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Plant–soil interactions limit lifetime fitness outside a native plant's geographic range margin

John W. Benning [1] and David A. Moeller

Department of Plant and Microbial Biology, University of Minnesota, 140 Gortner Labs, 1479 Gortner Avenue, Saint Paul, Minnesota 55108 USA

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Abstract. Plant species' distributions are often thought to overwhelmingly reflect their climatic niches. However, climate represents only a fraction of the *n*-dimensional environment to which plant populations adapt, and studies are increasingly uncovering strong effects of nonclimatic factors on species' distributions. We used a manipulative, factorial field experiment to quantify the effects of soil environment and precipitation (the putatively overriding climatic factor) on plant lifetime fitness outside the geographic range boundary of a native California annual plant. We grew plants outside the range edge in large mesocosms filled with soil from either within or outside the range, and plants were subjected to either a low (ambient) or high (supplemental) spring precipitation treatment. Soil environment had large effects on plant lifetime fitness that were similar in magnitude to the effects of precipitation. Moreover, mean fitness of plants grown with within-range soil in the low precipitation treatment approximated that of plants grown with beyond-range soil in the high precipitation treatment. The positive effects of within-range soil persisted in the second, wetter year of the experiment, though the magnitude of the soil effect was smaller than in the first, drier year. These results are the first we know of to quantify the effects of edaphic variation on plant lifetime fitness outside a geographic range limit and highlight the need to include factors other than climate in models of species' distributions.

Key words: Clarkia xantiana *ssp.* xantiana*; edaphic; geographic range limit; local adaptation; mutualism; range expansion; species distributions.*

Introduction

Species' geographic range limits, the perimetric lines that delimit taxa's geographic distributions, are relatively simple patterns resulting from the complex interplay of genetics, ecological interactions, and demography. For terrestrial plants, the most oft-assumed drivers of geographic distributions are temperature and precipitation, and these climatic variables underlie most species distribution models (SDMs) (Pearson and Dawson 2003, Sexton et al. 2009, Louthan et al. 2015). However, it is increasingly recognized that nonclimatic factors likely play underappreciated roles in limiting species' large-scale distributions (Parker 2001, Araújo and Luoto 2007, Gravel et al. 2011, Bertrand et al. 2012, Louthan et al. 2015, Staniczenko et al. 2018, Benning et al. 2019). One environmental variable that is potentially pivotal in influencing plant species' distributions is the edaphic (soil) environment in which almost all terrestrial plants complete their life cycle (Bertrand et al. 2012, Thuiller 2013, Diekmann et al. 2015). However, the role of plant–soil interactions in modulating plant species' geographic distributions remains sorely understudied.

Soils exhibit remarkable diversity in biotic (Fierer and Jackson 2006, Tedersoo et al. 2014) and abiotic (Palm et al. 2007) properties, and these vary at both small and large scales. It is widely recognized that variation in the hyperdimensional soil environment can drive ecosystem-level patterns in productivity and terrestrial community composition (Ettema and Wardle 2002, Zak et al. 2003, Güsewell 2004, Hawkes et al. 2005, Palm et al. 2007, Van Der Heijden et al. 2008, Wubs et al. 2019), and that biotic (Lugtenberg and Kamilova 2009, Hayat et al. 2010, Miransari 2010, Jung et al. 2012) and abiotic (Passioura 1991, Mengel et al. 2001) components of soil have a range of potentially large effects on individual plant phenotypes and fitness. However, the potential role soil factors play in the colonization of, and fitness within, novel environments outside a taxon's range limit has received surprisingly little attention (but see Nuñez et al. 2009, Peay et al. 2010, Brown and Vellend 2014, Ford and HilleRisLambers 2020).

Given the demonstrated effects of soil microbial communities on plant performance (Wolfe et al. 2005, Jung et al. 2012, Lau and Lennon 2012, Pain et al. 2018) and the high spatial turnover of these communities (Noguez

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[1] E-mail: jwbenning@gmail.com

et al. 2005, Wolfe et al. 2007), plant–soil microbe interactions could play an underappreciated role in modulating plant distributions (Parker 2001, Van der Putten 2012). If microbial mutualists are absent or less abundant outside a plant species' range limit, novel soil microbial assemblages could impair fitness outside that limit (Peay et al. 2010, Brown and Vellend 2014, Lankau and Keymer 2016). The presence of mutualists may be especially important for ameliorating increased abiotic stress that often occurs at and beyond range margins, like that experienced by plants distributed across gradients in aridity (Augé 2001, Yang et al. 2009, Miransari 2010, Lau and Lennon 2012). Similarly, if pathogens are more abundant or novel beyond a range limit, they could also hinder plant fitness and successful colonization. Finally, variation in abiotic properties of soil across a distributional boundary, such as nutrient and organic matter content, could also influence plant performance outside the range. Including abiotic edaphic factors in SDMs often improves their performance over climate-only models (Bertrand et al. 2012, Dubuis et al. 2013, Walthert and Meier 2017), suggesting that these factors play roles in structuring plant species' geographic distributions. Abiotic edaphic factors are known to structure local/population range limits, like those of plants adapted to serpentine soils (Lau et al. 2008, Lazarus et al. 2011), but their potential effect on plant species' distributions remain underexplored. Overall, we largely lack the necessary experiments to test the potential for biotic/abiotic edaphic variation across a plant's geographic range boundary to limit colonization outside that boundary. Especially important are field experiments that replicate natural conditions as closely as possible, given that responses of plants in field vs. greenhouse conditions can vary strongly (Dawson and Schrama 2016, Poorter et al. 2016).

Manipulative field transplant experiments let us ask directly: what environmental variables limit lifetime fitness and prevent range expansion beyond a taxon's current geographic range limit? Factorial experiments manipulating multiple putatively important environmental variables also let us assess the *relative* magnitude of these effects on fitness, and potential interactions between them, in a way that correlative approaches cannot. We designed an experiment to disentangle the role of edaphic environment and precipitation in limiting the distribution of a California annual plant by experimentally manipulating these two niche variables in a transplant experiment beyond the plant's geographic range boundary. We grew plants in large mesocosms installed in the soil that allowed us to manipulate complete soil environments and precipitation for individual plants. The plant, *Clarkia xantiana* ssp. *xantiana*, is distributed across an aridity gradient, with lower precipitation near and outside its range edge, and SDMs indicate this aridity gradient is strongly correlated with the subspecies' distribution (Eckhart et al. 2011). We quantified the relative, and potentially interactive effects of edaphic environment and precipitation on *C. x. xantiana* lifetime fitness outside this range boundary in the first year of the experiment.

Even short-term historical precipitation patterns can influence future soil abiotic and biotic properties (e.g., Cavagnaro 2016, Hicks et al. 2018). This may be especially important during climate change if interannual variability increases and historically rare climatic events become more frequent. For example, in California, anthropogenic forcing has already increased precipitation volatility and the frequency of extremely wet (and dry) years (Swain et al. 2018). If high-precipitation years, despite being relatively infrequent, have lasting legacy effects on soil properties outside the range margin of *C. x. xantiana*, this could modify plant–soil interactions important for mediating the plant's distribution. For instance, relatively high precipitation in one year could favor the increased growth of mutualistic (or pathogenic) microbial symbionts outside a plant's range edge, effects which could "spill over" into the next growing season(s). These legacy effects of precipitation could thus potentially dampen intergenerational environmental variation and alter the probability of successful colonization outside the range margin. Thus, we continued the experiment, without manipulating precipitation, in a second year to test for temporal variation in the effect of edaphic factors on plant fitness, and to ask if legacy effects of precipitation in the prior growing season affected plant fitness in the subsequent year.

Methods

Study system

Clarkia xantiana ssp. *xantiana* A. Gray (hereafter, *xantiana*) is a primarily outcrossing winter annual native to the southern Sierra Nevada foothills of California (United States). *Xantiana* is most commonly found on steep slopes at low to intermediate elevations (350–1,650 m) in grasslands, oak and pine woodlands, and openings in chaparral (Lewis and Lewis 1955, Eckhart and Geber 1999). The subspecies is distributed between California's Central Valley to the west and the Mojave Desert to the east, with the greatest density of populations occurring within the Kern River Valley. Most populations occur on sandy, fast-draining soils derived from igneous rock (granodiorite, granite, quartz monzonite, and/or gabbro; Eckhart et al. 2010). In the Mediterranean climate of the southern Sierra Nevada, *xantiana* germinates in the relatively wet winter, maturing and setting seed in June.

The eastern range edge of *xantiana* is stark (Fig. 1a) and extensive searching over the past 20+ yr has uncovered no *xantiana* populations beyond this limit. The largely selfing *Clarkia xantiana parviflora*, a sister subspecies of *xantiana*, is distributed mainly to the east of *xantiana*, and the two taxa are in secondary contact within a narrow (approximately 10 km) zone of

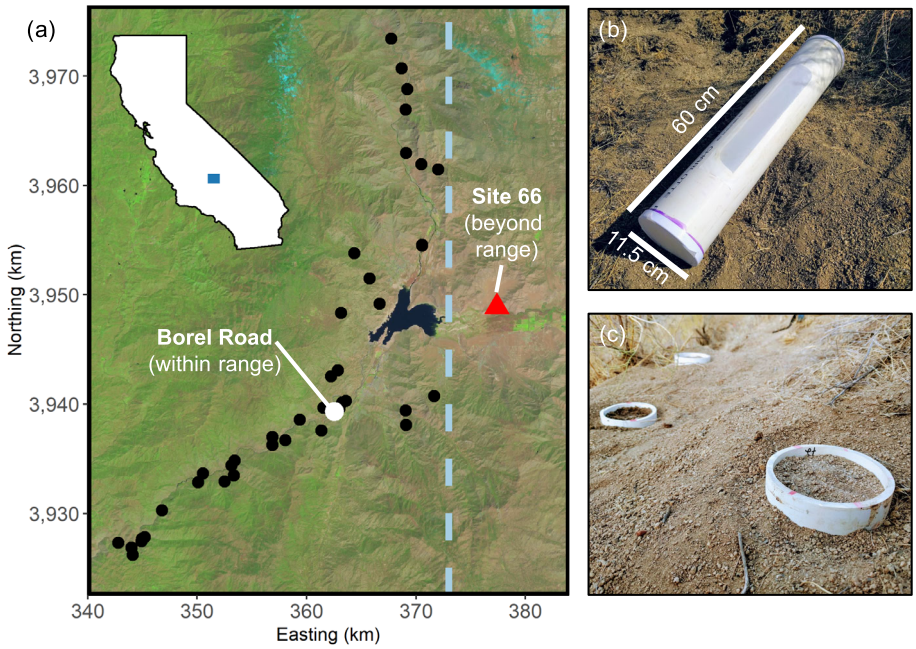

FIG. 1. (a) Overview of study area in southern California and the locations of sites used in the field experiment. Seeds were sourced from the Borel Road site (large white circle) and the experiment took place at Site 66 (red triangle), 4 km outside the eastern range limit of *Clarkia xantiana* ssp. *xantiana* (marked by the dashed blue line). Small black circles mark a representative geographic sample of 42 populations across the main portion of the subspecies' distribution. Background image is 19 April 2016 LANDSAT imagery of study area. Axes are Universal Transverse Mercator coordinates; Zone 11 S. (b) One of the mesocosms used to manipulate edaphic environments in the field, before installation in the ground. Note the mesh-covered openings on two sides (only one shown) and bottom. (c) Mesocosms installed in the ground at Site 66 and filled with soil.

sympatry at the eastern range edge of *xantiana* (and the western range edge of *C. x. parviflora*; Pettengill and Moeller 2012, Briscoe Runquist et al. 2014). *Xantiana* is distributed across a west–east aridity gradient (with precipitation lower and more variable toward and outside its eastern range edge) that contributes to reduced performance at the range edge and beyond (Fig. 1a; Eckhart et al. 2010, 2011). In addition, mutualistic interactions with pollinators are weaker at and beyond the range limit, resulting in greater pollen limitation of reproduction (Moeller et al. 2012, Anderson et al. 2015, Benning and Moeller 2019), and antagonistic interactions with mammalian herbivores are stronger at and beyond the range limit (Benning et al. 2019). Multiple lines of evidence (transplant experiments, Geber and Eckhart 2005, Benning and Moeller 2019; distribution models, Eckhart et al. 2011; and population genetics, Moeller et al. 2011) indicate the subspecies' range is limited primarily by adaptation and not dispersal.

Overview of experimental design

We conducted the experiment at a site 4 km beyond the eastern range edge of *xantiana* that hosts a population of *C. x. parviflora* (Site 66; Fig. 1a). In order to manipulate edaphic environments and water availability, we installed 160 mesocosms in 20 blocks across a large slope (approximately 100 × 30 m) where natural vegetation was allowed to remain intact. The field site is an arid shrubland dominated by sagebrush (*Artemisia tridentata*), longspine horsebrush (*Tetradymia axillaris* var. *longispina*), and sparse annual vegetation. The mesocosms were filled with soil from one of two sites: the focal site (Site 66), 4 km outside the eastern range edge of *xantiana*, or from a site toward the center of the geographic range (11 km west of the eastern range edge of *xantiana*), that hosts a natural *xantiana* population (Borel Road). All mesocosms were planted with seeds from the same within-range population (Borel Road); seeds for each year of the experiment were collected the preceding June from at least 20 maternal plants and bulked before planting. Both the beyond-range experimental site and the within-range source population occur on fast-draining soils derived from Mesozoic granite.

Mesocosm construction and installation

We based our mesocosm design on the in-growth cores of Johnson et al. (2001), with some modifications. Each mesocosm was constructed from 60-cm-long sections of PVC pipe (10-cm interior diameter; 11.5-cm exterior diameter) in order to afford plants a large belowground environment that allowed for natural root growth (Fig. 1b, c). One end of the section was capped with PVC caps, which were glued to the sections using PVC glue. To allow water movement across the mesocosm

exterior, we cut two openings (32 × 5 cm) into the sides of each mesocosm, and one large hole (8-cm diameter) into the bottom cap. These slits and holes were covered with 0.5 micron nylon mesh (Plastok Associates, Ltd., England), which was attached to the mesocosm with an elastic adhesive (Lexel; Sashco, Brighton, Colorado, United States). This mesh kept *xantiana* roots from growing outside the mesocosms and should have prevented most fungi (Teste et al. 2006, Islam et al. 2017) and many bacteria (Levin and Angert 2015) from entering the mesocosms from the surrounding soil environment. We installed mesocosms at the site in October 2017. We prepared holes for each mesocosm using an auger powered by a portable drill and set mesocosms into the hole such that about 3 cm of the mesocosm protruded above the soil surface. We tamped the soil around the perimeter of each mesocosm to ensure contact between the mesocosm and the surrounding soil.

We collected soil from the focal site, and the seed source site, to fill the mesocosms. Soil was collected from the top 60 cm at multiple locations within the natural *xantiana* population at Borel Road, and from multiple locations within the transplant site (>10 locations per site). Soil was manually homogenized on tarps. We filled mesocosms with 5 L of soil each; there were 80 mesocosms in each within- and beyond-range soil treatment ($N = 160$). Soil and precipitation treatments were assigned randomly across 20 blocks within the site using a complete randomized block design (precipitation $n = 80$). All mesocosms were caged to protect plants from mammal herbivory, which can be very common in this region (Benning et al. 2019). Despite this effort, some cages were breached by small rodents; any plants that were eaten were removed from analyses below (Year 1, final $N = 136$; Year 2, $N = 156$).

Sowing, precipitation treatment, and phenotyping

Year 1.—In October 2017, 15 seeds (collected June 2017) were sown into each mesocosm. Because conditions were so dry (Fig. 2) and germination did not occur in all mesocosms, we added an additional 10 seeds to mesocosms that had fewer than two germinants in February ($n = 128$ mesocosms). These varying seed numbers are accounted for in analyses of germination (see Statistical analyses). Despite the seed addition, only 18 mesocosms that did not have germinants in February contained seedlings in April.

We implemented precipitation treatments to mimic the winter rains and spring drought that characterize this Mediterranean ecosystem. The treatments differed in the severity of spring drought to examine how the edaphic environment might modulate plant–water relations during the primary period of plant growth and thus influence lifetime fitness. Precipitation in the winter of 2017–2018 was very low (51% of the long-term average; Fig. 2; Results), so we watered all mesocosms monthly in December, January, and February to promote germination. Each monthly watering

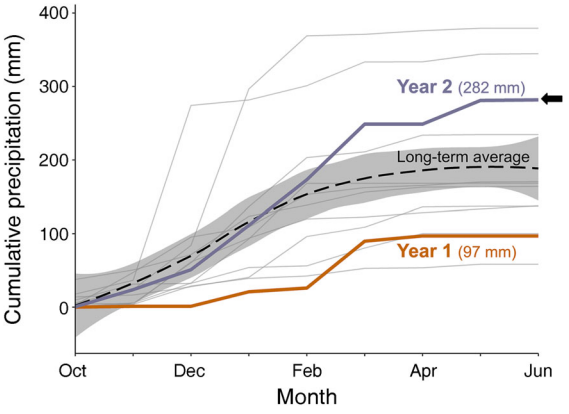

FIG. 2. Growing-season precipitation at the experimental site (Site 66) for Years 1 (orange line) and 2 (purple line), and long-term trends for years 2008–2017 (thin gray lines). Dashed black line is long-term average with 95% confidence band, as determined by loess smoothing. Black arrow indicates average growing season precipitation for Borel Road (284.6 mm; measured 2008–2019), the within-range site where seeds and within-range soil were sourced. Precipitation in Year 2 at the experimental site was very similar to Borel Road average precipitation.

added approximately 525 mL of water to each mesocosm. In March, when plants begin to grow quickly aboveground, we initiated the watering treatment. All low-precipitation mesocosms received approximately 175 mL of water in March and no supplemental water thereafter, and high-precipitation mesocosms received approximately 525 mL once in March, April, and May. All watering treatments were applied to mesocosms regardless of whether they contained germinants. We culled each mesocosm to one seedling in March. We recorded germination and survival monthly February–June. We collected all fruits from each plant in late June. We estimated seed set in each collected fruit using a linear model that predicted seed set as a function of individual fruit weight (Benning and Moeller 2019). A plant's lifetime fitness was equal to the sum total seeds contained in all of its fruits. Seventeen plants were part of a separate experiment quantifying the magnitude of pollen limitation outside the range; each of these plants had one pollen-supplemented and one control (unmanipulated) fruit. For these 17 plants, we assumed "natural" seed set of the supplemented fruit was equal to seed set of the control fruit. Both soil treatments were represented in these 17 plants, but they were largely from the high precipitation treatment.

Soil volumetric water content (VWC) was measured with a Decagon GS1 soil moisture meter (METER Group, United States) in a subset of mesocosms in April and May, approximately 24 h after imposing the watering treatment, in order to measure differences in mesocosm VWC between low- and high-precipitation treatments.

Year 2.—We reseeded all mesocosms with an additional 15 seeds (collected June 2018) in October 2018. In analyses below, we assume that seeds sown in Year 1 that did not germinate survived to Year 2. We did not include a

precipitation treatment in Year 2, but rather tested for legacy effects of the previous year's precipitation treatment—that is, did mesocosm precipitation treatment in Year 1 influence plant fitness in Year 2? We recorded germination in February and culled each mesocosm to one seedling. We recorded survival in May and collected all fruits from each plant in late June. Collected fruits were lost for one plant; we estimated that plant's total seed set by taking the product of its number of fruits and the average individual fruit seed set of all other experimental plants that year. Soil VWC was measured with a Decagon GS1 soil moisture meter (METER Group) in a subset of mesocosms in February and May, as in Year 1. Thirty mesocosms from four haphazardly chosen blocks were exhumed in May to harvest soil for nutrient analyses, and roots for later microbiome analyses. Using data from the remaining mesocosms, we predicted final seed set for removed mesocosms using a linear model of seed set given number of flower buds in May. Number of buds in May was strongly correlated with final seed set (model adjusted $R^2 = 0.65$). We used these predicted values in the analyses below to retain these individuals in the data; analyses omitting these exhumed mesocosms produced very similar results (Appendix S1: Fig. S1). Soil from 25 of these exhumed mesocosms (12 with beyond-range soil, 13 within range) was used for analyses of soil pH, macro- (nitrate, phosphorus, potassium, calcium, magnesium, and sulfur) and micronutrient (aluminum, boron, iron, manganese, lead, and zinc) content, and estimated cation exchange capacity (CEC). We also measured soil organic matter (SOM) in soils from six mesocosms of each soil type. All soil analyses were performed at the University of Connecticut Soil Nutrient Analysis Laboratory. Soil nutrients were quantified using a modified-Morgan solution, SOM was determined by loss on ignition, and CEC was estimated with the summation method based on levels of Ca, Mg, and K.

We obtained daily precipitation data for the transplant site during the 2 yr of the experiment from a weather monitoring station (HOBO Onset) at the site. We also obtained precipitation records for the transplant site in years 2008–2017, and the seed source/within-range site in years 2008–2019, in order to interpret precipitation patterns during the experiment relative to long-term trends.

Statistical analyses

All analyses were conducted in R (R Development Core Team 2013). We used *aster* life history models (Geyer et al. 2007, Shaw et al. 2008) in R to evaluate the effects of soil environment and precipitation treatments on *xantiana* lifetime fitness. *Aster* models use a graphical approach that links sequential components of lifetime fitness, each modeled with its appropriate statistical distribution. Our *aster* model incorporated four components of lifetime fitness (*nodes* in the graphical model) for this experiment: germination, late survival (May), fruit production (i.e., did the plant produce any seed-bearing fruits), and total seed set. The first three components were modeled as Bernoulli variables (0,1), and total seed set was modeled as a zero-truncated negative binomial variable (below, "1" is the root node indicating the presence of sown, but ungerminated seeds):

$$\begin{array}{ccccc} \textit{germination} & & \textit{late survival} & & \textit{fruit production} \\ (0,1)\text{Bernoulli} & \rightarrow & (0,1)\text{Bernoulli} & \rightarrow & (0,1)\text{Bernoulli} \\ & & \textit{seeds produced} & & \\ & \rightarrow & \text{zero}-\text{truncated negative binomial} & & \end{array}. \quad (1)$$

For Year 1, we built an *aster* model with soil treatment, precipitation treatment, and their interaction as predictors; response variables were those associated with each component of lifetime fitness. To estimate the effects of each predictor on lifetime fitness, each predictor was fit at the level of total seed set in the model (Shaw et al. 2008). We did not include block as a random effect in these models because random effects cannot be estimated in *aster* models that include nodes modeled with negative binomial distributions (C. Geyer, *personal communication*). We used likelihood ratio tests (LRTs) comparing submodels to fuller models to test each term of interest. For these and all analyses below, we use $\alpha = 0.05$.

For Year 2, we built an *aster* model as above with soil treatment, precipitation treatment, and their interaction as predictors. Here, precipitation treatment indicated the "legacy" precipitation treatment from Year 1. We used LRTs comparing submodels to fuller models to test each term of interest. A significant precipitation or soil × precipitation term would indicate legacy effects of precipitation in Year 1 on plant fitness in Year 2. We found no evidence that the presence of a plant in a mesocosm in Year 1 affected lifetime fitness in that mesocosm in Year 2 (Appendix S1: Table S1).

Individual life history components.—Because effects of soil and precipitation treatments may manifest at different stages of a plant's life, we also tested the influence of soil and precipitation treatments at each life-history stage separately for both years of the experiment (in Year 2, precipitation treatment was the "legacy" precipitation treatment from Year 1). We used mixed-effect logistic regression models (lme4 package; Bates et al. 2015) and Type II ANOVAs (car package; Fox and Weisberg 2019) to test the effects of soil treatment, precipitation treatment, and their interaction, on our Bernoulli life history components (germination through fruit production), including a random block term: glmer(response ~ Soil * Precipitation + (1|Block). Using the same model structure, we used negative binomial regression to model seed production, using the *glmer.nb( )* function in the MASS package (Venables and Ripley 2002). Estimated

marginal means were calculated with *emmeans* in the emmeans package (Lenth 2020). These separate fitness component analyses are "conditional" in the sense that, for each component after germination, we only used the subset of records that survived the previous life-history stage (e.g., analysis of the probability of fruiting only included those plants that survived to March). For fruit production in both years, there was complete separation in the models (i.e., one treatment combination had no variation in response). Thus, we added one "pseudorecord" with the opposite response for that treatment combination to enable the models to converge, but we do not include that pseudorecord in Fig. 3.

Predicting mean lifetime fitness.—The fitness metric of most interest was mean seeds produced per planted seed. Because we planted multiple seeds per mesocosm, and culled extra germinants, fitness predictions from our *aster* model (where germination was treated as presence/absence for each mesocosm) would be inflated relative to this metric. Thus, we obtained predicted values for lifetime fitness and their associated standard errors by taking the product of germination probabilities (see Individual life history components) and unconditional parameter estimates from a full *aster* model that did not include a germination node. Standard errors for these products were calculated using the Delta method (Buehler, 1957).

VWC and soil nutrient analyses.—To quantify differences in VWC between precipitation treatments and soil types, for each year we built a linear model with VWC as the response and soil treatment, precipitation treatment, the soil × precipitation interaction, and sampling month as predictors: lm(VWC ~ Soil * Precipitation + Month). We used Type II ANOVA (car package; Fox and Weisberg 2019) and *emmeans( )* (Lenth 2020) to test for differences in VWC between treatments.

We used Student's *t* tests to test for differences in soil pH, macro- and micronutrient content, soil organic matter, and CEC of the within- and beyond-range soils in the mesocosms exhumed in Year 2. To determine if differences in these abiotic soil variables were related to fitness differences between soil treatments, we used linear regression to test the effects of each variable on plant height in May (which is highly correlated with final seed set; $r = 0.72$).

Results

Year 1

During the Year 1 growing season, the beyond-range transplant site received 97.0 mm of precipitation (51% of the 12-yr average of 189.5 mm; Fig. 2). There was at least one germinant in 104 mesocosms (76%), and a fruiting plant in 78 mesocosms (57%). Both soil and precipitation treatment had large effects on lifetime fitness as modeled by *aster* analyses (both $P < 0.01$), but there was no evidence of a significant interaction between the two treatments (Table 1, Fig. 3). Overall, within-range soil increased lifetime fitness about 170% relative to plants grown with beyond-range soil (21.4 vs. 7.8 seeds per planted seed, respectively). Plants in the high-precipitation treatment had lifetime fitness values about 280% higher than those plants in the low-precipitation treatment (23.1 vs. 6.1 seeds per planted seed, respectively). Interestingly, lifetime fitness of plants grown with beyond-range soil and high precipitation was not significantly different from that of plants grown with within-range soil and low precipitation (12.4 vs. 9.1 seeds per planted seed, respectively; LR dev = 1.6, $P = 0.2$; Fig. 3).

The effects of soil and precipitation treatments varied among life-history stages. Precipitation treatment had no effect on germination, late survival, or probability of fruiting, but increased precipitation resulted in a more than 200% increase in seed set (estimated marginal means of 364 vs. 111 seeds; $P < 0.001$; Table 2, Fig. 3). Within-range soil increased probability of germination (within range: 0.08, beyond range: 0.06; $P = 0.01$; Fig. 3b) and seed set (256 vs. 157; $P < 0.01$; Fig. 3e) relative to beyond-range soil.

Year 2

In Year 2, the transplant site received 281.8 mm of precipitation, 49% more than the site's long-term average and roughly equal to the long-term average (284.6 mm) of Borel Road, the within-range site where seeds and within-range soil were sourced (Fig. 2). There was at least one germinant in 150 mesocosms (96%), and a fruiting plant in 116 mesocosms (74%). Average lifetime fitness was more than twice as high as in Year 1 (37.6 vs. 14.6 seeds per planted seed, respectively; Fig. 3a, f). Mesocosm precipitation treatment in Year 1

Table 1. Summary of results from likelihood ratio test *aster* model comparisons testing effects of soil and precipitation treatments, and their interaction, on lifetime fitness in *xantiana* in Years 1 and 2.

Term	Residual df	Test df	Year 1 $N = 136$ Dev	Year 2 $N = 156$ Dev
Full model	7			
Soil × Precipitation	6	1	3.1†	0.1
Main effects only	6			
Soil	5	1	9.9**	4.9*
Precipitation	5	1	24.1***	1.1

Notes: The Year 2 model is testing for a legacy effect of precipitation treatment in the previous year. The germination node of these *aster* models is modeled as a Bernoulli variable (i.e., germinants were or were not present). Because we sowed multiple seeds into each mesocosm, for Fig. 3, estimates of seeds produced per planted seed were calculated as the product of germination probabilities and fitness estimates from an *aster* model including only those plants that germinated (see Methods).

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; †$P < 0.1$.

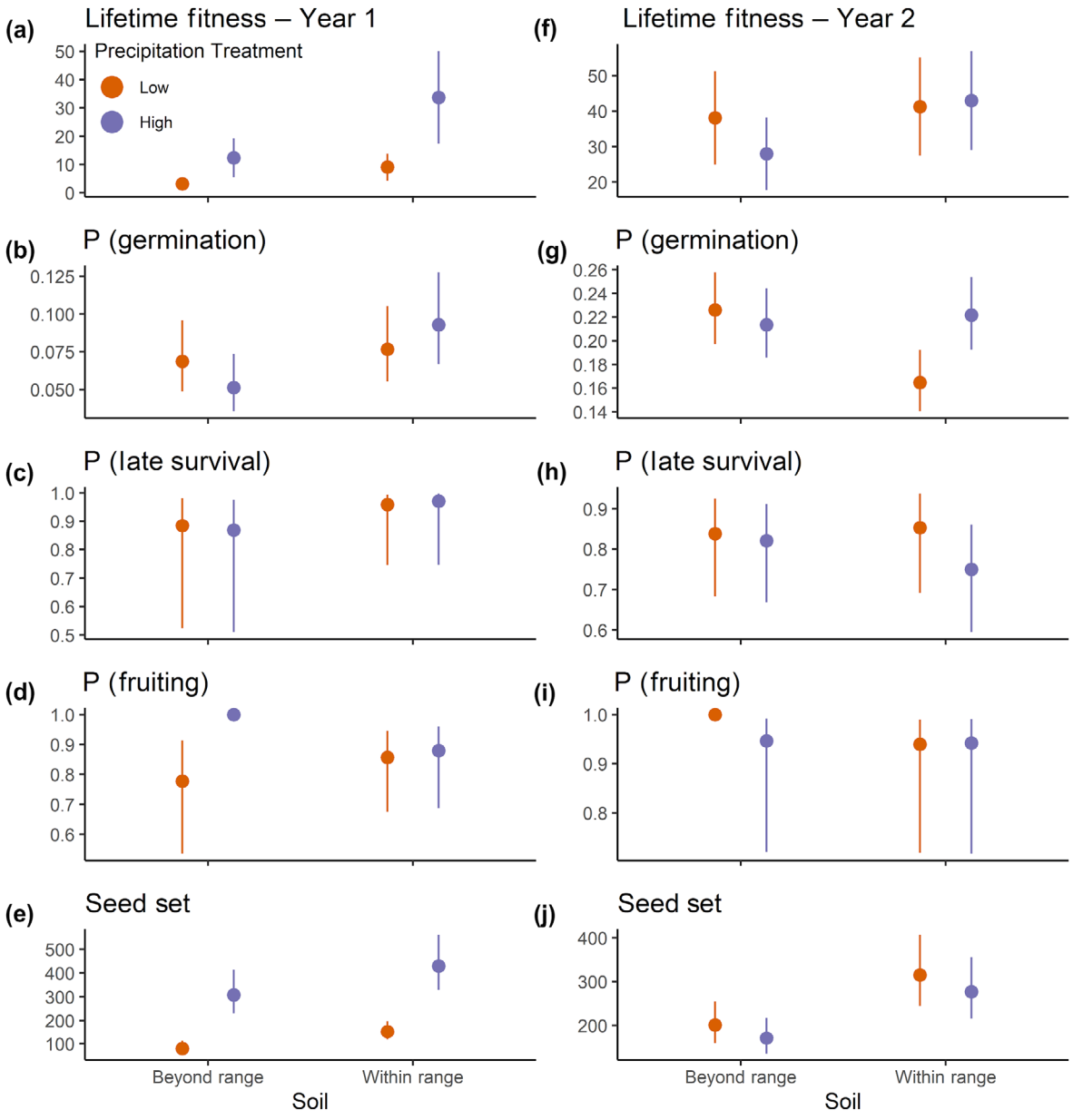

FIG. 3. Effects of soil and precipitation treatments on (a) lifetime fitness (seeds per planted seed) and (b–e) conditional components of lifetime fitness in Year 1 of the experiment, and effects of soil treatment and precipitation legacy treatment on (f) lifetime fitness and (g–j) conditional components of lifetime fitness in Year 2 of the experiment. Note that in Year 2, precipitation treatments reflect "legacy" effects of precipitation treatments in Year 1; that is, we did not differentially water mesocosms in Year 2. Estimates of seeds produced per planted seed (lifetime fitness) were calculated as the product of germination probabilities and fitness estimates from an *aster* model including only those plants that germinated (see Materials and Methods). Estimates for conditional components of fitness are estimated marginal means. All error bars are 95% confidence intervals.

("legacy" precipitation) did not have significant effects on plant lifetime fitness in Year 2 (precipitation $P = 0.3$, precipitation × soil $P = 0.8$; Table 1). Soil treatment had a more modest effect on lifetime fitness than in Year 1, but in the same direction: within-range soil increased lifetime fitness about 30% relative to beyond-range soil (42.1 vs. 33.1 seeds per planted seed, respectively; $P = 0.03$; Table 1, Fig. 3f).

The effect of soil treatment on lifetime fitness was largely driven by increased seed set in within-range soil relative to beyond-range soil (295 vs. 185 seeds, respectively; $P < 0.001$; Table 2, Fig. 3j). There was a significant soil × (legacy) precipitation interaction for germination ($P < 0.01$; Table 2), whereby mesocosms with within-range soil that had received the low-precipitation treatment in Year 1 had reduced probability of

TABLE 2. Summary of Type II analysis of deviance for logistic regressions (germination through fruit production) and negative binomial regression (seed set) testing effects of soil treatment, precipitation treatment, and their interaction, on sequential components of *xantiana* lifetime fitness in Year 1, and the effect of soil treatment and legacy precipitation treatment on these fitness components in Year 2.

	Conditional lifetime fitness components									
	Year 1					Year 2				
	df	Germination (132)	Late survival (100)	Fruit production (85)	Seed set (74)	df	Germination (154)	Late survival (148)	Fruit production (120)	Seed set (114)
Fixed effects										
Soil	1	**6.4***	2.8*	0.0	**10.5****	1	5.4*	0.2	0.2	**13.9*****
Precipitation	1	0.0	0.0	1.0	**64.0*****	1	3.3	0.8	0.1	1.4
Soil × Precipitation	1	3.3†	0.1	1.0	1.1	1	**10.1****	0.4	0.2	0.0
Random effects										
Block	1	25.2***	9.0**	0	0	1	30.2***	0	0.1	0

Notes: Values are Wald χ^2 statistics. Bolded values remain significant at $P < 0.05$ after Holm adjustment. Numbers in parentheses after fitness components indicate the residual df for that model. The random effect of block was tested with likelihood ratio tests; values are χ^2 statistics.

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; †$P < 0.1$.

germination (0.17 vs. ~0.22 in other treatment combinations; Fig. 3g).

Soil abiotic properties

In Year 1, the high-precipitation treatment increased mesocosm VWC (Θ) from 0.02 to 0.15, averaging across soil types and measurements in April and May (soil $P < 0.001$; Appendix S1: Table S2). Note that measurements were taken about 24 h after each monthly watering treatment, and that soil VWC likely equilibrated between treatments sometime afterward. The main effect of soil treatment and the soil × precipitation interaction were both marginally significant ($P = 0.07$ and $P = 0.06$, respectively; Appendix S1: Table S2). VWC in mesocosms with within-range soil was higher after watering relative to beyond-range soil (0.16 vs. 0.13; Tukey $P = 0.05$); there was no difference in VWC between soil types in the low precipitation treatment. In Year 2, VWC in mesocosms with within-range soil was again higher than with beyond-range soil (0.15 vs. 0.13, respectively; $P < 0.01$; Appendix S1: Table S2), averaging across measurements in February and May. There was no legacy effect of precipitation treatment on VWC ($P = 0.27$; soil × precipitation interaction $P = 0.88$).

Though both soils were, overall, nutrient poor, within-range soil was more nutrient rich than beyond-range soil, had a slightly lower pH, higher soil organic matter (SOM), and higher CEC (Appendix S1: Fig. S2). The largest significant differences in nutrient content between within- and beyond-range soils were for magnesium (108.0 vs. 55.2 ppm, respectively), calcium (1,040.3 vs. 554.0 ppm), sulfur (20.4 vs. 11.0 ppm), and nitrate (4.0 vs. 1.5 ppm). Within-range soil had double the CEC of beyond-range soil (7.0 vs. 3.5 cmole+/100 g, respectively), and within-range soil had higher SOM than beyond-range soil (1.1 vs. 0.2%, respectively). Plant height in exhumed mesocosms in Year 2 was significantly positively correlated with mesocosm soil CEC ($P = 0.01$), calcium ($P < 0.01$), magnesium ($P < 0.01$), sulfur ($P = 0.02$), and nitrate ($P < 0.01$; Appendix S1: Fig. S3). The relationship of height with nitrate was driven by one within-range soil outlier with a nitrate level 47% higher than the next highest nitrate record; when this outlier was removed, the relationship between height and nitrate was not significant ($P = 0.2$).

DISCUSSION

The question of why, in the absence of obvious barriers, an organism occurs on one side of its range margin and not the other is a perennial one. In many cases, the simple answer is that the organism is adapted to environments inside its range, and maladapted to the environment outside its range. However, determining the particular environmental variables underlying these patterns in adaptation is a more difficult, but necessary task. Manipulative field experiments are especially useful in going beyond correlative models to test specific hypotheses regarding the environmental factors underlying maladaptation and restricting range limits. Using a manipulation of whole soil environments in the field across 2 yr, we found evidence that (1) lifetime fitness of transplants outside a native plant's geographic distribution was limited by plant–soil interactions, (2) fitness effects of treatments were large, and (3) plant–soil interactions had effects similar in magnitude to those caused by precipitation, the key climatic driver. Importantly, the effect of plant–soil interactions varied across 2 yr that differed greatly in precipitation, indicating that the relative importance of environmental constraints on range expansion will vary through time.

Soil and precipitation treatments have large fitness effects in the field

In Year 1, increased precipitation and within-range soil each more than doubled mean lifetime fitness in *xantiana* growing outside its range limit. The precipitation gradient across which *xantiana* is distributed is well characterized (Eckhart et al. 2010, 2011), and the first year of this experiment confirmed experimentally what correlative approaches have previously suggested; that is, that decreased precipitation limits fitness outside the range margin of *xantiana*. What is more surprising is that soil moved from just 18 km southwest of the beyond-range transplant site more than doubled lifetime fitness beyond the range, despite the soils being derived from the same parent material and of similar age. Calls to explore the potential for edaphic factors to limit plant geographic distributions (Lafleur et al. 2010, Thuiller 2013, Diekmann et al. 2015) have been answered to some extent by incorporating soil variables into SDMs, which often improves model fit (Bertrand et al. 2012, Dubuis et al. 2013, Beauregard and de Blois 2014, Buri et al. 2017, Walthert and Meier 2017). However, field experiments are lacking (but see Brown and Vellend 2014, Ford and HilleRisLambers 2020), and to our knowledge, ours is the first to directly quantify the effect of edaphic variation across a geographic range boundary on plant lifetime fitness outside that boundary. Our results suggest that the edaphic environment has effects on fitness that are comparable to that of a climatic factor despite no underlying variation in soil parent material, and little overt differentiation in soils (as opposed to, e.g., serpentine outcrops). More generally, these results suggest that greater attention should be paid to edaphic factors in studies of plant geographic ranges.

Beyond the overall fitness advantage conferred by within-range soil, two observations in particular are of note: first is the contrast between beyond-range soil with the high-precipitation treatment, and within-range soil with the low-precipitation treatment—lifetime fitness estimates within these two treatment combinations were similar and not significantly different from each other. Second, in the low-precipitation treatment, which produced extremely low levels of soil moisture, within-range soil increased fitness about 180% relative to beyond-range soil. These results suggest that edaphic factors can mediate stressful conditions resulting from low precipitation outside the range of *xantiana* and can functionally "erase" the negative effects of a dry year on fitness. There is increasing evidence that soil microbial communities can alleviate drought stress in plants (Augé 2001, Lau and Lennon 2012, Gehring et al. 2017, Fitzpatrick et al. 2019), and *xantiana* may benefit from interactions with soil microbes from within its range that are absent or less abundant outside its range limit. Increased mineral nutrition of plants growing in within-range soil could also contribute to increased drought tolerance, either through direct mechanisms modulated by specific nutrients or simply because of overall increased nutrition, especially if this results in larger root systems with more capacity for water and nutrient uptake (Waraich et al. 2011, Ahanger et al. 2016).

In Year 2, when precipitation was 49% higher than average, seed set was still improved about 60%, and lifetime fitness about 30%, when plants were grown with within-range vs. beyond-range soil. This highlights how the relative importance of environmental variables regulating plant population dynamics can change over time, and that identification of constraints on species' distributions greatly benefits from multiyear studies. For instance, the effects of mammalian herbivory in this system are severe in years of higher rainfall, but minimal in low-rainfall years (Benning et al. 2019). This temporal variation in the importance of different limiting environmental factors could even directly contribute to the formation of range limits—if selective environments are inconsistent across generations, adaptation to the novel environments beyond range may be even less likely (e.g., Kirkpatrick and Peischl 2013, Hao et al. 2015). Temporal environmental variation in the current study also affected the life stages at which soil treatment effects were realized. In Year 1, within-range soil positively affected germination and seed set. In Year 2, all positive effects of within-range soil were realized at seed set. Interestingly, though there was no evidence of a legacy effect of precipitation treatment on lifetime fitness in Year 2, there was a significant interaction of soil and (legacy) precipitation treatment on germination. Mesocosms with within-range soil that had received the low-precipitation treatment in Year 1 had a lower probability of germination in Year 2 than the other three treatment combinations. It is difficult to know the underlying mechanism, but there is accumulating evidence that soil microbes can affect seed germination rates and early survival (Gallery et al. 2007, Sarmiento et al. 2017, Osborne et al. 2018), and their effects are very likely to be dependent on environmental context (Johnson et al. 1997, Hoeksema et al. 2010). The low-precipitation treatment in Year 1 may have increased the relative prevalence of pathogens that, in turn, decreased the survival of seedlings upon germination, or alternatively decreased the prevalence of microbes promoting germination. Sequencing of mesocosm soils collected at the end of the experiment will help to shed light on microbial compositional changes potentially underlying this legacy effect of precipitation. Although this is not the sort of legacy effect that could mediate establishment outside the current range limit (i.e., there was no legacy effect in beyond-range soil), it is informative as to how precipitation could influence plant–microbe interactions within range.

Secondary nutrients may play an underappreciated role in limiting fitness in natural populations

Both soils used in the experiment are derived from the same parent material (Mesozoic granite), are fast draining with little clay content, and can be considered "nutrient poor," but they did differ in some abiotic properties. We note that these nutrient analyses reflect soil nutrient status at the end of the 2-yr transplant experiment, and that overall nutrient levels may have decreased by the end of the experiment. Thus, in comparing within- and beyond-range soils we are assuming relative differences in nutrient content did not change significantly across the timeline of the experiment. Within-range soil had slightly greater water-holding capacity (as indicated by higher soil VWC), likely because of its higher SOM content relative to beyond-range soil. Differences in SOM between these soils are to be expected given the gradient in primary productivity that separates the sites from which they are sourced (Fig. 1a). However, it is unlikely that the large differences in fitness between soil types was primarily due to their relatively small difference in soil VWC, especially given that fitness differences persisted in Year 2, when water was not likely limiting (Fig. 2). Within-range soil was also more fertile, though only a subset of soil variables was significantly associated with differences in plant height. Interestingly, these were the secondary nutrients calcium (Ca), magnesium (Mg), and sulfur (S), all of which are strongly related to soil SOM in most soils.

Though these secondary nutrients (Ca, Mg, and S) receive less attention than N, P, and K for their roles in plant nutrition, they are all essential for plant growth and required in relatively large amounts. When we examined the relationship of Ca, Mg, and S with plant height and fit trend lines for each soil type separately (Appendix S1: Fig. S4), an interesting pattern emerged. For beyond-range soil, increasing amounts of these nutrients lead to increased plant height; however, there was no indication of a positive relationship with height for those plants grown with within-range soil. This suggests that, if these nutrients are limiting, the relationship with plant growth might not be linear, but rather asymptotic—that is, there is a threshold quantity of soil Ca, Mg, and S necessary for optimal *xantiana* growth. This could indicate that this *xantiana* population is well adapted to the full range of Ca, Mg, and S values that occur in soils from within its source site, but maladapted to lower soil fertility levels that occur outside its range.

Plant–microbe interactions could influence current and future range limits

The effects of edaphic environment on *xantiana* fitness are likely due to a combination of abiotic and biotic properties differing between the soils. Though field experiments are rare, there is mounting evidence that variation in microbial communities across range boundaries could influence the location of current range limits (Afkhami et al. 2014, Lankau and Keymer 2016) and affect future range shifts (Van Nuland et al. 2017). For *xantiana*, there is evidence from amplicon sequencing that soil microbial communities differ strongly across the range boundary (Benning and Moeller, *in press*). We do not have data to compare microbial communities from the two sites in the current experiment directly, but the available evidence suggests that communities of root-colonizing fungi are less rich (i.e., fewer taxa) outside the range margin. If the results of the current study are in part due to plant–microbe interactions, the direction of effect suggests that important microbial mutualists present at the within-range site were absent or in lower abundance at the beyond-range transplant site. An alternative explanation is that beyond-range soil contained relatively higher pathogen loads, leading to low plant fitness. However, given the preponderance of evidence for negative plant–soil feedback (Kulmatiski et al. 2008) and the relatively high potential for enemy escape outside a plant's range limit (Van der Putten 2012, Mlynarek et al. 2017), we believe this scenario is less probable. Though the potential of microbial mutualists to contribute to a plant taxon's range boundary has theoretical and conceptual support (e.g., Parker 2001, Van der Putten 2012), empirical tests of this hypothesis are scarce. At a local scale, Parker et al. (2006) showed that success of an invasive legume is limited by availability of rhizobial mutualists in old-field habitats. Afkhami et al. (2014) provided evidence from observational studies and greenhouse experiments that the geographic range of *Bromus laevipes* may be mediated by interactions with a mutualistic fungal leaf endophyte. The hypothesis that microbial mutualist limitation could constrain colonization outside of plant distributional limits needs more empirical tests, especially manipulative experiments in the field, and the current study provides strong impetus to test this hypothesis explicitly for *xantiana*. Furthermore, inclusion of more *xantiana* populations and their respective home soils would allow future studies to test the extent of population-specific local adaptation vs. range-wide adaptation to edaphic environments.

Niche variables will not shift synchronously with climate change

Research on species' geographic range limits is increasingly spurred by a desire to predict species' distributions under future climatic conditions, usually using SDMs based on climatic variables. Though approaches like SDMs can identify putatively important environmental variables, they are correlative, confounded by covarying environmental gradients, and usually lacking information on nonclimatic environmental variables. An underlying assumption of climatic SDMs is that if populations' ranges shift along with their optimal climatic isotherms, their future distribution will reflect the future location of these climatic niche envelopes. However, unless all aspects

of the *n*-dimensional environment shift synchronously, species will *always* encounter novel environments, to varying extents, regardless of whether they disperse to new areas. If factors other than climate significantly influence a species' distribution, predictions from climate-based SDMs are likely to be poor. Thus, determining the relative importance of various environmental variables for restricting a species' distribution is essential to forecast the movement of geographic range limits accurately.

There is no a priori reason to believe that environment variables will shift synchronously. There is little inherent limit on the rate of change of climatic variables like temperature and precipitation. However, other environmental axes, such as belowground biotic and abiotic properties, may change much more slowly, if at all, with climate change (Van der Putten 2012). For example, soil temperature responds more slowly than air temperature (Gehrig-Fasel et al. 2008), soil nutrients often have limited responses to experimental temperature manipulations (Lamb et al. 2011, Zamin et al. 2014), and soil microbial communities may respond slowly to even sudden shifts in the abiotic environment (Waldrop and Firestone 2006, Rinnan et al. 2007, Cruz-Martínez et al. 2009, Cregger et al. 2012). When nonclimatic factors are disregarded in discussions of shifting species' distributions, an organism's *n*-dimensional niche is collapsed down to just a few axes, and researchers run the risk of greatly overestimating their ability to predict future distributions accurately (Van der Putten et al. 2010, Bertrand et al. 2012). Further, if organisms within a habitat do not migrate or respond at the same rate as the climate changes, the complex web of species interactions within which every species is situated will change. There is mounting evidence that the decoupling of historical biotic interactions (e.g., herbivory, Visser and Holleman 2001; and competition, Alexander et al. 2015) will likely complicate predictions of species range shifts (Van der Putten et al. 2010).

Conclusion

Organismal niches are hyperdimensional, and as researchers increasingly test for influences other than climate on species' large-scale distributions, evidence for their importance accumulates. For *xantiana*, in addition to drought stress, herbivory and pollen limitation reduce fitness outside its range margin (Geber and Eckhart 2005; Eckhart et al. 2011, Moeller et al. 2012, Benning et al. 2019, Benning and Moeller 2019), and the current experiment demonstrates the further contribution of plant–soil interactions. These observations hint at geographic range limits perhaps representing a "perfect storm" of maladaptation along multiple environmental (and trait) axes (sensu Antonovics 1976). Here we show that plant–soil interactions can have large effects on plant fitness outside the range, similar in magnitude to the effects of precipitation, and that the relative effects of plant–soil interactions vary among years. The logistical hurdles involved in manipulating soil environments in the field has led to a paucity of experiments in natural populations, and in general, little consideration of edaphic variation in most research on current and future species' distributions. Our approach of replacing the entire soil environment experienced by a plant via large mesocosms, while growing plants in natural field conditions, provided an unusually holistic test of the hypothesis that edaphic variation across a range boundary contributes to maladaptation beyond that boundary. Moving forward, increased use of field experiments will be key to a more comprehensive understanding of how plant–soil interactions affect distributional patterns of both native and invasive plant species.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3254/suppinfo

Data Availability

All data and code for statistical analyses are available on Figshare https://doi.org/10.6084/m9.figshare.c.5204297.v1 (Benning 2020).