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INVITED PAPER

For the Special Issue: Evolutionary Insights from Studies of Geographic Variation

What can local and geographic population limits tell us about distributions?¹

Jason P. Sexton² and Erin E. Dickman

PREMISE OF THE STUDY: Understanding the evolutionary and ecological factors that determine plant distributions is of primary importance in botanical research. These factors may vary in predictable ways across different spatial scales, and thus, we can leverage scale to reveal the underlying processes limiting plant distributions.

METHODS: We review various research considerations across local and geographic scales, including the investigation of dispersal and habitat limitation, evolutionary factors, abiotic and biotic factors, and research logistics. We also present two case studies, slender monkeyflower (*Mimulus leptaleus*) and cut-leaf monkeyflower (*Mimulus laciniatus*), in the California Sierra Nevada.

KEY RESULTS: At a local spatial scale (within 50 m), no seeds were produced from plants sown at sites located just beyond known patches of *M. leptaleus*, but within the species' geographic range. At a much broader spatial scale (kilometers), at the highest and lowest elevations of the species' range, we found greatly reduced abundance and fecundity in plants sown outside of the geographic range limits of *M. laciniatus*.

CONCLUSIONS: These cases illustrate two contrasting spatial scales, yet agree in their illustration of strong habitat limitation. We end by discussing future avenues of research and by suggesting ways botanical researchers can frame their studies to maximize information gained on species requirements, distribution limits, and conservation among varying spatial scales.

KEY WORDS dispersal limitation; evolution; habitat limitation; *Mimulus*; monkeyflowers; plant distribution; range limits; restoration; Sierra Nevada; spatial scale

Why are plants of a given species found in one patch of ground, but not in an adjacent patch? Species range limits can arise from a variety of factors, including abiotic and biotic factors and dispersal limitations (Sexton et al., 2009; Hargreaves et al., 2014). Limiting factors occur at all scales, locally, and up to the geographic scale. At the broadest scale, population limits are referred to as range limits, geographic limits, range margins, and species borders (Hoffmann and Blows, 1994; Gaston, 2003; Sexton et al., 2009). At smaller spatial scales, terms such as microsite limitation and local limits have been used with a variety of meanings (Münzbergová and Herben, 2005).

All species, having some distinguishing genetic or phenotypic property, should differ to some degree in their niche (Holt, 2009), distribution, and habitat availability, and so the distinction between local or internal range limits and external or geographic range limits

will vary greatly and will be relative for each species. Here we refer to "local" limits as those patterns and processes occurring at the scale limiting growth of individuals at one continuous local population or set of patches within seed dispersal distances common to a given species (Fig. 1). Species also differ greatly in the patchiness of their available habitat, and thus their distributions, so we acknowledge that "limits" may be difficult to define at any scale for some species. We contrast local limits with "geographic" limits, which we refer to as the ultimate extent of a geographic range (e.g., extremes of elevation or latitude). At geographic limits, populations will be similarly limited as in local scales, but if geographic limits represent the spatial extent of the species niche, then this scale may represent limitations on the species as a whole, as opposed to a given population. Many studies have examined what we term local scales of limitation (e.g., Stanton and Galen, 1997; Emery, 2009; Moore, 2009) and geographic scales of limitation (e.g., Prince and Carter, 1985; Etterson, 2004; Samis and Eckert, 2009; Stevens and Emery, 2015).

Here we review and discuss considerations for the investigation of plant distributions at local to geographic limits. We offer

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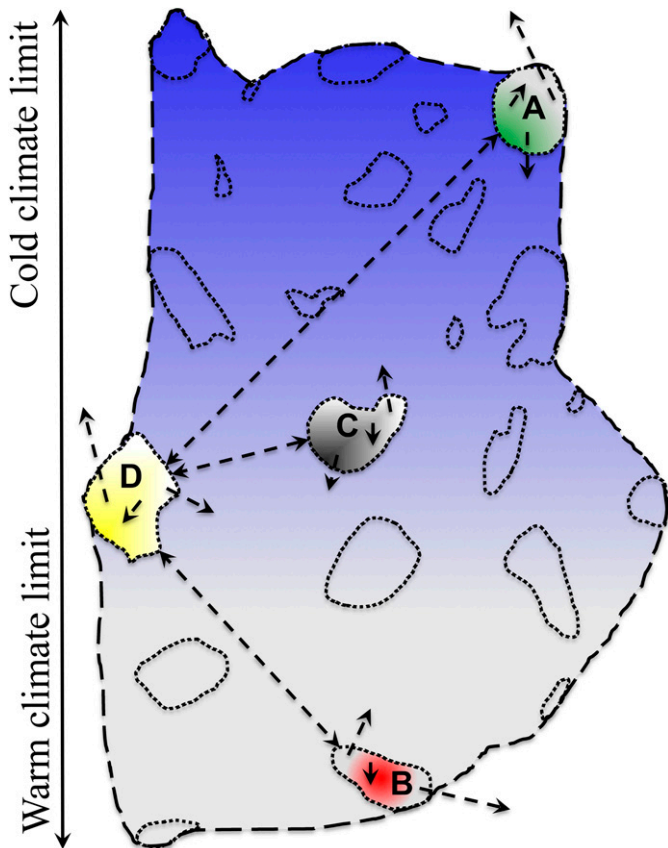


FIGURE 1 Variation in the scale and character of distribution limits. Species ranges are often delimited by an imagined external, geographic range limit (large-dashed line), and this polygon may contain much unoccupied space. Populations (outlined in dotted lines) can also include much unoccupied space and can vary greatly in size, shape, and isolation from other populations as well as proximity to geographic range limits. To understand niche characteristics and constraints on distribution, we can make contrasts within (short arrows), outside of (medium arrows), and between populations (connecting arrows), and beyond geographic limits (long arrows). Climate gradients exist across species ranges (blue shading), and important ecological gradients can exist within populations (shaded example populations A–D). Populations near geographic limits allow for testing the relative strength of local-scale and geographic-scale factors on distribution limits. (A) Example population at the cold climate limit having high potential gene flow due to many nearby populations. (B) A population at the warm climate limit and having high potential genetic isolation due to few neighboring populations. (C) A central population. (D) A peripheral population in a central climate location, which could be useful for parsing nonclimate factors (e.g., dispersal, biotic, soil, historical) from climate factors (comparing populations A and B) and from potential central–marginal factors on plant performance (comparing to population C) such as population size or isolation.

perspectives on dispersal and habitat constraints, evolutionary factors, climate, abiotic and biological interactions, environmental change, and experimental logistics. We then include two empirical case studies of monkeyflowers (*Mimulus* spp.) for comparison. We end by discussing how future work at various scales of limitation can enhance understanding of plant ecology and evolution, conservation, restoration, and responses to climate change.

LOCAL VS. GEOGRAPHIC RANGE LIMITS

Understanding the extent to which plant populations are limited by their niche requirements or dispersal capabilities has been a long-standing area of interest and is an important question because it addresses the difference between being able to live in a given habitat vs. being able to get there (Münzbergová and Herben, 2005; Hargreaves et al., 2014). If habitat limitation, sometimes referred to as “niche limitation” (e.g., Moore and Elmendorf, 2006), acts at local scales, then logically it should be expected at geographic scales where the species is likely encountering ecological conditions mainly found outside of the current geographic range. Similarly, dispersal limitation can occur from local to geographic scales (Primack and Miao, 1992; Hubbell et al., 1999; Turnbull et al., 2000) depending on species-specific dispersal capabilities (Hyatt et al., 2003; Hubbell, 2005). However, dispersal limitation should not be a limiting factor over very long time scales (i.e., many generations) for populations embedded within a species range since other populations of the species are already distributed more widely; that is to say, individuals have already migrated from or to a given locale in the recent or distant past (Cain et al., 1998). (An exception to this scenario may arise when species fragment into refugia during periods of extreme environmental change (i.e., during glaciation events), but dispersal limitation has prevented them from expanding again.) Rare, long-distance dispersal events are understudied and can be critical to expanding distributions (Clark et al., 1998; Cain et al., 2000; Nathan and Muller-Landau, 2000). Thus, we hypothesize that habitat limitation should be of ultimate importance in setting local limits and that dispersal limitation should be of lesser or proximate importance (see Table 1 for a summary of considerations at various scales of limitation). In this vein, local limits provide great opportunities for defining species niches and for designing experiments to test niche-limiting mechanisms. However, one local limit alone cannot provide a full picture of the ecological niche and habitat of a species. More informed niche evaluations require replication of local and geographic limits. Temporal variation can also be important and can be included in comparisons of scales of environmental limitation. From these arguments, it follows that geographic limits can be ideal for studying dispersal limitation, including the evolution of dispersal (e.g., Phillips et al., 2006; Darling et al., 2008). Indeed, constraints on dispersal at broad geographic scales become apparent where invasive species establish new distributions after human-assisted transport (Mack et al., 2000). Studies on the relative importance of dispersal vs. habitat limitation across geographic scales are needed, but a logical hypothesis is that dispersal limitation becomes increasingly important as spatial scale increases.

Considering evolutionary factors, several predictions can be made regarding local and geographic scales based on variation in migration (gene flow), selection, and drift (i.e., deviations from Hardy–Weinberg equilibrium). Regarding gene flow effects, due to closer proximity at local scales, gene flow should be greater across local gradients (i.e., microclimates) than across geographic gradients (e.g., climate gradients). Thus, we predict that the potential for swamping gene flow to stall adaptation along environmental gradients and distribution limits (sensu Kirkpatrick and Barton, 1997; Polechová and Barton, 2015) is more likely to act at local scales than geographic scales. Patterns consistent with gene swamping within local plant population gradients have been found in some studies (e.g., Stanton and Galen, 1997; Anderson and Geber, 2010), but not

TABLE 1. Hypotheses and considerations regarding the study of plants across local and geographic distribution limits. Investigations across scales of limitation may inform plant and conservation science about different ecological and evolutionary processes.

Scale	Dispersal and habitat limitation	Evolution	Climate and nonclimate factors	Logistics
Local limits	Habitat limitation is predicted to be of relatively greater importance; thus, local limits are ideal places to examine habitat attributes. Examinations at replicate population limits enable a holistic understanding of the species niche.	Genetic differentiation (i.e., microevolutionary variation) should be lower among individuals inhabiting a locality. Swamping gene flow may have important effects. Genetic drift is unlikely to have important effects.	Climate should not vary across a population or locality as much as across the geographic range, although microclimates may vary greatly. Local scales are good places to examine microclimate factors on survival and young plant establishment as well as to study biotic and nonclimate, abiotic effects such as soil variables.	Research conducted at local scales may have high cost and time efficiency relative to the study of geographic limits. At local scales, it is easier to replicate experiments and less expensive to carry them out in terms of travel and time costs.
Geographic limits	Dispersal limitation should be of greater importance at geographic limits than at local limits, although habitat limitation remains crucial. Geographic limits are ideal for examining dispersal evolution.	Genetic differentiation should be higher among individuals among different populations due to lower gene flow rates, differences in population size (drift), and broader variation in selective regimes at greater spatial scales. Swamping gene flow is unlikely to limit adaptation. Genetic drift is more likely to have important effects.	Geographic limits are ideal to examine effects of climate, climate change, and novel climates, and for testing limits of climate selection. Biotic effects may maintain or expand population limits. Comparisons of biotic effects at geographic vs. local limits can reveal their nature, consistency, and strength on plant growth and fitness.	Research conducted at geographic scales may be more intensive in travel and time costs compared with local scales. Despite higher time and travel costs, geographic scales should yield strongest effects or responses if geographic limits lie at the threshold of species habitat and dispersal limits.

in others (e.g., Emery, 2009). However, despite great emphasis in the scientific literature on gene swamping to potentially cause geographic range limits, we know of no plant studies that have demonstrated this effect in nature. On the contrary, the widespread pattern of genetic isolation by environment among populations (the pattern of higher gene flow among similar environments) likely precludes swamping gene flow from being a ubiquitous mechanism causing geographic range limits (Sexton et al., 2014).

Species' geographic ranges, by definition, include all within-population environmental variation plus all among-population environmental variation. The isolating effects of distance and environment between populations (Shafer and Wolf, 2013; Sexton et al., 2014; Wang and Bradburd, 2014), plus a wider breadth of selection regimes across broader scales than local scales, act to differentiate populations and likely underlie the commonly observed patterns of local adaptation in plants (Clausen et al., 1940; Leimu and Fischer, 2008; Hereford, 2009). Due to variation in habitat availability across landscapes, population sizes vary and so the strength of genetic drift should vary among populations. Genetic drift may have greater influence at geographic range limits than at local range limits, a prediction supported by general patterns of increased genetic differentiation in neutral loci toward species range limits (Eckert et al., 2008). This pattern is expected in situations where habitat quality or carrying capacity is reduced in marginal areas of species ranges, also known as the abundant center hypothesis (Brown, 1984; Keitt et al., 2001; Case et al., 2005), although central areas are often not the most abundant areas of species ranges (Channell and Lomolino, 2000; Sagarin and Gaines, 2002; Sexton et al., 2009). The hypothesis that genetic drift operates strongly at local spatial scales in plants (Wright, 1943) has not been supported in light of evidence of strong, local natural selection (Schemske and Bierzychudek, 2007). Genetic differentiation that is the result of natural selection appears to be common at the scale of centimeters to meters in plant populations (Linhart and Grant,

1996; Schemske and Bierzychudek, 2007; Moyle et al., 2012). Additionally, local ecological gradients may be quite steep, and in many cases, local gradients may be much steeper (e.g., slope or aspect) than broad ecological gradients (e.g., latitude) (Halbritter et al., 2013). Moreover, local habitat heterogeneity can be so great that it may commonly allow speciation at local or sympatric scales (Anacker and Strauss, 2014; Baldwin, 2014; Ferris et al., 2014; Grossenbacher et al., 2014). Whether adaptive change occurs likely depends on dispersal capacity relative to the scale of the selective landscape (Richardson et al., 2014). Nevertheless, we predict genetic differentiation to be relatively greater across geographic scales due to a higher potential for drift and a lower potential for gene flow.

There are several implications of these evolutionary influences on plant distributions across local to geographic scales. First, studies of the effects of isolation, selection, and drift may find the strongest examples at geographic scales and approaching geographic limits. Second, geographic selection regimes can be compared with local gradients to quantify variation in the relative strength of selection for different agents of selection such as edaphic and biotic factors (Sexton et al., 2009). Finally, local populations that experience a range of drift, gene flow, and selection responses can act as replicate cases for understanding the relative roles of these factors on adaptation. Thus, different experimental outcomes can lead to contrasting conclusions about the factors that form local and geographical limits. For example, populations that experience varying levels of gene flow across gradients may exhibit corresponding patterns of local adaptation to those gradients. In this case, experimental gene flow (sensu Emery, 2009; Sexton et al., 2011; Volis, 2011) may have greater effects on plant fitness (and thus greater potential to expand population limits) in systems having lower gene flow rates if our above assumptions are correct. In another hypothetical example regarding the expectation that dispersal limitation is more important at geographic scales than at local scales, we would predict that experimental transplants outside of local populations (but

within species ranges) would result in fewer successful cases than transplants outside of the geographical range (e.g., long-distance transplants that can result in biological invasions).

We assume that climate should not vary across a single population as much as across the geographic range of a species, although more research on this topic is needed. Geographic limits are thus ideal for examining species-level effects of climate, climate change, and novel climates (e.g., Etterson and Shaw, 2001). Geographic limits are also ideal for monitoring populations for climate change responses since these are areas where population contractions and expansions may be occurring (Hampe and Petit, 2005; Sexton et al., 2009; Cahill et al., 2012). For example, populations at “leading edges” with climate warming (at highest latitudes or elevations) may exhibit less climate habitat limitation outside of population boundaries than central or “rear-edge” (at lowest latitudes or elevations) populations. Microclimates vary greatly within and among localities (Dingman et al., 2013), and so local scales are ideal places for examining the effects of microclimate factors (e.g., soil temperature, aspect, slope, or air temperature at small heights above the ground) on survival and establishment of young plants while keeping the regional climate constant and for understanding whether microclimates can buffer shifts in regional climate shifts (Ford et al., 2013; Stevens and Emery, 2016). One surprisingly underexplored question is how the variation of microclimates (e.g., temperature, relative humidity, etc.) found within populations relates to the variation among populations across the geographic range. The answer to this question would improve our ability to forecast range shifts under climate change scenarios. A natural expectation is that spatial environmental variance should increase from local to geographic scales (i.e., environmental variance increases with geographic area), but it is important to know how these relationships may differ among various factors that influence plant distributions. Several studies have investigated the effects of microclimate on plant establishment and distribution (e.g., Drezner and Garrity, 2003; Cavieres et al., 2007; Graae et al., 2011), but only for a portion of a species range. To our knowledge, none have empirically measured environmental variables within and adjacent to local populations and across the geographic range of a species simultaneously.

Local and geographic scales are advantageous for studying non-climate effects such as biological interactions and soil factors influencing or setting species range limits (e.g., Pelini et al., 2009; Stanton-Geddes et al., 2012). Biotic factors affecting geographic range limits include competition, predation, disease, mutualism, and the interaction of these with abiotic factors (Sexton et al., 2009). Biotic limitations may follow biogeographic patterns (i.e., habitats, communities, etc.) or areas where species ranges intersect (Case et al., 2005). Comparisons of biotic interactions at local and geographic scales can illuminate how these effects can limit or expand populations (Afkhami et al., 2014) and whether the nature of these phenomena differs among scales (Belmaker et al., 2015). For example, if plants are limited locally and geographically by competition, are they the same competitors or functional groups? In what situations might scale \times biotic interactions (or scale \times biotic \times abiotic interactions) be important? Moreover, biological interactions and other nonclimate effects can impose strong limitations, yet such effects are often missing from species distribution or prediction models related to climate change, causing gross over-predictions or under-predictions of species' realized niches and range shifts under climate change (Nuñez et al., 2009; Afkhami et al., 2014; Brown and Vellend, 2014).

Finally, logistical considerations are important in deciding at what scale one should frame studies of limits to plant distributions. Local limits may be easier to study than geographic ones since they require less time and travel within the smaller scale, yet can still exhibit strong limitations on plant performance (see *Mimulus leptaleus* example below). Alternatively, gradients of interest may be weak at a local scale, requiring a broader geographic investigation. Additionally, at geographic limits, one may find the benefit of both scales; that is to say, a single population at a geographic limit will likely experience steep ecological gradients and may lie at the threshold of the species' ecological niche, allowing the strongest responses of plants (and genotypes) to variables of interest (Fig. 1). In the following section, we compare two empirical cases examining habitat limitation at two different scales in two species of monkeyflowers in the California Sierra Nevada.

MATERIALS AND METHODS

Genus *Mimulus* is highly diverse, with many species specialized to particular habitats (Wu et al., 2007), and thus offers many interesting cases to study distribution limits. We examined slender monkeyflower (*Mimulus leptaleus*; Phrymaceae, section *Eunanus*), an annual plant that occurs mainly in the California Sierra Nevada in montane environments between ca. 2000–3400 m a.s.l. (Fig. 2A). Not much is known of the autecology of *M. leptaleus*, but it is distributed in granitic soils within high-elevation, open conifer forests where it is often found in disturbed soil patches. It is most closely related to *M. constrictus* and *M. whitneyi*, with which it is interfertile (Beardsley et al., 2004; Thompson, 2005). Based on its diminutive stature, flower size, and floral architecture, *M. leptaleus* is likely to be self-fertilizing (see Thompson, 2005). We also examined the cut-leaf monkeyflower, *Mimulus laciniatus* (Phrymaceae, section *Simiolus*), an annual plant that is endemic to the Sierra Nevada occurring between ca. 800–3300 m a.s.l. (Fig. 2B). *Mimulus laciniatus* is typically distributed on granitic rocky slopes within seeps, to which it is specialized, and often grows in patches of moss (*Bryum* spp.) and spikemoss (*Selaginella* spp.). *Mimulus laciniatus* is within the *M. guttatus* species complex, a group that is often bee-pollinated (Wu et al., 2007). *Mimulus laciniatus* is known to be highly self-fertilizing and has been the subject of prior studies examining its habitat preferences and geographic range limits (Sexton et al., 2011, in press; Peterson et al., 2013). We were interested in studying the nature of distribution limits of these two monkeyflower species due their well-defined species ranges and their patchy, local distributions. *Mimulus* seeds are generally spheroidal and possess no hooks, wings, or other types of projections to aid dispersal. Nevertheless, *Mimulus* has been shown to achieve passive seed dispersal (≥ 1 km) through water, deer, and migratory birds (Lindsay, 1964; Waser et al., 1982; Vickery et al., 1986). Given these attributes, we believe these species allow compelling case studies for the examination of dispersal and habitat limitation (Table 1).

First, at a local scale, we asked whether *M. leptaleus* could grow and reproduce in habitat patches that do not currently contain *M. leptaleus* yet appear identical to those that do contain it. Seeds of *M. leptaleus* were randomly collected from 50 plants (maternal families) at a central population near Kaiser Pass (37.290633°N, 119.10865°W; 2700 m a.s.l.) within the Sierra National Forest in August 2005. In November 2005, half of the families were selected, and one seed from each maternal family was glued to a toothpick



FIGURE 2 (A) Site of slender monkeyflower (*Mimulus leptaleus*, inset photograph courtesy of Keir Morse, 2009) local limits experiment within California Sierran lodgepole pine (*Pinus contorta*) and limber pine (*Pinus flexilis*) habitat at ca. 2700 m a.s.l. (B) Example habitat (at low-elevation range limit, ca. 1000 m a.s.l.) of cut-leaf monkeyflower (*Mimulus laciniatus*, inset photograph courtesy of Ron Wolf, 2015) within ghost pine (*Pinus sabiniana*) granite seep foothills habitat.

and planted just under the soil surface within 5×5 grids (blocks). Twelve replicate blocks, each containing representatives of the 25 families, were randomly placed among three habitat patches (four blocks within each patch) where *M. leptaleus* was observed the previous growing season. We refer to these as “within” patch blocks. Additionally, 12 replicate blocks were placed among three sites at ca. 15, 22, and 50 m (termed “close,” “middle,” and “far,” respectively)

from where *M. leptaleus* occurred. We refer to these as “beyond” patch blocks. These sites beyond patches were deemed suitable by having similar ground cover (light pine needle duff), slope, surface soil, and exposure. Seeds were left to overwinter, and plants were monitored once during the growing season and again at fruiting stages in 2006. Within each block, we measured shoot mass, total mass, and number of seeds. The six sites were visited again in 2007 and 2015 to check for the presence of plants that recruited naturally in either within- or beyond-habitat patches.

At a much broader geographic scale, we examined fitness at the high and low elevation limits (referred to as “limit,” “high limit,” or “low limit”) of the *M. laciniatus* species range. We also established two experimental sites higher and lower in elevation (referred to as “beyond” or “beyond-limit”) to test dispersal and establishment capabilities. Seeds of *M. laciniatus* were randomly collected from 50 to 100 maternal families at each of two populations occurring at elevation limits of the species range (high limit site: 37.36328°N, 118.85703°W, 3293 m a.s.l.; low limit site: 37.03977°N, 119.40857°W, 1000 m a.s.l.). In 2009, two seed mixes were created from all collected families within each of the two populations from which to sow into respective beyond-range limit gardens. For example, seeds were pooled from the high-limit population to sow into the high-elevation beyond-limit garden. A large volume of seed stock was produced through a generation of self-fertilization (the common mode of reproduction for *M. laciniatus*) in common conditions within growth chambers. The high-elevation beyond-limit garden (37.366174°N, 118.854078°W; 3393 m a.s.l.) was ca. 0.4 km from the high-edge population. The low-elevation beyond-limit garden (37.036160°N, 119.429616°W; 628 m a.s.l.) was ca. 2.0 km from the low-edge population. The two beyond-limit planting sites were deemed suitable by having similar moss or spikemoss cover in similar granite seep habitats compared with their respective source populations for seed sowing. However, due in part to differences in elevation, climate differed between nearby sites; BIOCLIM climate values (data for years 1950–2000 at ~1 km scale; Hijmans et al., 2005) are given in Table S1. At each beyond-limit garden 0.25

mL of seeds (ca. 6000 seeds) were sprinkled into each of 10 seeding locations (ca. 100 cm² areas within mossy patches typical of *M. laciniatus* habitats) and marked with toothpicks. We sowed this quantity of seeds because it grossly exceeds the number of mature *M. laciniatus* plants observed within 100 cm² (typically <100 plants). To compare this quantity of seeds sown in beyond-limit plots to the number of seeds produced annually within natural,

at-limit reference populations, we estimated the mean number of seeds produced within these populations. For this estimate, we used the expected linear relationship of the number of seeds produced from a given fruit mass (number of seeds = $9.31 + 11.12 \times \text{fruit mass [mg]}$; regression $R^2 = 0.61$, $N = 140$, $P < 0.0001$), the relationship of the total fruit mass produced by plants with a given number of fruiting pedicels (fruit mass [mg] = $-2.17 + 2.70 \times \text{number of pedicels}$; regression $R^2 = 0.88$, $N = 700$, $P < 0.0001$), the mean number of pedicels produced by plants at each population (see Results), and the mean number of plants observed within plots at each population (see Results). Seeds of *M. laciniatus* germinate readily after overwintering under field conditions (Sexton et al., 2011), and a long-lived seed bank is not expected based on prior studies of its interfertile relative, *M. guttatus* (Vickery, 1999). Thus, we expect this first-year germination response to beyond-limit conditions to be a reasonable representation of the capacity of plants to survive and reproduce in those conditions with the caveat that environmental conditions vary greatly by year and that these conditions will likely influence germination. We did not introduce seeds to natural range (geographic) limit populations to avoid altering population attributes since they are the subjects of long-term investigations. We compared naturally occurring *M. laciniatus* plants emerged in those populations to emerged sown plants at the nearby beyond-limit gardens. All plants found near the 10 seeding locations in each beyond-limit garden were measured at the end of the growing season and compared with naturally emerged plants within edge populations in 10 randomly positioned 100-cm² plots. To estimate lifetime fitness in *M. laciniatus*, we counted the number of reproductive branches (pedicels) in developed, senescent plants at the end of the growing season. The total number of pedicels is strongly related to total fruit mass (see above), and total fruit mass is a strong predictor of total seed mass in *M. laciniatus* (Sexton et al., 2011; Peterson et al., 2013).

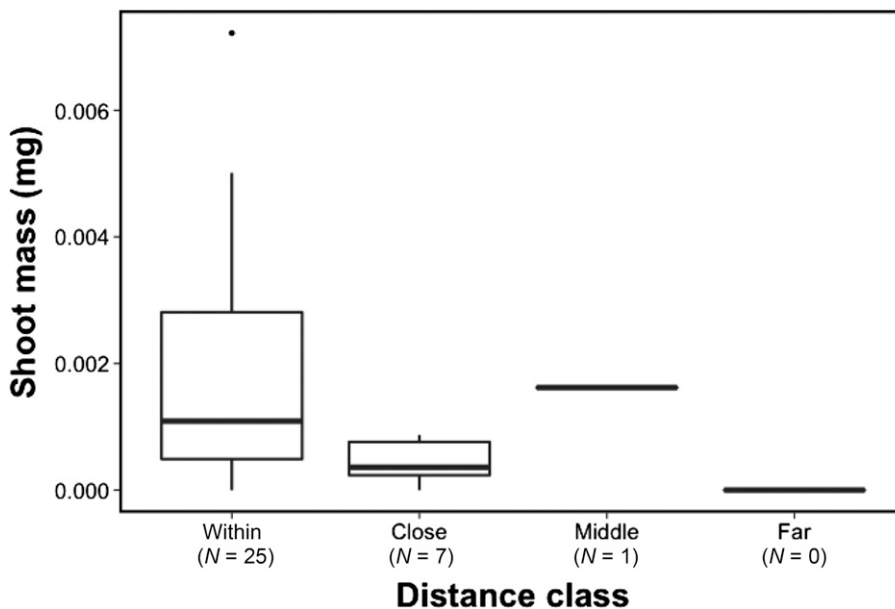


FIGURE 3 Shoot mass response box plots for *Mimulus leptaleus* plants in the local-scale experiment among plots within habitat patches and at three distances beyond habitat patches: close = 15 m; middle = 22 m; far = 50 m. No plants were observed in the far-distance plots; only one plant was observed in the middle-distance plots.

Data analysis for *M. leptaleus* (within/beyond habitat patches) and *M. laciniatus* (at limit/beyond-limit) experiments consisted of Kruskal–Wallis rank sum tests for non-normal data to test for differences in reproduction, growth, and survival to reproduction between respective habitats or gardens of comparison. For the *M. leptaleus* experiment, tests were used to detect significant differences in the number of seeds produced, shoot mass, and total mass between plots within and beyond the patch boundary. We also conducted a Levene’s test of homogeneity of variance between inside and outside patches to understand whether variance in growth differed among locations across the local patch boundary (Moore and Stanton, 2014). For the *M. laciniatus* experiment, we compared the number of reproducing plants (i.e., plants possessing pedicels) and the fitness of plants (i.e., number of pedicels) between respective limit and beyond-limit gardens (e.g., high limit population vs. high beyond-limit garden) and between different limit populations (i.e., high limit population vs. low limit population). Analyses were conducted with R statistical software (R Core Team, 2014) using the packages plyr (Wickham, 2011), rmisc (Hope, 2013), and car (Fox and Weisberg, 2011).

RESULTS

For both *Mimulus* species, and at two very different spatial scales (patch borders for *M. leptaleus* and species borders for *M. laciniatus*), we found strong evidence for habitat limitation maintaining distributions. The *M. leptaleus* experiment had poor germination and survival with only 33 of 620 seeds surviving (ca. 5%) to maturity. Those that survived were examined for differences in fitness and fitness-related traits. Significant differences between within-patch and beyond-patch areas were observed in the number of seeds produced ($df = 1$; $\chi^2 = 5.48$; $P = 0.019$). The mean number of seeds produced within patch habitats was 5.16 (± 1.561 SE) and no seeds were produced in beyond-patch habitats. Significant differences between within and beyond were also observed for shoot mass ($df = 1$; $\chi^2 = 5.02$; $P = 0.025$). The mean shoot mass for within-patch habitat was 0.00189 mg (± 0.00037 SE) and beyond-patch habitat was 0.00061 mg (± 0.00018 SE). Differences in total mass were marginally nonsignificant ($df = 1$; $\chi^2 = 3.42$; $P = 0.064$). The mean for total mass within patch habitat was 0.00211 mg (± 0.00040 SE) and beyond patch habitat was 0.00079 mg (± 0.00020 SE). No plants were observed in the far beyond plots (50 m from patch boundary) and only one plant was observed in the middle beyond plots (22 m from patch boundary), suggesting strong habitat limitations with spatial distance. Figure 3 shows shoot mass among the varying distance classes. Levene’s tests for homogeneity of variance were nonsignificant between within-patch and beyond-patch plots for shoot mass ($df = 1$; $F = 2.93$; $P = 0.097$) and total mass ($df = 1$; $F = 2.60$; $P = 0.117$). In return visits during the 2007 and 2015 growing seasons, no *M. leptaleus* plants were observed in beyond patches, whereas plants were again found growing in within patches.

In the *M. laciniatus* experiment, from natural seed rain estimates (see Materials and Methods), the expected mean number of seeds produced per 100 cm² in natural populations was ca. 1189 and 3985 seeds at the low-limit and high-limit populations, respectively. The estimated range of seeds produced was ca. 90–5406 and 311–23,035 seeds at the low-limit and high-limit populations, respectively. These values indicate that our estimated sowing input of 6000 seeds at beyond-limit plots was well above average for both reference populations and within the range of natural variation for annual seed production.

The *M. laciniatus* experiment exhibited strongly reduced growth and fitness beyond geographic range limits at both the low-elevation and high-elevation limits, indicating habitat limitation. At the high-elevation limit and beyond the limit, the mean observed number of plants emerged and surviving to produce pedicels differed significantly ($df = 1$; $\chi^2 = 12.46$; $P < 0.001$; Fig. 4A) and was 12.8 (± 6.082 SE) and 0.8 (± 2.828 SE) for the high-limit and high beyond-limit sites, respectively. All plots at the high-limit population had reproductive plants growing in them (range = 1–74 plants), whereas only one plot (of 10) in the beyond-limit garden supported reproducing plants (range = 0–8 plants). The mean number of pedicels differed significantly ($df = 1$; $\chi^2 = 35.47$;

$P < 0.0001$; Fig. 4C) and was 10.867 (± 0.905 SE) and 1.059 (± 0.473 SE) for the high-limit and high beyond-limit sites, respectively. At the low-elevation limit and beyond the limit, the mean number of plants emerged and surviving to produce pedicels differed significantly ($df = 1$; $\chi^2 = 12.71$; $P < 0.001$; Fig. 4B) and was 13.7 (± 4.752 SE) and 0.5 (± 1.374 SE) for the low-limit and low beyond-limit sites, respectively. All plots at the low-limit population had reproductive plants growing in them (range = 1–60 plants), whereas only three plots (of 10) in the beyond-limit garden supported reproducing plants (range = 0–3 plants). The mean number of pedicels differed significantly ($df = 1$; $\chi^2 = 18.39$; $P < 0.0001$; Fig. 4D) and was 3.496 (± 0.230 SE) and 0.750 (± 0.305 SE) for the low limit and low beyond-limit sites, respectively. High-limit and low-limit populations did not differ in the number of reproducing plants observed within plots ($df = 1$; $\chi^2 = 0.58$; $P = 0.448$), but did differ in lifetime fitness ($df = 1$; $\chi^2 = 70.13$; $P < 0.0001$), with high-limit plants producing ca. three times more pedicels than low-limit responses in Figs. 4C and D; note scale differences). In return visits during the 2014 and 2015 growing seasons, no *M. laciniatus* plants were observed in the beyond-limit localities, whereas plants were again found growing at the range limit sites.

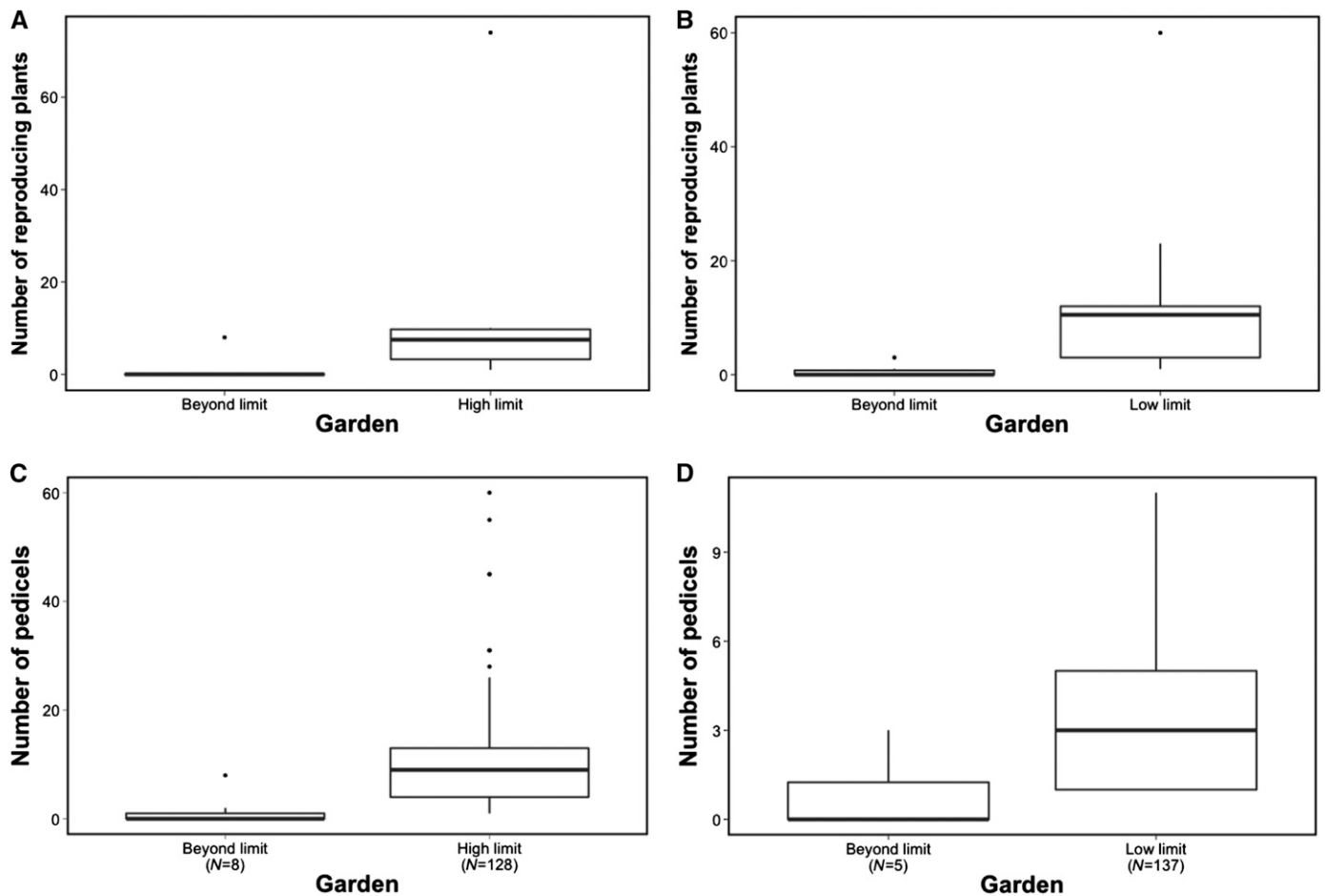


FIGURE 4 (A, B) Mean number of *Mimulus laciniatus* reproductive plants observed at end of growing season in the geographic-scale experiment among plots at and beyond high-elevation (A) and low-elevation (B) species range limits. (C, D) Mean number of pedicels produced (a proxy for lifetime fitness) from surviving plants at and beyond high-elevation (C) and low-elevation (D) species range limits. The total number (*N*) of plants observed among plots surviving to reproduction is given below each garden site.

DISCUSSION OF CASE STUDIES

From these experiments, there are several findings relevant to issues and hypotheses raised earlier (see Table 1). First, logistically, the local-scale experiment was low cost and time efficient. That is to say, one location was visited, but it revealed very strong effects of habitat limitation. The geographic-scale experiment also revealed strong effects, but required much more time, travel and expense to yield results from its four field sites. Second, the local-scale experiment demonstrated a good candidate system for studies on nonclimatic distribution limits such as microclimate, soil, or symbiotic factors. In contrast, the geographic-scale experiment is a good candidate for understanding how climate differences (e.g., at warm and cold extremes of a species range) may translate into reduced growth and fitness, in addition to nonclimate factors that may be limiting the species range. Regarding evolutionary processes, both experimental scales revealed very strong fitness effects, which could be further leveraged to understand if evolutionary change (e.g., increased genetic variation in phenotypic traits) could expand these local and geographic population limits through fitness increase. Finally, dispersal limitation appeared to be a partial limiting factor at the geographic scale (*M. laciniatus*), but not at the local scale (*M. leptaleus*). For example, plants were able to produce seeds (however, much fewer than within the species range) at only one seeding station beyond the high-elevation limit site of *M. laciniatus*, suggesting that there is rare, supportive habitat outside of the local range if seeds can travel to it. In this way, reduced propagule pressure (dispersal limitation) and reduced habitat availability (habitat limitation) may combine to form a geographic limit.

At both beyond-limit scales, plants were able to germinate and flower, but seed set was low to nonexistent, suggesting that these habitats did not have all of the resources to support populations; that is, they may be sink habitats (sensu Holt and Gomulkiewicz, 1997). These examples highlight the advantage of measuring lifetime fitness in such assessments, which is of course more difficult for long-lived plants, and that early life history stages (e.g., germination, flowering) alone may not accurately predict the niche. Understanding dispersal is certainly important for tracking species habitat (e.g., Gómez-Aparicio, 2008; Pinto et al., 2014), but more studies are needed on the importance of dispersal limitation in setting geographic range limits (Hargreaves et al., 2014). Additionally, dispersal limitation and habitat limitation are not mutually exclusive (Moore and Elmendorf, 2006). One caveat for the *M. laciniatus* experiment is that the initial seed inputs, including seed banks, was not known for the natural reference populations near the range limits against which the beyond-limit plots were compared. Thus, the number of starting seeds necessary to produce the number of plants observed in reference populations could be higher than estimated, complicating comparisons between reference and experimental populations. Given the ready field germinability of *M. laciniatus*, we do not expect seed bank effects to have played a major role in differences between range limit and beyond-limit plots. During return visits in 2014 and 2015, we confirmed the presence of *M. laciniatus* in range limit populations and its absence in beyond-limit sites. Nevertheless, standardized, experimental seed inputs between sites (as in the *M. leptaleus* experiment) are necessary to accurately measure and test differences in habitat suitability. Our goal in the *M. laciniatus* experiment was to create a comparable seed rain in beyond-limit sites to test whether dispersal

limitation or habitat limitation was more likely in setting geographic limits.

IMPLICATIONS AND FUTURE RESEARCH

Examining and comparing local (internal) and geographic (external) population limits allows us to determine the relative strength of selection from myriad agents of interest, the scales at which dispersal and habitat limitation vary in importance and how populations evolve to respond to these limitations, and the relative roles of climate, small-scale abiotic variation (e.g., microclimates and soils) and biotic factors (e.g., competitors and soil microbes) on plant distributions. We know of no studies that have investigated different scales of limitation simultaneously, yet this approach could provide great insights for plant ecology, evolution, and conservation science. For example, a long-standing hypothesis is that abiotic factors (e.g., cold-related stress) play a more important ecological and evolutionary role for populations than biotic interactions (e.g., competition or predation) at higher latitudes, and vice versa for lower latitudes (e.g., Darwin, 1859; Schemske et al., 2009). Investigating such questions at multiple scales within and across species ranges could illuminate whether such biogeographic hypotheses are consistently supported among varying ecological contexts (e.g., climate gradients, biomes, communities, topography). In our *Mimulus* experiments, we saw that both local and geographic limits can impose severe habitat restrictions within habitats that are adjacent to and appear very similar to those within the species' borders. Further experiments are then possible to understand which factors or variables and their interactions and values circumscribe the niche.

Studying local and geographic limits can greatly inform us about the likely success of conservation strategies such as restoration (Harris et al., 2006; Benayas et al., 2009) and assisted migration (McLachlan et al., 2007; Mueller and Hellmann, 2008; Vitt et al., 2010). Assisted migration outside of a species' current range is controversial (Ricciardi and Simberloff, 2009) and may not work even with strong support from environmental niche models if the variables circumscribing the niche have not been accounted for (e.g., microsite soil chemistry, soil mycorrhizae) at the intended destinations. Additionally, establishing plant populations requires high confidence that microsite properties are favorable, and even then, recruitment may be low due to natural mortality, seed dormancy, or absence of microbial mutualists. In this vein, specific, local information (at very small scales) of habitat requirements is necessary for restoration or assisted migration. Moore and Elmendorf (2006) showed that species distribution models could accurately predict dispersal limitation and habitat limitation given enough local environmental data. Filling such data gaps can require a great deal of information about co-occurring species and the environmental components of occupied and unoccupied habitats, and illustrates why broad-scale niche modeling (i.e., at the scale of hundreds of meters) will not suffice if steep, unmeasured local gradients determine plant performance.

Belowground niche factors or axes of variation can be critical to plant success (Janssens et al., 1998; Turnau and Haselwandter, 2002; Potthoff et al., 2006; Heneghan et al., 2008; Hufford et al., 2014). At our *M. leptaleus* site, no obvious factors (e.g., herbivory or plant competition) were observed that could explain the inability of plants to develop seeds. For plants, steep habitat-limiting factors may occur on the scale of meters, even in the absence of competitors and with

no obvious aboveground transition. Such phenomena can indicate soil-based or belowground heterogeneity (e.g., soil nutrients or belowground biological interactions) or microclimate variation. If our *M. leptaleus* site were being restored, specific location information would be crucial. More investigations at the soil–root interface, and with microbial associations, are needed, and such studies will be interesting to compare within and beyond species ranges.

In conclusion, great opportunities to build understanding of the distributions of plants can be found by identifying places where plants cannot grow or only grow with difficulty, on the margins of their local and geographic distributions. Examining a variety of distribution limits is important and replication is essential. Due to habitat limitations, sample sizes of surviving plants may be low at and beyond distribution limits, but the strength of effects between patches may be quite large. Carefully considering and combining multiple scales and types of limitation, with replication, investigators can tune their sampling to solve the mysteries of plant distributions.

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