, there is some evidence that LA is stronger between than within habitat types (Sambatti & Rice, 2006; Hereford &

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Winn, 2008) or at greater geographic or environmental distances (Galloway & Fenster, 2000; Hereford, 2009; Anderson *et al.*, 2015). However, comparative approaches that test for LA vs FA at multiple ecological scales within a single species remain rare and are necessary to test these predictions.

We took advantage of a hierarchy of nested ecological contrasts within common monkeyflower (*Mimulus guttatus* DC, Phrymaceae) – from widespread life history races to elevational ecotypes to local populations – to test for LA vs FA at each of these scales. *Mimulus guttatus* is a highly polymorphic and geographically widespread herb that occupies a diverse range of mesic habitats, including coastal bluffs, serpentine seeps, and montane streams (Grant, 1924; Wu *et al.*, 2008). Populations of *M. guttatus* exhibit one of two life history strategies, annual or short-lived perennial, determined primarily by their genotypes at a chromosomal inversion region that controls several key life history traits (Lowry & Willis, 2010; Friedman, 2014; Oneal *et al.*, 2014). Within these general life history races, however, populations vary in traits associated with specific habitats. Among annual populations, clinal variation in flowering time and size at reproduction is associated with elevational and latitudinal gradients (Kooyers *et al.*, 2015). Similarly, perennial populations in coastal and montane habitats have each been recognized as distinct taxa relative to inland, low-elevation perennial populations (Nesom, 2012). Thus, populations of *M. guttatus* exhibit habitat-associated ecotypic divergence nested within more general life history divergence.

We compared the performance of 11 populations of *M. guttatus* in a common garden field experiment at the site of a montane perennial population. We estimated population growth rates as a comprehensive fitness measure. The population growth rate (λ) integrates different components of fitness, including survival, reproduction, and growth, that vary between life history races, and thus is a more appropriate fitness measure than any single component (Stearns, 1992). We compared relative λ values between native and foreign genotypes to test for LA vs FA at a series of nested scales: between annual and perennial races, between low-elevation perennial and montane perennial ecotypes, and between local and foreign montane perennial populations. We use the term 'local adaptation' here to refer to a pattern where local genotypes outperform foreign genotypes within a single environment (also referred to as home-site advantage). Although we did not test for fitness trade-offs in other environments, previous transplant studies in this species have demonstrated these trade-offs for late-flowering perennials in seasonally drying annual environments (Hall & Willis, 2006; Lowry *et al.*, 2008).

In addition to testing for patterns of LA vs FA, we also used life table response experiments (LTREs) to dissect the contributions of specific vital rates to differences in performance. We predicted that fitness differences between life history races would occur through vital rates, such as adult survival and vegetative growth, that distinguish these strategies. Finally, because there was extensive fitness variation within groups, we constructed a continuous measure of phenotypic divergence across all 11 populations to test whether patterns of LA were related to continuous variation in life history. We predicted that LA would be stronger at greater ecological scales (between life history races and elevational ecotypes), whereas FA would be more likely at finer ecological scales (between populations within the montane perennial ecotype). Correspondingly, we predicted that the magnitude of LA between population pairs would increase with greater phenotypic divergence.

Materials and Methods

Study system

In 2010, we collected maternal seed families from 11 populations of *Mimulus guttatus* DC in the central Sierra Nevada of California and surrounding foothills. These populations span the range of life history variation among inland populations of *M. guttatus* in California (Supporting Information Table S1). We classified each population as annual or perennial based on duration (i.e. senescence at fruit maturity) in the field and further divided montane and low-elevation perennials based on morphology and habitat (Fig. 1). Montane perennials (*M. corallinus sensu* Nesom, 2012) occur above 1450 m elevation in the Sierra Nevada and produce few flowers, investing instead in extensive below-ground mats of branching rhizomes. Low-elevation perennials (*M. guttatus sensu* Nesom, 2012) are more morphologically and ecologically variable but generally occur along lakes and streams and produce horizontal stems (i.e. stolons) that root at nodes and give rise to clonal rosettes. Annual plants (*M. micranthus sensu* Nesom, 2012) are highly variable in phenological and morphological traits, but occupy seasonally drying habitats and senesce after fruiting.

Given extensive phenotypic variation in these and other traits and incomplete reproductive barriers, taxonomists have variously recognized between four and 20 species in the *M. guttatus* complex (reviewed in Nesom, 2012). Although the most recent taxonomic treatment splits *M. guttatus* into multiple morphological species (Nesom, 2012), recent genomic evidence suggests extensive introgression among these taxa (Oneal *et al.*, 2014; Twyford & Friedman, 2015). For this reason, we treat different life history races and elevational ecotypes as within the broader circumscription of *Mimulus guttatus sensu lato* (Grant, 1924).

Common garden transplant experiment

We transplanted cohorts of seedlings from each of 11 populations over 2 yr into a common garden field experiment to test for LA vs FA. The common garden site was a montane meadow surrounding a small stream supporting a native population of montane perennial *M. guttatus* in Stanislaus National Forest (38.32107N, 119.91607W; 2040 m asl). This native population (Eagle Meadows) was included as one of the 11 experimental populations to assess local adaptation at the population level within the montane perennial ecotype.

In 2012 and 2013, we transplanted 40 seedlings from each population into experimental plots located along the stream bank and within the distribution of native *M. guttatus* at this site. Each experimental plot contained one individual from each population in a fully randomized position, for a total of 40 plots yr^{-1}. To

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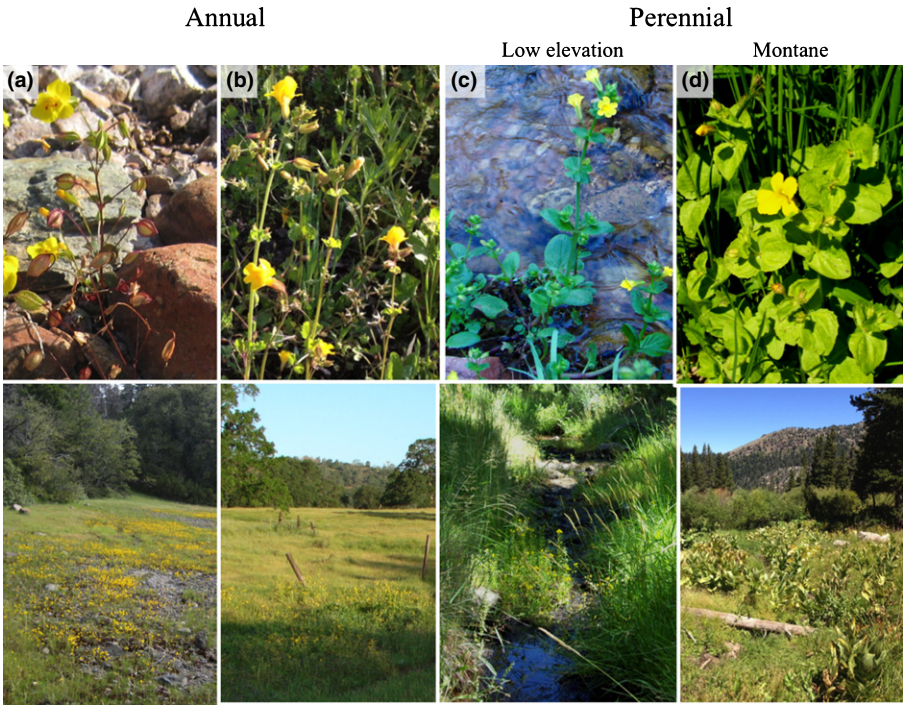

Fig. 1 Characteristic growth form (upper panels) and habitat (lower panels) of the populations of *Mimulus guttatus* used in this study. (a, b) Annuals occupy seasonally drying seeps or meadows and exhibit variation in the timing and size at flowering associated with variation in the length of the growth season. (c, d) Perennials occupy more mesic stream banks or meadows and survive and reproduce over multiple years. (c) Low-elevation populations overwinter as aboveground rosettes connected by stolons whereas (d) montane populations produce few flowers and overwinter as belowground rhizomes.

prevent genetic contamination of the native population, we emasculated all flowers on experimental plants and transplanted all seedlings into 4-inch round pots (Kord, Ontario, Canada) buried within the local substrate (to contain belowground rhizomes from nonnative genotypes). This site is inundated with snowmelt at the start of the growth season and slowly dries as stream flow decreases throughout the summer. Thus, to reduce transplant shock and mitigate any effects of pots on root development, we watered all plots to field capacity at the time of transplant and at each subsequent census. The use of pots and supplemental watering may have obscured some aspects of the local environment, including competition and the magnitude or timing of drought stress. However, in both years, experimental plants from montane perennial populations exhibited similar timing of flowering, fruiting, and dormancy as the surrounding native *M. guttatus*, as well as similar degrees of drought stress (indicated by wilting and die-back) in 2013 when low snowpack accelerated drying at this site (M. DeMarche, pers. obs.). Thus, we do not believe that supplemental watering substantially altered experimental plots relative to the native population.

Experimental seedlings in 2012 were derived from field-collected seeds pooled from 30 maternal families within each population and germinated in the glasshouse at UC Santa Cruz. In 2013, seedlings were randomly sampled from among the germinants in the seed germination experiment (see 'Seed germination experiment' in Methods) to allow natural variation in the timing of germination following snowmelt. By using field-collected seeds, this design captures the relative fitness of a foreign seed dispersing into the common garden habitat, and observed fitness differences are driven by a combination of genetic and maternal effects. Transplants occurred following snowmelt on 14 June 2012 and 26 May 2013.

Vital rates

We estimated vital rates by tracking the survival and reproduction of each experimental individual at 3–10 d intervals from the time of transplant to the end of the growth season (the first snowfall on 21 October 2012 and drought-induced mortality of all experimental individuals by 27 September 2013). In a few cases, we excluded transplanted seedlings that were destroyed or unidentifiable and included seedlings from populations that had been accidentally transplanted twice within the same plot. For these reasons, the number of seedlings per population and year varied from 38 to 42 (mean = 39.8; Table S2). All analyses were conducted in R v.3.1.2 (R Core Development Team, 2015).

Survival and growth We recorded adult overwinter survival as the presence of at least one rosette following snowmelt each year (11 May 2013 and 1 May 2014), and counted the number of additional vegetative rosettes as a measure of growth. Low-elevation perennials overwinter as vegetative rosettes, whereas montane perennials usually regenerate from belowground rhizomes each spring (M. DeMarche, pers. obs.). Belowground rhizomes were contained within experimental pots, allowing survival and vegetative growth to be scored for montane perennial individuals.

Fecundity Experimental flowers were emasculated to avoid pollen contamination, preventing measures of seed set. Instead, we estimated two components of fecundity: flower number (F) and ovule number per flower (O). In each year, we counted the total number of flowers produced by each experimental individual (individuals that died before flowering or failed to flower were scored as zero) and estimated ovule number per flower from a

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subset of individuals in each population (n per population: mean = 14; range = 3–31; Table S2). We collected ovaries from second flowers and preserved them in ethanol, then scraped ovules from each locule onto separate microscope slides using clean forceps. Ovules were dyed with lactophenol aniline blue and counted under a dissecting microscope. Sample sizes for ovule number were generally low in montane perennial populations because few individuals flowered. In 2013, we were only able to collect a single flower from the Silver Creek population, so for this population we estimated mean ovule number for 2013 from flowers collected in both years. We fitted linear mixed models with population and year as fixed effects and plot as a random effect to estimate mean ovule number (O).

Seed germination experiment We estimated seed overwinter survival and germination rates from 96 field-collected seeds per population during the winter of 2012–2013. We pooled seeds from 10 to 30 maternal families within each population and planted single seeds into separate plug tray cells (98 cell plug trays; TO Plastics, Ostego, MN, USA) filled with HP Sunshine Potting Mix (Pro-Mix, Quebec, Canada) in a fully randomized design. Plug trays were placed in the field before the first snowfall on 21 October 2012, and germinants scored following snowmelt on 11 May 2013. We fitted generalized linear mixed models with a binomial error distribution and tray as a random effect to estimate seed germination rates for each population.

Recruitment plots Because *Mimulus* individuals produce hundreds of ovules per flower, raw ovule estimates and experimental germination rates would wildly inflate our estimates of fecundity. In reality, pollen and resource limitations on seed set, safe-site limitation, and seed predation and dispersal will act to reduce the proportion of ovules that successfully recruit as seedlings. Further, *Mimulus* seeds are small and easily dispersed by wind and water (Waser *et al.*, 1982; Truscott *et al.*, 2006), suggesting that many seeds may be lost from the relatively narrow band of suitable stream bank habitat at this site. We established five recruitment plots within the native *M. guttatus* population to better understand recruitment dynamics in this site. Following snowmelt in the spring of 2014, we set up plots at 1-m intervals along the stream bank in the area of peak *M. guttatus* abundance. We sampled natural *M. guttatus* recruits by collecting 10 × 10 cm soil cores from each plot on 1 May and again on 16 May. In each core, we excavated every *M. guttatus* recruit to determine whether it was a seedling or a clonal rosette arising from a belowground rhizome (Fig. S1). For each rosette, we traced its network of rhizomes to determine whether it was physically connected to any other rosettes. Both stolons and rhizomes root at nodes and can readily fragment to become physiologically independent but genetically clonal rosettes (i.e. ramets) (Truscott *et al.*, 2006). From these data, we estimated the total proportion of *M. guttatus* recruits that were seedlings vs clonal rosettes and calculated a retention rate A that captures the proportional recruitment success of ovules relative to rosettes as $A = 6.7 \times 10^{-4}$ seedlings per ovule (i.e. scaling seedling/rosette recruitment by rosette/ovule production; Methods S1).

Comparing demographic performance

We constructed matrix projection models and used LTREs (Caswell, 2001) to compare demographic performance between life history races, ecotypes, and populations in each year.

Matrix projection models We modeled the growth of each stage-classified population as $\mathbf{N}(t+1) = \mathbf{A}\mathbf{N}(t)$, where $\mathbf{N}(t)$ is a vector of stage-classified individuals at time t and $\mathbf{A}$ is a 3×3 matrix of transition rates. We collapsed census data collected throughout each year to estimate yearly transitions based on a pre-reproductive census (i.e. at the start of the growth season right after snowmelt). At this time, individuals can exist in one of three stages: seed in the seed bank, newly germinated seedling, or vegetative rosette (Fig. 2). Either seedlings or rosettes can flower and contribute to the seed or seedling class or survive to produce vegetative rosettes in the subsequent time step, while the transition from seed to seed reflects seed dormancy (matrix 1).

We assembled separate transition matrices for each population in each year and also pooled individuals across populations to construct matrices for higher level contrasts between races and ecotypes. For the comparison within montane perennials, we focused on population-level comparisons and tested the relative fitness of each foreign montane perennial population (Silver Creek and Silver Fork) separately. However, pooling these populations into a single local vs foreign contrast did not alter qualitative results or the level of significance, probably because sample sizes within the local Eagle Meadows population were still limiting.

We parameterized the transition matrices according to Fig. 2. Seed germination rate G was estimated as the mean germination rate for each population from the seed germination experiment (see 'Seed germination experiment' in Methods). Yearly seed

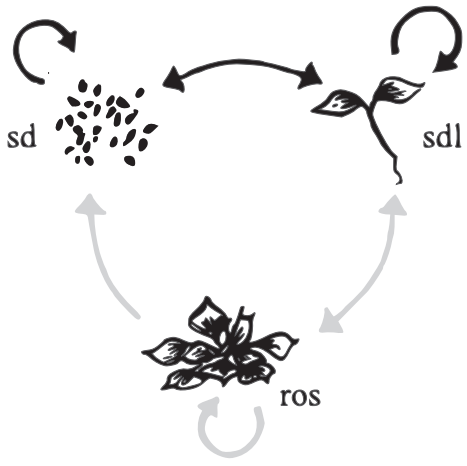

Fig. 2 Life cycle graph for *Mimulus guttatus* based on a yearly census at the start of the growing season. Annual populations (black arrows only) can exist as seeds (sd) in the seed bank or newly germinated seedlings (sdl), whereas perennial populations (black and gray arrows) can also exist as vegetative rosettes (ros) that have successfully overwintered. Either seedlings or rosettes can flower to produce seeds or seedlings, or survive and grow to produce rosettes, the following year. Vital rate parameters are given in matrix 1.

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bank survival D was treated as a constant across all years and populations; we used 0.534 based on a seed viability study using *M. guttatus* seeds from multiple Sierra Nevada populations (Elderd & Doak, 2006). Flower production (F), overwinter survival (S), and rosette production (R) were estimated from the observed per capita transition frequencies in each seedling cohort (e.g. F = the total number of flowers/the total number of individuals, etc.). Pooled matrices were constructed by using population-specific germination and ovule rates to estimate individual seed and seedling production, then averaging across pooled individuals to estimate matrix transitions.

Sample sizes for estimating performance of second-year individuals were small (n = 4–7 per perennial population) and estimates were limited to 2013 when overall performance was low (because of drought; see Results). However, there was no evidence that fecundity, survival, or growth differed between rosettes and seedlings in 2013 (low-elevation perennial: fruits: $F_{1,88} = 2.44$, $P = 0.12$; survival and rosette production were zero for all individuals; montane perennial: fruits: $F_{1,137} = 0.77$, $P = 0.38$; survival: $\chi^2_{1,137} = 0.22$, $P = 0.64$; rosettes: $F_{1,137} = 0.58$, $P = 0.45$). Thus, rather than ignoring rosette production as a component of fitness in perennial populations, we chose to set the value of a rosette as equal to the value of a seedling by assuming that rosette performance was equivalent to seedling performance within each population and year. Under this assumption, a perennial plant may produce new individuals either sexually by producing a viable seed or seedling, or clonally by producing a new vegetative rosette.

Transition matrices took the general form:

$$\begin{array}{c} \\ \text{Seed}_{t+1} \\ \text{Seedling}_{t+1} \\ \text{Rosette}_{t+1} \end{array} \begin{array}{c} \begin{array}{ccc} \text{Seed}_t & \text{Seedling}_t & \text{Rosette}_t \end{array} \\ \begin{pmatrix} \text{D}(1-\text{G}) & \text{FOA}(1-\text{G}) & \text{FOA}(1-\text{G}) \\ \text{DG} & \text{FOAG} & \text{FOAG} \\ 0 & \text{SR} & \text{SR} \end{pmatrix} \end{array}$$

(Matrix 1)

Life table response experiments We tested the fitness effects of a foreign group relative to a native group using fixed-effect LTREs (Caswell, 1989, 2001). Fixed-effect LTREs are retrospective analyses that decompose the effect of a treatment (in this case, native vs foreign genotypes) on λ into contributions from specific vital rates (Caswell, 1989, 2001). Large contributions may arise through large observed differences in a vital rate between treatments and/or high elasticity of λ to that vital rate. Preliminary analyses demonstrated a large effect of year on variation in λ, so we constructed separate models for each contrast within each year. We modeled the population growth of a group i as:

$$\lambda_i = \lambda_\bullet + \alpha_i \qquad \text{Eqn 1}$$

($\lambda_\bullet$, the population growth rate of a reference matrix; α_i, the effect of the ith treatment relative to that matrix.) We used the transition matrix of the native group as the reference matrix, so that the α estimate for the native group becomes 0 and the α estimate for the foreign group captures the magnitude of either FA (positive values) or LA (negative values). We decomposed the effect of the foreign group into contributions from specific vital rates. Matrices for each group were constructed by pooling across populations as appropriate. For example, to compare life history races we constructed a foreign matrix by pooling individuals from all annual populations and compared its performance to that of a reference matrix constructed by pooling individuals from all perennial populations. All analyses were conducted with the LTRE function in the POPBIO package (Stubben & Milligan, 2007).

Bootstrapping We constructed bias-corrected 95% confidence intervals around all estimates of λ and LTRE contributions by resampling 10 000 bootstrap replicates. For each replicate, we created a new data set by randomly sampling with replacement experimental individuals stratified by population and year to preserve the sample sizes of the original data set. We generated a distribution of estimates and used the 95th percentile confidence intervals (corrected for bias following Caswell, 2001) as an indication of statistical significance.

Phenotypic divergence and local adaptation

Given extensive fitness variation within groups, particularly annuals (see the Results section), we also tested whether fitness relative to the native Eagle Meadows population was explained by continuous, rather than discrete, phenotypic divergence in life history traits across all populations. For each experimental individual in the common garden field experiment, we measured four traits related to life history strategy: flowering time, flower size, flowering stem diameter, and rosette production. In a survey of 74 populations of *M. guttatus*, Friedman *et al.* (2015) found that perennial genotypes flower later and produce larger flowers, thicker primary stems, and more vegetative growth than annual genotypes. We measured flowering time as the number of days from the transplant date to the first census interval with at least one open flower, and also measured the corolla width of the first flower and the diameter of the primary flowering stem at the basal node on the same day. We used principal components analysis (PCA) on population means for each of these four traits. We transformed trait values across all populations in each year to z-scores and used the mean values for each population to estimate principal components using the princomp function. Thus, populations were the unit of replication in this analysis (n = 11). We quantified divergence in these life history traits by calculating the Euclidean distance between each population and the native Eagle Meadows population in a phenotypic space defined by the first two principal components. We estimated relative fitness for each population following Hereford (2009) as:

$$(\lambda_N - \lambda_F)/\bar{\lambda} \qquad \text{Eqn 2}$$

(λ_N and λ_F, the growth rates of the Eagle Meadows and each foreign population, respectively; $\bar{\lambda}$, the mean of λ_N and λ_F.) We fitted linear models with relative fitness as the response variable and phenotypic divergence, its square, and year as explanatory variables.

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Results

Local adaptation at nested ecological scales

Evidence for LA was mixed and depended on the level of comparison. In the contrast between life history races, annual populations contributed negatively to λ relative to perennial populations, indicating LA at the level of life history race (Table 1; Fig. 3a). However, this effect was only significantly different from zero in 2013. Conversely, the contrast between perennial ecotypes indicated FA. Low-elevation populations contributed positively to λ relative to montane populations, and this difference was statistically significant in both years (Fig. 3b). Within the montane perennial ecotype, both foreign populations (Silver Fork and Silver Creek) had negative but nonsignificant effects on λ in comparison with the native Eagle Meadows population in 2012, indicating a trend towards LA among montane populations (Fig. 3c). In 2013, fitness differences between populations were small and variable.

Different vital rates contributed to the emergent differences in λ that caused LA vs FA at different scales. LA of the perennial life history race was driven by perennial vital rates, including rosette production and fertility, whereas annuals exhibited FA in the seedling-to-seedling vital rate (Fig. 4a,b). Within the perennial life history race, greater seedling and rosette fertility contributed to the FA of the low-elevation ecotype (Fig. 4c,d). Conversely, the native montane ecotype only exhibited LA through rosette production in 2013. Within the montane ecotype, rosette production had the greatest effect on fitness differences between populations. However, contributions at this scale were nonsignificant. In general, large LTRE contributions reflected both large differences in vital rates between groups and high elasticities for those vital rates (Table S2).

Vital rates

In general, year had a profound effect on the performance of all individuals. There was a severe drought in the year 2013, and estimates of λ were consistently lower in 2013 compared with 2012 (Table S2). Both flower number and ovule number per flower decreased in 2013 relative to 2012 (Table S2). Drought conditions in 2013 increased mortality in August and September, truncating the growing season compared with 2012, when many individuals continued to flower into the late fall. In fact, all aboveground biomass died back by the end of September 2013. One consequence of this drought was that low-elevation perennials were unable to overwinter or produce clonal rosettes through aboveground stolons. By contrast, some montane perennials regenerated from belowground rhizomes the following spring (Table S2). Vital rates, elasticities, and λ estimates are available in Table S2.

Phenotypic divergence and local adaptation

Overall, variation in flowering time, inflorescence diameter, flower size, and rosette production captured life history and ecotypic divergence. The first principal component separated annual and perennial life history races (Fig. 5a), from small, early-flowering individuals with low rosette production (negative values) to larger, later flowering individuals with high rosette production (positive values). The second principal component reflected trait variation within life history races, including variation in reproductive size traits and 2013 rosette production. Low-elevation and montane ecotypes were separated along this axis (Fig. 5a), from individuals with thick inflorescences, smaller flowers, and less rosette production in 2013 (low-elevation ecotype; negative values) to individuals with thin inflorescences, larger flowers, and greater rosette production in 2013 (montane ecotype; positive values). In addition, annual populations were separated along both principal 'components 1 and 2', indicating variation in life history traits within the annual race (Fig. 5a).

Foreign populations varied in fitness relative to the native Eagle Meadows population, from LA to FA, and this variation was associated with phenotypic divergence in life history traits (Fig. 5b). Relative fitness had a significantly quadratic relationship with phenotypic distance (phenotypic distance: $\beta = -3.51$; $t = -4.25$; $P < 0.01$; phenotypic distance ^2: $\beta = 0.58$; $t = 4.55$; $P < 0.01$), with ecologically intermediate populations exhibiting FA (Fig. 5b). Year had a marginally significant effect on relative fitness, with greater FA in the severe drought of 2013 (year: $\beta = -0.30$; $t = -2.01$; $P = 0.06$).

Discussion

Multiple ecological and evolutionary processes structure fitness variation within species. Testing for LA vs FA at multiple ecological scales is necessary to understand the net outcome of conflicting evolutionary forces. Here, we used a common garden experimental approach to test for LA, measured as a home-site advantage, vs FA in *M. guttatus* at a series of nested scales: between life history races, between elevational ecotypes within a perennial life history race, and among populations within a montane ecotype. We predicted that divergent selection would cause LA to predominate at greater scales (between life history races and ecotypes), whereas nonselective processes would be more likely to generate FA at the finest scale (among populations within an ecotype). Instead, we found some evidence for LA at the largest and smallest scales (between life history races and among populations within the montane ecotype, respectively), whereas comparisons at the intermediate scale (between perennial ecotypes) exhibited FA. At the population level, we found nonlinearity in the relationship between relative fitness and phenotypic divergence, with ecologically intermediate populations exhibiting FA. We discuss potential explanations for this pattern in greater detail in subsequent sections.

Fitness variation for different ecological contrasts in *Mimulus guttatus*

In concordance with previous transplant studies in this species (Hall & Willis, 2006; Lowry *et al.*, 2008), we found evidence that a perennial life history strategy is locally adaptive in mesic

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Table 1 Demographic parameters for each group and year for three nested ecological scales

Year	Ecological scale	λ	*G*	*O*	*F*	*S*	*R*	*n*	***e*** *sd, sdl*	***e*** *sdl, sdl*	***e*** *sd, ros*	***e*** *sdl, ros*	***e*** *ros, sdl*	***e*** *ros, ros*
2012	Annuals	1.63 (1.40, 1.86)	0.732	363	8.59	0	0	239	0.08 (0.07, 0.09)	0.84 (0.81, 0.86)	0	0	0	0
	Perennials	1.95 (1.47, 2.52)	0.549	662	3.12	0.152	1.03	197	0.02 (0.01, 0.04)	0.20 (0.11, 0.33)	0.02 (0.02, 0.03)	0.22 (0.21, 0.23)	0.24 (0.24, 0.24)	0.26 (0.13, 0.42)
	Low elevation perennials	3.06 (2.19, 4.09)	0.652	621	6.88	0.162	1.04	80	0.02 (0.01, 0.05)	0.40 (0.22, 0.60)	0.01 (0.01, 0.02)	0.20 (0.13, 0.23)	0.22 (0.14, 0.24)	0.11 (0.03, 0.26)
	Montane perennials	1.18 (0.69, 1.91)	0.478	690	0.56	0.145	1.02	117	0.00 (0.00, 0.03)	0.01 (0.00, 0.05)	0.03 (0.01, 0.07)	0.09 (0.05, 0.12)	0.11 (0.06, 0.18)	0.72 (0.39, 0.87)
	Silver Fork	0.98 (0.40, 2.02)	0.552	803	0.40	0.100	0.82	40	0.01 (0.00, 0.12)	0.02 (0.00, 0.10)	0.03 (0.01, 0.09)	0.10 (0.04, 0.15)	0.13 (0.04, 0.20)	0.67 (0.07, 0.92)
	Silver Creek	0.84 (0.45, 1.69)	0.410	650	0.63	0.158	0.66	38	0.02 (0.00, 0.15)	0.03 (0.00, 0.11)	0.06 (0.01, 0.09)	0.09 (0.05, 0.14)	0.15 (0.07, 0.20)	0.54 (0.02, 0.89)
	Eagle Meadows	1.71 (0.59, 3.67)	0.469	614	0.64	0.179	1.56	39	0.00 (0.00, 0.07)	0.01 (0.00, 0.06)	0.01 (0.00, 0.08)	0.07 (0.02, 0.13)	0.08 (0.02, 0.18)	0.82 (0.21, 0.96)
2013	Annuals	0.54 (0.49, 0.61)	0.732	157	4.91	0	0	240	0.19 (0.17, 0.20)	0.56 (0.52, 0.61)	0	0	0	0
	Perennials	0.72 (0.56, 0.92)	0.549	523	2.27	0.052	0.19	199	0.10 (0.05, 0.17)	0.29 (0.18, 0.41)	0.04 (0.02, 0.06)	0.12 (0.05, 0.18)	0.16 (0.07, 0.22)	0.07 (0.01, 0.21)
	Low-elevation perennials	1.06 (0.79, 1.34)	0.652	494	5.34	0	0	77	0.14 (0.11, 0.18)	0.69 (0.60, 0.76)	0	0	0	0
	Montane perennials	0.47 (0.34, 0.81)	0.478	542	0.28	0.086	0.32	122	0.03 (0.00, 0.11)	0.02 (0.00, 0.08)	0.08 (0.05, 0.09)	0.06 (0.02, 0.11)	0.14 (0.10, 0.19)	0.38 (0.03, 0.84)
	Silver Fork	0.38 (0.24, 0.78)	0.552	635	0.29	0.048	0.17	38	0.09 (0.00, 0.24)	0.06 (0.00, 0.24)	0.08 (0.08, 0.09)	0.05 (0.00, 0.15)	0.13 (0.00, 0.21)	0.12 (0.00, 1.00)
	Silver Creek	0.58 (0.34, 1.67)	0.410	525	0.27	0.083	0.46	42	0.01 (0.00, 0.11)	0.01 (0.00, 0.04)	0.05 (0.01, 0.09)	0.05 (0.02, 0.09)	0.10 (0.04, 0.17)	0.65 (0.00, 0.98)
	Eagle Meadows	0.46 (0.34, 0.79)	0.469	479	0.29	0.122	0.31	42	0.03 (0.00, 0.13)	0.02 (0.00, 0.06)	0.09 (0.07, 0.09)	0.06 (0.02, 0.09)	0.14 (0.11, 0.18)	0.36 (0.01, 0.85)

λ and elasticities (***e*** stage_{t+1}, stage_t) and 95% bias-corrected confidence intervals (from 10 000 bootstrap samples) for each group and year. Pooled estimates of *G*, germination rate and *O*, ovule number per flower are averages across population means. *F*, flower number; *S*, overwinter survival; and *R*, rosette production, are estimates from observed seedling transition rates for each group and year based on *n* individuals. Note that the germination rate *G* was estimated in 2012 and did not vary between years in matrix models. Vital rates for each population are given in Supporting Information Table S2, along with SE and sample sizes for estimation of *G* and *O* population means (from generalized and linear mixed models, respectively).

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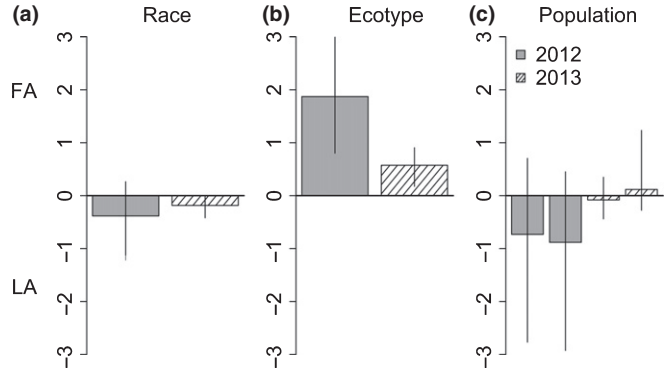

Fig. 3 Local adaptation vs foreign advantage in three ecological contrasts in *Mimulus guttatus*. Data are the life table response experiment (LTRE) contribution of the foreign group to variation in population growth (λ) relative to the native group in each year, with bias-corrected 95% confidence intervals. Positive values indicate foreign advantage (FA) and negative values indicate local adaptation (LA). (a) Race: annuals relative to perennials. (b) Ecotype: low-elevation relative to montane perennials. (c) Population: foreign montane (left to right: Silver Fork and Silver Creek) relative to the native (Eagle Meadows) population.

environments. Together, perennial populations outperformed annual populations in both years, although this was only significant in 2013. Further, the advantage of perennial populations was attributable to perennial vital rates, including rosette fertility and production, rather than differences in first-year reproduction. Previous transplant experiments between coastal perennial and inland annual populations have demonstrated strong, divergent selection on flowering time (Hall & Willis, 2006). This trait is pleiotropically linked to other life history traits, including vegetative growth, through a chromosomal inversion region across a range of annual and coastal and inland perennial populations (Friedman, 2014; Friedman *et al.*, 2015). Thus, LA at this scale is probably facilitated by strong, consistent divergent selection on genetically coupled traits.

In comparisons between perennial ecotypes, however, we found that low-elevation populations outperformed the native montane populations in both years. FA at this scale was driven by differences in seedling and rosette fertility, rather than rosette production, suggesting that low-elevation perennials were able to achieve higher reproductive success. Montane perennials produced few flowers and invested in extensive mats of belowground rhizomes, from which new rosettes regenerated each spring (Table S2). In 2012, however, there was no evidence that rosette production contributed to fitness variation, suggesting that the low-elevation ecotype achieved higher reproductive success without incurring trade-offs in survival and growth. In 2013, severe drought resulted in the death of all aboveground tissue; all low-elevation perennials died whereas montane perennials regenerated the following spring from belowground rhizomes. Correspondingly, rosette production contributed to LA in this year. However, low-elevation populations still exhibited FA in overall fitness in 2013 despite these differential drought responses.

We found a trend towards LA among native and foreign populations within the montane perennial ecotype in 2012, although small sample sizes at this scale resulted in large confidence intervals around LTRE estimates. Additional transplant experiments with larger sample sizes are necessary to make robust inferences about fitness variation at this scale. However, observed trends were largely consistent between population pairs and hint towards some potential patterns. Estimates of LTRE effects were negative for both population pairs in 2012, indicating LA. Conversely, LTRE effects were small and variable in 2013, suggesting that drought may have suppressed fitness differences among montane populations. Further, rosette production rates had the largest effects on fitness variation between montane populations; this pattern is consistent with the evolution of increased rhizome growth and decreased flower production in the montane ecotype. One intriguing possibility suggested by this result is that the vital rates that determine fitness variation within an ecotype (e.g. rosette production) are less important in determining fitness differences between ecotypes.

In this study, we used local vs foreign fitness differences within a single environment (i.e. home-site advantage) as our measure of LA. This broader definition has been used to distinguish between the magnitude of LA within an environment and the strength of fitness trade-offs between environments (Hereford, 2009), as well as cases where comparisons of many populations preclude reciprocal transplants (Galloway & Fenster, 2000; Anderson *et al.*, 2015). Given that we include multiple populations within each of our contrasts, a consistent fitness advantage of the local group implies adaptation to the local environment (Galloway & Fenster, 2000). Local vs foreign contrasts provide a measure of the strength of adaptation to a local environment, but do not test whether such adaptation confers a fitness disadvantage in other environments. Other transplant experiments in *M. guttatus* have found that late-flowering perennials have low relative fitness in seasonally drying annual environments (Hall & Willis, 2006; Lowry *et al.*, 2008). However, transplant experiments at low elevation and additional montane environments would be necessary to test for LA of low-elevation perennials or fitness trade-offs among montane perennial populations. Thus, it is important to note that other definitions of LA, including home vs away, sympatric vs allopatric, or reciprocal fitness trade-offs between environments (Kawecki & Ebert, 2004; Lowry, 2012; Blanquart *et al.*, 2013), are not tested by our common garden design.

Fitness variation among annual populations

We used LTREs to test for LA vs FA for three discrete ecological contrasts – life history race, ecotype, and population. However, we also observed extensive fitness variation among annual populations (Table S2), suggesting some ecological divergence within this general life history race. We found that relative fitness of foreign populations was quadratically related to a continuous measure of phenotypic divergence in life history traits. Thus, the most ecologically divergent annual populations (e.g. earliest flowering at smaller sizes) resulted in stronger estimates of LA whereas those with more perennial-like life history traits (e.g. later flowering at larger sizes) exhibited weaker LA or even FA. Transplant experiments between discrete groups, such as ecotypes or

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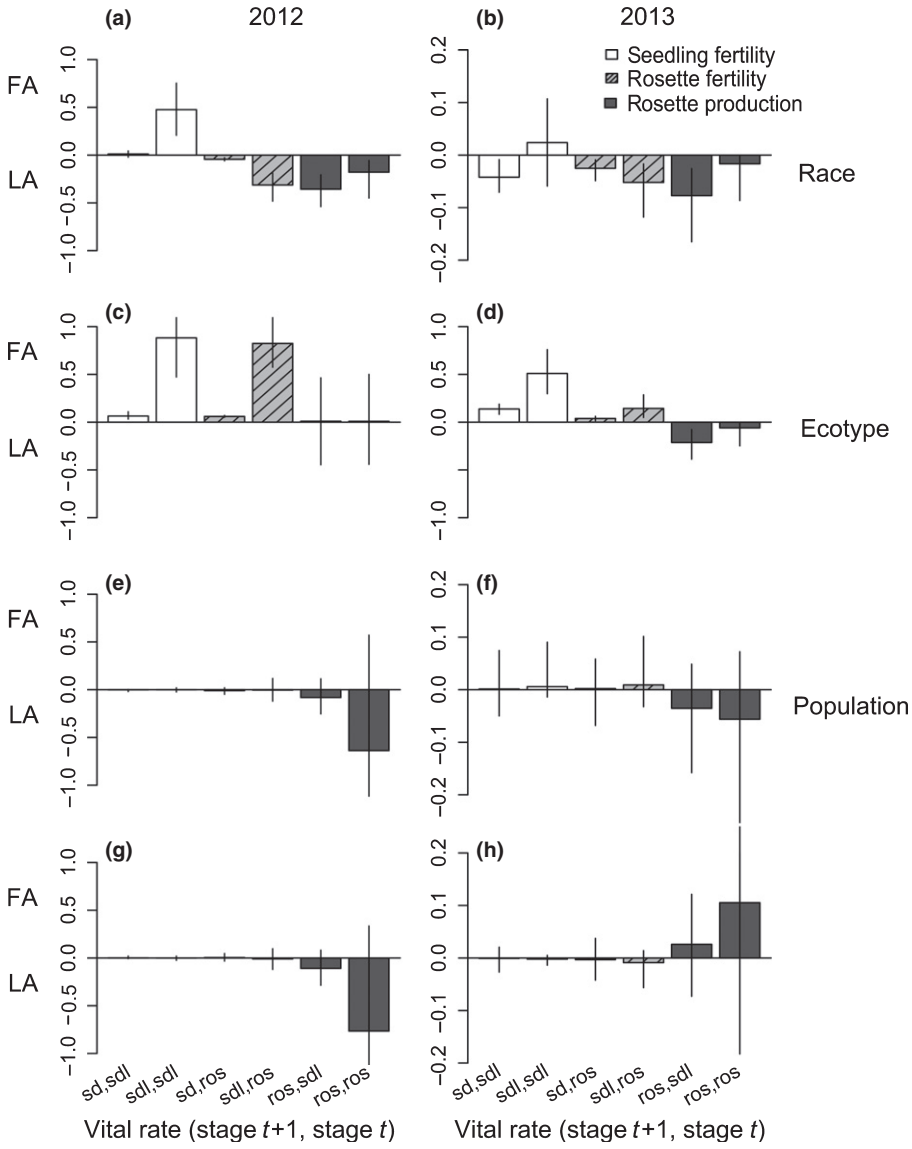

Fig. 4 Contributions of vital rates to variation in population growth for three ecological contrasts in *Mimulus guttatus*. Life table response experiment (LTRE) effects indicate vital rates that contribute to either foreign advantage (FA; positive values) or local adaptation (LA; negative values) in each year. Vital rates are coded as contributing to seedling fertility (white), rosette fertility (hatched gray), or rosette production (dark gray). Contributions for seed survival (sd, sd) and germination (sdl, sd) were small and are not shown. Error bars indicate bias-corrected 95% confidence intervals. Note different *y*-axis scales. (a, b) Race: annuals relative to perennials. (c, d) Ecotype: low-elevation relative to montane perennials. Population: foreign montane (e, f, Silver Fork; g, h, Silver Creek) relative to the native (Eagle Meadows) population.

habitats, often find variation in the strength of LA among replicates (Leimu & Fischer, 2008; Hereford, 2009). In these cases, additional information on phenotypic, genetic, or environmental distances can clarify such variation (e.g. Hereford, 2009).

What explains foreign advantage?

We observed a consistent fitness advantage of low-elevation perennials relative to montane perennials when grown in a montane habitat. FA can result from methodological biases in experimental design, recent environmental change, or nonselective processes in the evolution of fitness trade-offs. In transplant studies that utilize a single fitness component or time period, patterns of FA may in fact reflect an incomplete understanding of fitness in a given environment or the influence of year-to-year environmental variation. However, we observed FA even after integrating multiple fitness components to estimate population growth rate, and this effect was consistent over two years encompassing very different environmental conditions (normal vs drought). One potential explanation is that we did not accurately capture the fitness advantage of belowground rhizomes. Given the survival advantage of rhizomes relative to aboveground rosettes during the 2013 drought, it is possible that investment in rhizomes represents a bet-hedging strategy that would require much greater temporal and environmental sampling to detect. Another potential explanation is that recent trends toward warmer, drier conditions throughout the Sierra Nevada (Belmecheri *et al.*, 2015) have masked any adaptation to historical conditions in the montane ecotype. This study was carried out at the start of the 2012–2015 drought period in the Sierra Nevada, during which low precipitation and high temperatures combined to create extreme soil moisture deficits relative to the last 500–1000 yr (Griffin & Anchukaitis, 2014; Belmecheri *et al.*, 2015). As a result in part of the cumulative nature of moisture deficits, drought conditions in 2013 were much worse than in 2012, which was within the range of variation in the last 100 yr (Griffin & Anchukaitis, 2014).

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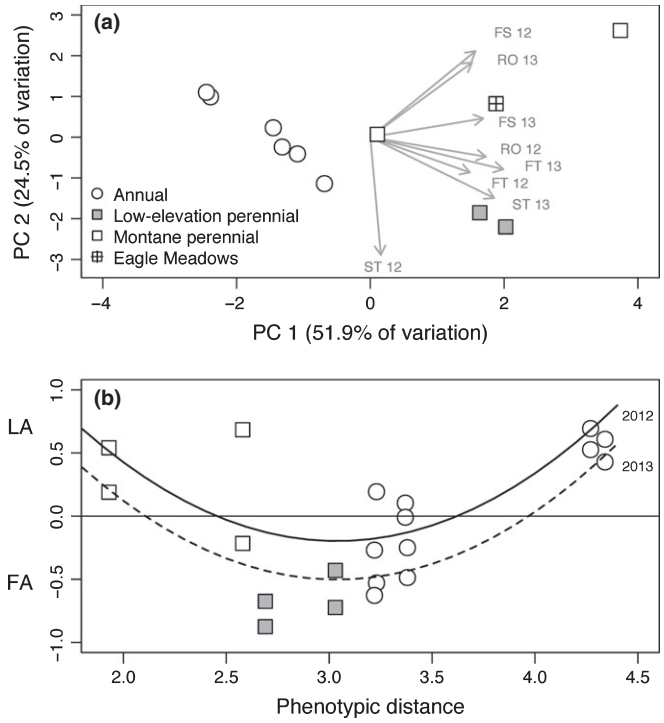

Fig. 5 Variation in relative population growth depends on divergence in life history traits in *Mimulus guttatus*. (a) Position of each experimental population in phenotypic space defined by two principal component (PC) axes. Gray arrows indicate loadings of each life history trait in each year (FT, flowering time; FS, flower size; RO, rosette production; ST, stem diameter). (b) Population growth rate (λ) relative to the native Eagle Meadows population (hatched square) as a quadratic function of Euclidean distance in phenotypic space for 2012 (solid line) and 2013 (dashed line).

Many species have responded to climate change by shifting ranges polewards or upwards in elevation (Parmesan & Yohe, 2003); the fitness advantage of lower elevation perennials may reflect changing environmental conditions in montane environments.

Alternatively, nonselective processes could drive the evolution of FA between perennial ecotypes. Dispersal limitation could prevent the introduction of low-elevation perennial alleles into montane populations. *Mimulus guttatus* is pollinated by large-bodied bees that could occasionally transport pollen over relatively long distances, whereas long-distance dispersal of seeds and vegetative fragments occurs primarily along water corridors and is thus less likely to occur upwards in elevation (Waser *et al.*, 1982; Vickery *et al.*, 1986; Truscott *et al.*, 2006). Montane populations, meanwhile, could be constrained by the evolution of a primarily clonal life history strategy from reaching a higher fitness peak involving greater reproductive investment. In addition, the evolution of mutational load driven by a more clonal life history could further depress reproductive output and local fitness (Muirhead & Lande, 1997; Dorken & Eckert, 2001; Willi *et al.*, 2005). Quantitative and population genetic studies would help distinguish among these hypotheses by addressing the roles of genetic drift, mutational load, and gene flow in shaping ecotypic divergence. In particular, studies that combine reciprocal transplants with quantitative trait locus (QTL) analysis can disentangle the roles of fitness trade-offs (i.e. antagonistic pleiotropy) vs conditional neutrality during LA (Anderson *et al.*, 2011, 2013; Ågren *et al.*, 2013). For example, in a comparison between coastal perennial and inland annual populations of *M. guttatus*, Hall *et al.* (2010) found little evidence for fitness trade-offs in locally adaptive alleles and several instances of FA for individual loci, suggesting that dispersal limitation and mutational load prevent the evolution of more globally fit genotypes.

LA vs FA and the design of transplant studies

The evolution of fitness trade-offs within species is the cornerstone of theory regarding speciation (Schluter, 2009), plasticity (Schlichting, 1986), and range limits (Kirkpatrick & Barton, 1997). Yet reviews of the transplant literature have highlighted extensive and largely unexplained variation in outcomes, from LA to FA (Leimu & Fischer, 2008; Hereford, 2009). Integrating multiple components of fitness (through population growth rates or lifetime reproductive success) will provide better estimates of fitness trade-offs than single components of fitness such as growth rate or seed set. Population growth rates incorporate variation in the timing of reproduction, allowing comparisons between life history strategies or within growing populations (Giske *et al.*, 1993), whereas lifetime reproduction (R_0) is an appropriate fitness measure within stable populations. Either can also be estimated using the aster statistical framework (Shaw *et al.*, 2008; Shaw & Geyer, 2010). In addition, LTRE analysis provides a powerful tool for quantifying the contributions of different fitness components to these emergent patterns across systems and scales. Finally, it is difficult to translate results from experiments designed to detect LA to make generalizations about the distribution and scale of LA in nature. Rather than focusing on the evolution of LA *per se*, a more comprehensive approach would be to quantify fitness trade-offs within species at a range of ecological scales (e.g. Galloway & Fenster, 2000; Sambatti & Rice, 2006; Hereford & Winn, 2008). By more closely approximating the distribution of populations within a plant species, through either random or stratified sampling, we can more clearly understand the distribution and underlying causes of fitness variation within species. This more agnostic approach will be useful in informing restoration and management efforts, which often seek to minimize fitness differences among source populations (McKay *et al.*, 2005), as well as testing hypotheses about the frequency of adaptive divergence in nature.

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Author contributions

MLD, KMK and ALA conceived the experiment and data analysis. MLD collected and analyzed the data. MLD wrote the first draft and all authors contributed to the final manuscript.

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Supporting Information

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

Fig. S1 Photographs of seedlings and rosettes from recruitment plots.

Table S1 Locality information for all populations used in the study

Table S2 λ and vital rates for all populations in the study

Methods S1 Results from recruitment plots with details for calculation of *A*.

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