VOL. 195, NO. 3 THE AMERICAN NATURALIST MARCH 2020

SYNTHESIS

Context Dependence of Local Adaptation to Abiotic and Biotic Environments: A Quantitative and Qualitative Synthesis

Ryan D. Briscoe Runquist,[1,*,†] Amanda J. Gorton,[2,*] Jeremy B. Yoder,[1,3,*] Nicholas J. Deacon,[2,4] Jake J. Grossman,[2,5] Shan Kothari,[1,2] Marta P. Lyons,[2,6] Seema N. Sheth,[2,7] Peter Tiffin,[1] and David A. Moeller[1,†]

1. Department of Plant and Microbial Biology, University of Minnesota, Saint Paul, Minnesota 55108; 2. Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, Minnesota 55108; 3. Department of Biology, California State University, Northridge, California 91330; 4. Biology Department, Minneapolis Community and Technical College, Minneapolis, Minnesota 55403; 5. Arnold Arboretum of Harvard University, Boston, Massachusetts 02131; 6. Department of Biology, University of Central Florida, Orlando, Florida 32816; 7. Department of Plant and Microbial Biology, North Carolina State University, Raleigh, North Carolina 27695

Submitted April 12, 2019; Accepted October 11, 2019; Electronically published January 29, 2020

Online enhancements: appendix, supplemental PDF. *Dryad data:* https://doi.org/10.5061/dryad.2v6wwpzh5.

ABSTRACT: Understanding how spatially variable selection shapes adaptation is an area of long-standing interest in evolutionary ecology. Recent meta-analyses have quantified the extent of local adaptation, but the relative importance of abiotic and biotic factors in driving population divergence remains poorly understood. To address this gap, we combined a quantitative meta-analysis and a qualitative metasynthesis to (1) quantify the magnitude of local adaptation to abiotic and biotic factors and (2) characterize major themes that influence the motivation and design of experiments that seek to test for local adaptation. Using local-foreign contrasts as a metric of local adaptation (or maladaptation), we found that local adaptation was greater in the presence than in the absence of a biotic interactor, especially for plants. We also found that biotic environments had stronger effects on fitness than abiotic environments when ignoring whether those environments were local versus foreign. Finally, biotic effects were stronger at low latitudes, and abiotic effects were stronger at high latitudes. Our qualitative analysis revealed that the lens through which local adaptation has been examined differs for abiotic and biotic factors. It also revealed biases in the design and implementation of experiments that make quantitative results challenging to interpret and provided directions for future research.

Keywords: meta-analysis, metasynthesis, reciprocal transplant, latitudinal gradient, life history, natural selection.

Introduction

Spatial variation in selection can shape phenotypic and genomic diversity through local adaptation. Local adaptation of populations is undoubtedly influenced by both abiotic and biotic factors, and most empirical studies cannot discern their relative contribution. In the subset of studies that manipulate environments, most have focused on either abiotic or biotic factors in isolation and have been informed by different bodies of literature (e.g., abiotic: Turesson 1922; Clausen et al. 1940; biotic: Van Valen 1973; Wolf et al. 1998; Thompson 2005).

Understanding the context dependence of local adaptation driven by abiotic and biotic factors not only provides insight about evolutionary processes but also may be important in applied settings. For example, large-scale restoration plantings (e.g., plant reintroductions: Godefroid et al. 2011; Guerrant 2012) attempt to maximize plant performance and reintroduction success by sourcing from natural populations physically close to the planting site or from similar abiotic environmental conditions. However, rarely do restoration planners have the information to fully account for local adaptation or maladaptation to biotic factors (Handel 2012; Perring et al. 2015). Similarly, the interaction of abiotic and biotic factors may drive the evolution of species distributions and range boundaries under climate change. For example, establishment of new populations of *Clarkia xantiana* beyond its current range boundary was limited by herbivory, the influence of which depended on the abiotic environment (Benning et al. 2019;

---

[*] These authors contributed equally to this work.

[†] Corresponding authors; email: rbriscoe@umn.edu, moeller@umn.edu.

ORCIDs: Briscoe Runquist, https://orcid.org/0000-0001-7160-9110; Gorton, https://orcid.org/0000-0002-4101-2257; Yoder, https://orcid.org/0000-0002-5630-0921; Deacon, https://orcid.org/0000-0002-6180-9888; Grossman, https://orcid.org/0000-0001-6468-8551; Kothari, https://orcid.org/0000-0001-9445-5548; Lyons, https://orcid.org/0000-0002-8117-8710; Sheth, https://orcid.org/0000-0001-8284-7608; Tiffin, https://orcid.org/0000-0003-1975-610X; Moeller, https://orcid.org/0000-0002-6202-9912.

Am. Nat. 2020. Vol. 195, pp. 000–000.
DOI: 10.1086/707322

Benning and Moeller 2019). With global climate change, species distributions and biotic interactions will continue to shift and influence local adaptation (Thuiller et al. 2008; Tylianakis et al. 2008; Yates et al. 2010; Valladares et al. 2014).

Evolutionary ecologists have used both theoretical and experimental approaches to explore the conditions under which local adaptation is expected to occur and how it can be detected (reviewed in Kawecki and Ebert 2004; Poulin and Forbes 2012; Savolainen et al. 2013; Tiffin and Ross-Ibarra 2014). Multiple meta-analyses have quantified local adaptation and spatially variable selection in response to either the abiotic or the biotic environment (Hoeksema and Forde 2008; Leimu and Fischer 2008; Hereford 2009; Siepielski et al. 2013) and have identified key factors that affect the likelihood of observing that adaptation. Consistent with expectations on the efficacy of selection, local adaptation to abiotic environments is more likely when populations are large (Leimu and Fischer 2008) and environmental differences between habitats are more extensive (Hereford 2009). Adaptation to biotic variation is more likely for specialized interactions (Lajeunesse and Forbes 2002) and for the species that have a higher rate of migration over a given distance (e.g., a parasite that has a greater dispersal distance than its host: Greischar and Koskella 2007; Hoeksema and Forde 2008). Last, local adaptation may depend on the interaction between the abiotic and biotic environment. For example, a recent meta-analysis focusing on arbuscular mycorrhizal fungi showed that local adaptation to host plants depended on the soil environment (Rúa et al. 2016). Nevertheless, these meta-analyses do not allow for direct comparison of the relative importance of abiotic and biotic factors in driving local adaptation. To fill this gap, we integrated a quantitative meta-analysis and a qualitative metasynthesis to summarize the findings of local adaptation experiments that explicitly consider both the abiotic and the biotic environment.

When and where abiotic versus biotic environments are expected to be the primary driver of adaptation has been the subject of considerable debate. For instance, life-history variation has been argued to modulate the extent to which organisms experience biotic challenges. Ephemeral life histories may reduce the importance of biotic factors by allowing organisms to escape exposure to enemies, whereas biotic factors may be more important for long-lived organisms that are exposed to a broader array of predators, parasites, and competitors (e.g., Feeny 1976; Smilanich et al. 2016). Researchers also have argued that biotic interactions are stronger in the tropics, where abiotic environments are more stable, whereas abiotic challenges may more strongly influence the evolution of organisms at high latitudes (Darwin 1859; Wallace 1878; Dobzhansky 1950). MacArthur (1972) and Janzen (1973) both hypothesized that this latitudinal variation explains greater specialization and stronger coevolution in the tropics, a hypothesis supported by studies showing that biotic interactions are stronger at low than at high latitudes (Schemske et al. 2009; LaManna et al. 2017; Roslin et al. 2017; Hargreaves et al. 2019; but see HilleRisLambers et al. 2002; Anstett et al. 2016).

A growing body of studies testing for local adaptation examine both abiotic and biotic sources of selection using fully factorial designs. These studies provide direct comparisons of abiotic and biotic sources of selection under conditions in which researchers have an a priori expectation that both factors will have measurable effects on fitness. In this article, we use both a quantitative meta-analysis and a formal qualitative metasynthesis (fig. 1) to summarize and synthesize the findings of these studies. The studies we examined were designed to test for local adaptation, but they could have revealed local maladaptation or a lack of local adaptation (Brady et al. 2019). A quantitative meta-analysis allows for a fair comparison across experiments and systems (Hillebrand and Gurevitch 2016) because it statistically combines weighted effect sizes from individual studies into standardized effect sizes (Côté and Reynolds 2012; Koricheva and Gurevitch 2014). We use a quantitative meta-analysis to test whether (1) there is greater local adaptation to abiotic or biotic factors, (2) the magnitude of fitness effects (e.g., local adaptation or maladaptation) is greater in response to abiotic versus biotic factors, (3) the magnitude of local adaptation and fitness effects are mediated by life history and taxonomy, and (4) the strength of local adaptation (and fitness effects of treatments) is related to latitude and whether those relationships differ for abiotic and biotic factors.

A qualitative metasynthesis also uses a systematic approach to extract content from articles; however, metasyntheses focus on extracting text from the introduction, methods, and discussion sections rather than summarizing quantitative results (Dixon-Woods et al. 2005). The primary goal of a qualitative metasynthesis is to identify common themes and areas of divergence emerging from the literature and to develop new interpretations on a topic. This approach has rarely been applied in ecology and evolutionary biology. With our qualitative analysis, we address how the context and framing of studies testing for local adaptation to abiotic and biotic factors (1) influences the design, results, and interpretation of those results and (2) contributes to the interpretation of the quantitative meta-analyses.

Methods

Literature Review

We collected relevant studies and made initial decisions about their inclusion based on prevailing standards for

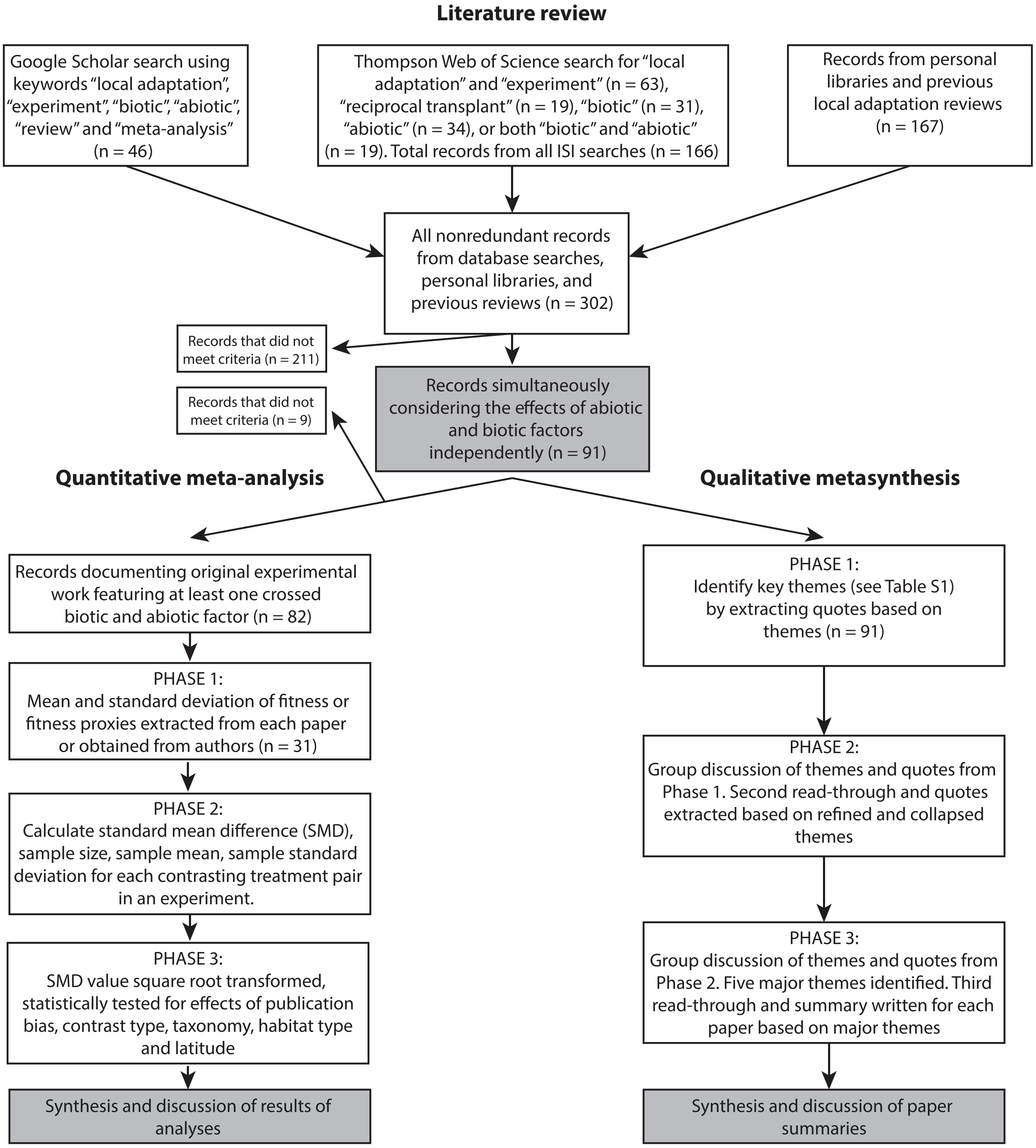

Figure 1: PRISMA (preferred reporting items for systematic reviews and meta-analyses) diagram explaining selection of articles for literature review as well as the quantitative meta-analysis and qualitative metasynthesis approaches.

both quantitative meta-analysis (Koricheva and Gurevitch 2014) and qualitative metasynthesis (fig. 1; Noblit and Hare 1988). We conducted searches in February 2015 using both Google Scholar (https://scholar.google.com/) and ISI Web of Science (https://webofknowledge.com/). We conducted a second search in March 2019 to update the database using Google Scholar and our personal libraries. On Google Scholar, we conducted a single search for the terms "local adaptation," "experiment," "biotic," and "abiotic," with records excluded if they included the term "review" or "meta-analysis." This Google Scholar search returned tens of thousands of relevance-ranked records. We reviewed these in descending order of relevance until approximately 30 consecutive records were not suitable for inclusion, about 300–350 records deep in the list for both search rounds. On ISI Web of Science, we conducted five searches, each of which included "local adaptation" paired with another one or two keywords: "experiment," "biotic," "abiotic," "biotic" and "abiotic," or "reciprocal transplant." These searches returned 2005 records, all of which we reviewed for initial suitability. Finally, we added a number of articles included in previous meta-analyses of local adaptation or that we had previously identified as being relevant.

A single investigator (J. B. Yoder) briefly reviewed the search results (2015: $n = 357$; 2019: $n = 390$) to identify all articles that appeared to describe original work that involved a measure of fitness in response to at least one abiotic and at least one biotic manipulation, with abiotic and biotic manipulations crossed. This selection process resulted in 91 articles that were included in the qualitative analysis; further inspection revealed that 82 articles were experimental and were included in the quantitative analysis (table A1, available online).

Quantitative Meta-analysis

Data Extraction. First, we quantified the magnitude of local adaptation to abiotic and biotic environments, which required the strict criterion that we could identify "home" versus "away" environments for each genotype/population (Kawecki and Ebert 2004; Leimu and Fischer 2008). Second, we relaxed that criterion to include more experimental comparisons and more broadly examine whether the effect sizes of fitness contrasts differed between abiotic versus biotic environments. Both of these contrast types were also parsed by taxonomic group (plants, bacteria, animals). Third, we tested the hypothesis that the effect size of biotic contrasts was greater at low than at high latitudes and that abiotic contrasts were greater at high than at low latitudes, consistent with the hypothesis that the strength of biotic interactions is greater in the tropics than in the temperate zone and that abiotic factors have greater influence in temperate zones. There were 51 articles where we were unable to obtain the appropriate data either because the experiments were not fully factorial or because the data were not presented in the article or an online archive and authors did not reply to our requests. In total, we extracted data from 31 articles representing 57 species (compiled by four authors: J. B. Yoder, N. J. Deacon, S. Kothari, S. N. Sheth; table A1). Four species were each represented in two studies (*Chamaecrista fasciculata*, *Daphnia magna*, *Elymus glaucus*, *Nassella pulchra*), which resulted in some nonindependence in our data set.

Several articles examined multiple abiotic or biotic factors, the same factors in multiple species, or the same factors in multiple populations of a single species. We defined an "experiment" as each iteration of the full factorial test for effects of a single biotic factor and a single abiotic factor on individuals within a single biological unit (i.e., the same species, population, or family). Thus, an article reporting experiments testing the effect of water supplementation and the presence of competitors on plants grown from seed originating from two source populations would count as two separate experiments: effects of water and competitors on samples from each of the two populations.

Local-Foreign Contrasts. To determine whether there was greater local adaptation to abiotic or biotic factors, we used the local-versus-foreign criterion because it is most relevant to the process of local adaptation—natural selection acts on genetically based variation in fitness within habitats (Kawecki and Ebert 2004). To do this, we compared the mean fitness or fitness proxy of the "local" genotype/population with the "foreign" genotype/population within the same environment ("local-foreign criterion"; fig. 2*A*, 2*B*; Kawecki and Ebert 2004). Higher fitness of the local genotype compared with the foreign genotype (i.e., positive contrasts) was considered evidence of local adaptation, whereas the opposite pattern (i.e., negative contrasts) indicated maladaptation (Leimu and Fischer 2008). The use of this contrast type required that we could identify either the abiotic or biotic "home" environment in the experiment. Genotypes/populations where we could not identify a home experimental environment were not included for these contrasts. There were three mutually exclusive types of local-foreign contrasts: (1) genotype is local to abiotic environment, (2) genotype is local to biotic environment, and (3) genotype is local to both abiotic and biotic environments.

In a subset of experiments from which we extracted local-foreign contrasts, biotic environments were treated as a presence/absence variable (e.g., herbivory vs. no herbivory). In these cases, there was no clear home biotic environment. For these studies, we quantified the contribution of biotic interactions to the degree of local adaptation to abiotic environments by comparing the local-foreign contrasts from the same abiotic environment in the presence versus absence of the biotic interaction (i.e., "biotic influence contrasts"; fig. 2*A*, 2*B*).

Fitness Contrasts in Abiotic and Biotic Environments. To determine whether the magnitude of fitness effects of abiotic and biotic factors differ even if those differences are not consistent with strict local adaptation, we compiled a data set for which we no longer required genotypes/populations

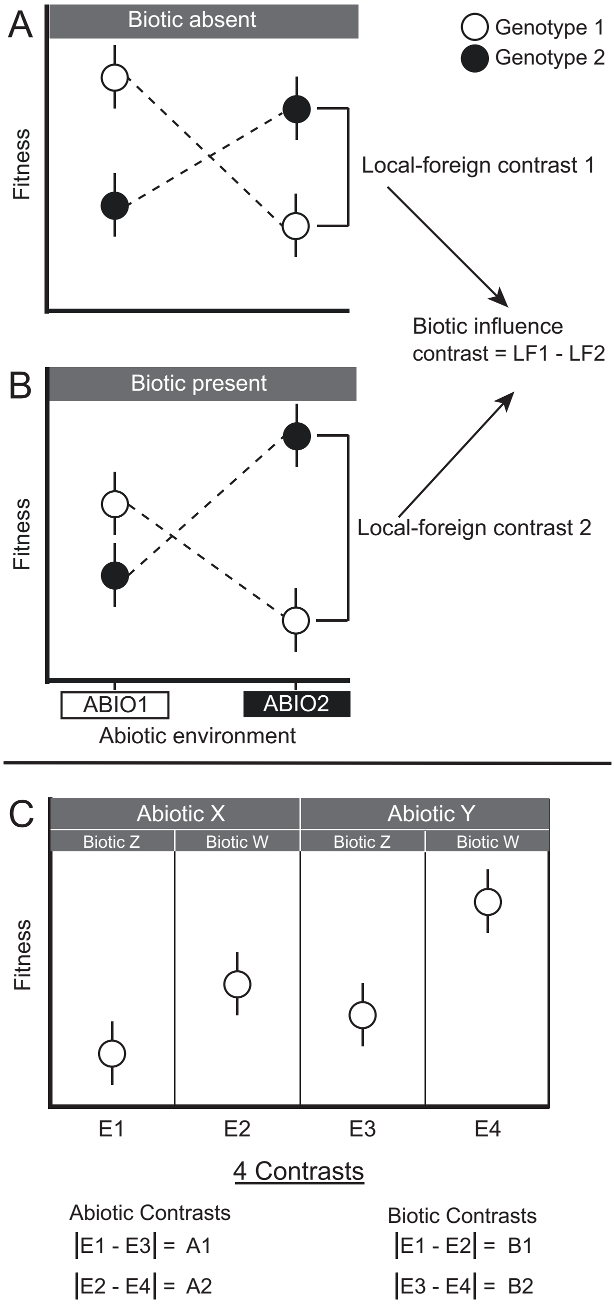

Figure 2: Diagrams illustrating contrast types used in our quantitative meta-analysis. *A* and *B* depict local-foreign contrasts and biotic influence contrasts, and *C* depicts the fitness contrasts in abiotic and biotic environments. In *A* and *B*, genotype 1 is the local genotype for abiotic environment 1 (ABIO1), and genotype 2 is the local genotype for abiotic environment 2 (ABIO2). Contrasts in *A* and *B* were calculated within one environment between different genotypes/populations. Local-foreign contrasts in these examples are positive and indicative of local adaptation; however, contrasts in the data set could also be negative, indicating local maladaptation, or zero, indicating a lack of local adaptation. Contrasts in *C* were calculated between environments on the same genotype/population. In *A*, biotic absent refers to experimental treatments where there was no biotic interaction (e.g., no competition). In *B*, biotic present refers to experimental treatments where there was a biotic interaction (e.g., competition). The biotic influence contrast was calculated by subtracting the difference between the value of the local-foreign contrast with and without a biotic interaction. In *C*, E1–E4 refers to four unique contrasts that combine the different abiotic and biotic treatment levels.

to have a home environment. We then estimated the strength of the effect as the absolute value of the difference in mean fitness of a single genotype/population between environments (either abiotic or biotic; fig. 2*C*).

Many articles contained complex designs with multiple experimental setups. For each experiment (defined above, in "Data Extraction"), we identified two types of contrasts: (1) the genotype/population experienced different abiotic treatments and the same biotic treatment (abiotic contrasts; fig. 2*C*) and (2) the genotype/population experienced different biotic treatments and the same abiotic treatment (biotic contrasts; fig. 2*C*).

Calculation of Standardized Effects. For each contrast (local-foreign and fitness contrasts), we calculated the standard mean difference (SMD) between treatment groups *i* and *j* as

$$\mathrm{SMD} = \frac{\bar{X}_i - \bar{X}_j}{S_{\mathrm{within}}}, \tag{1}$$

where n is the sample size, $\bar{X}$ is the sample mean, and S_{within} is the sample standard deviation within treatment, calculated as

$$S_{\mathrm{within}} = \sqrt{\frac{(n_i - 1)^2 S_i + (n_j - 1)^2 S_j}{n_i + n_j - 2}} \tag{2}$$

(Lipsey and Wilson 2001, eqq. [3.21]–[3.24]). For local-foreign contrasts, a larger SMD would be consistent with greater local adaptation; for fitness contrasts, a larger SMD would be consistent with a greater effect of abiotic or biotic environments.

Statistical Analysis. We conducted all data analysis in R (ver. 3.3.2; R Core Team 2016). For fitness contrasts in abiotic and biotic environments (i.e., the absolute value of the fitness difference between the same genotype/population in different environments), we used square-root-transformed SMD values so that the residuals of the analysis better approximated a normal distribution; local-foreign contrasts and biotic influence contrasts were not transformed. We tested for a publication bias by determining whether the absolute value of SMD was correlated with the mean sample size for each pair of contrasted treatment groups ($(n_i + n_j)/2$). A significant negative correlation between reported effect sizes and sample size is consistent with a bias toward publication of statistically significant effects (Nakagawa et al. 2017).

For the local-foreign and biotic influence contrasts, we used linear mixed effects models to test for the effects of taxonomy (plant, animal, bacteria) and local environment (abiotic, biotic, both). For the fitness contrasts in abiotic and biotic environments (i.e., the same genotype/populations in different environments), we tested for the effects of taxonomy plant, animal, bacteria and treatment type (abiotic, biotic). For both the local-foreign and the fitness contrasts from plant studies, we used linear mixed effects models and tested for an effect of life history (annual, perennial) as well as local environment (local-foreign contrasts, biotic influence contrasts) or treatment type (fitness contrasts).

In all models, we tested both main effects and interactions. We tested the effects of each variable by comparing corrected Akaike information criterion (AICc) values (Cavanaugh 1997) of fitted models and estimated the variation in SMD explained by the best-fit models within each comparison as total adjusted R^2 (conditional R^2 for generalized linear mixed models: variance explained by entire model, including fixed and random effects). We fitted all models using the lmer function from the lme4 package (Bates et al. 2015) and calculated R^2 using the r.squaredGLMM function provided in the MuMIn package (Barton 2009). In all models, we included experiment identity as a random effect to account for possible nonindependence of treatment groups of the same species within the same experiment and account for within-study variation. To test post hoc hypotheses about factors that explained variation in SMD, we used the bootstraps function provided in the rsample package (ver. 0.0.2; Kuhn and Wickham 2017) to bootstrap the data, stratifying the bootstrap randomization by the articles from which the data were drawn.

We also tested for an association between latitude and mean SMD for local-foreign contrasts and fitness contrasts in abiotic and biotic environments. For field experiments, latitude was the location of the common gardens, and for laboratory experiments latitude was the location of the source populations. Biotic interactions have been hypothesized to be stronger at low latitudes. If this was reflected in our data, we would expect a negative relationship between biotic SMDs and latitude. We would also expect the correlation with latitude for biotic SMDs to be more strongly negative than that for abiotic SMDs. To test whether there was a negative relationship between biotic SMDs and latitude and whether latitude was more strongly negatively correlated with biotic than abiotic SMDs, we calculated the Pearson's correlation coefficient for abiotic and biotic contrasts separately. These correlations were calculated for both the local-foreign contrasts and the fitness contrasts. For local-foreign contrasts, we excluded contrasts with a local environment of "both." Because latitude and experiment are highly colinear, we did not include experiment in this analysis and calculated correlation coefficients using all SMDs as independent data points; we assessed the significance of observed correlations using stratified bootstrapping. We then tested for the difference between correlation coefficients using a Fisher z-transformation and a one-tailed test.

We also subsetted the data set of local-foreign contrasts to include only contrasts that were potentially indicative of local adaptation (i.e., SMD > 0) and biotic influence contrasts to include at least one contrast potentially indicative of local adaptation (i.e., one of the pair of local-foreign contrasts used in the metric had SMD > 0). We used these data sets to investigate how abiotic and biotic environments may influence the magnitude of local-foreign contrasts where local adaptation may be occurring. We present the results of these analyses in the supplemental PDF (available online).

Qualitative Metasynthesis

A qualitative metasynthesis differs from less formal literature reviews that are commonly published in ecology and evolutionary biology (Vetter et al. 2013). Both approaches involve discussion of the major themes of a given topic, but metasynthesis uses a structured process for selecting articles and considering research questions and so is more similar to a quantitative meta-analysis (Noblit and Hare 1988; Dixon-Woods et al. 2005; see table S5 for a comparison of a literature review, a meta-analysis, and a metasynthesis; tables S1–S13 are available online).

The qualitative metasynthesis (completed by R. D. Briscoe Runquist, A. J. Gorton, J. J. Grossman, and M.P. Lyons) consisted of an iterative process of group discussions followed by extraction of direct quotes or paraphrases from each article using the original 69 articles from the 2015 search. The metasynthesis had three phases (fig. 1). In phase 1, we identified key themes that we deemed were important to the local adaptation literature as well as themes that emerged from our initial reading of articles (table S6: phase 1 themes). Two readers then read each article and identified and extracted quotes that were relevant to each theme. In phase 2, we discussed the quotes extracted from the phase 1 reading and refined our themes into broader categories (table S6: phase 2 themes, headers). The purpose of this was both to avoid splitting content across similar themes and to eliminate themes that were relevant to only a few articles. We then repeated the approach from phase 1 and conducted a second reading (with the same two readers per article) to extract quotes based on the refined themes.

We began phase 3 with a discussion of the themes and quotes extracted during phase 2 and then identified five major themes that captured and synthesized the content of the quotes (table S6: phase 3 themes; table S7). A single reader then read each article and used the quotes generated from the two readers in phase 1 and 2 to write a summary of each of the five themes. We used these summaries as our final "data set." With the updated database in 2019, two authors (R. D. Briscoe Runquist, D. A. Moeller) read each article to check for themes identified in the original analysis and note any additional themes that emerged. New articles highlighted the same general themes identified previously, and we did not find any new thematic elements in the updated set.

Results

Quantitative Meta-analysis

Our final round of data extraction yielded 31 articles (published from 1995 to 2018; table A1), which reported 62 experiments containing 389 local-foreign contrasts (from 24 articles), 179 biotic influence contrasts (from 13 articles), and 4,890 fitness contrasts in abiotic and biotic environments (from all 31 articles). Seventeen articles reported on field experiments, nine reported on greenhouse experiments, and five reported on laboratory experiments. Plants were the focus of 21 articles, whereas invertebrates, vertebrates (all amphibians), and bacteria were the focus of five, three, and two articles, respectively. Studies included a wide range of biotic interactions, including competition, mutualism, parasitism, and predation (table A1). Of the biotic influence contrasts, 141 involved plants, 26 involved animals, and 12 involved bacteria. Given the large number of studies of plants, we parsed these by life history. Of 47 species represented, 17 were annuals and 30 were perennials or biennials. There was also a strong bias toward species from the Northern Hemisphere; all articles for which we could ascertain locations reported experiments on populations from 20° latitude or farther north, with the median of 38.9°.

Publication Bias. For the local-foreign contrasts, the correlation between mean SMD within experiments and sample size was weak and not different from random expectation (Pearson's $r = -.07$, $P_{\mathrm{df}=26} = .69$). For fitness contrasts, the correlation between sample size and SMD in abiotic treatments was also weak and not different from random expectation ($r = -.06$, $P_{\mathrm{df}=60} = .66$). By contrast, in the biotic treatments this correlation was statistically significant ($P_{\mathrm{df}=58} = .03$) although not particularly strong ($r = -.29$). These results suggest that some publication bias affects estimates of the strength of local adaptation or maladaptation; however, this potential bias seems to be inconsistent across treatment types and not indicative for an overall signal of local adaptation (i.e., the local-foreign contrasts).

Local Adaptation. Across all experiments, approximately half of all local-foreign SMDs were positive ($N = 186/389$, or 47.8%), indicative of potential local adaptation. However, there was not strong overall evidence of local adaptation; the mean SMD of all local-foreign contrasts was greater than but not significantly different from zero ($N = 389$; mean ± SD: $.10 \pm .09$; stratified bootstrap $P = .13$). We note, however, that the estimated magnitude of the SMD was similar to that from previous meta-analyses of local adaptation (Hoeksema and Forde 2008; Leimu and Fischer 2008; Hereford 2009), and thus we consider the studies in our analysis to be broadly representative of local adaptation studies (i.e., those that examine both biotic and abiotic factors are not fundamentally different from those that examine only abiotic or biotic factors). We found a similar result when we excluded three studies of nonnative species (mean SMD ± SE: $.07 \pm .09$; $P = .25$); therefore, we included all species in our remaining analyses.

The mean SMD of local-foreign contrasts varied among local environments (abiotic, biotic, or both) and taxonomy (animal or plant; we excluded the single study on bacteria that provided local-foreign contrasts). The best-fitting model included taxonomic category, local environment, and their interaction (AICc = 1,391.4; $R^2 = .24$). This model was a better fit to the data than the next best model, which included only the effect of taxonomy ($\Delta\mathrm{AICc} = 15.5$; $R^2 = .32$; table S8; fig. 3). Across all taxa and for animals, there was a stronger signal of local adaptation to biotic environments than to abiotic environments or to both together, whereas for plants there was a weak signal of local maladaptation to biotic environments and local adaptation to abiotic environments (fig. 3); however, these differences were not greater than what would be expected by chance, based on the bootstrapping test of pairwise differences (bootstrap $P > .05$ in all cases). For plants, the inclusion of life history did not significantly improve model fit over a model including only the random effect of experiment (for the model with only random effect, AICc = 1,141.5, $R^2 = .02$; for the model with life history, $\Delta\mathrm{AICc} = 3.1$, $R^2 = .03$; table S9).

The magnitude of the local-foreign contrast was greater in the presence than in the absence of a biotic interactor (i.e., biotic influence contrasts); the effect was significant across taxonomic categories (mean ± SE: for presence, $.20 \pm .15$; for absence, $-.12 \pm .14$; bootstrap $P = .03$). This result suggests that foreign genotypes may not have the capacity to effectively tolerate combined abiotic

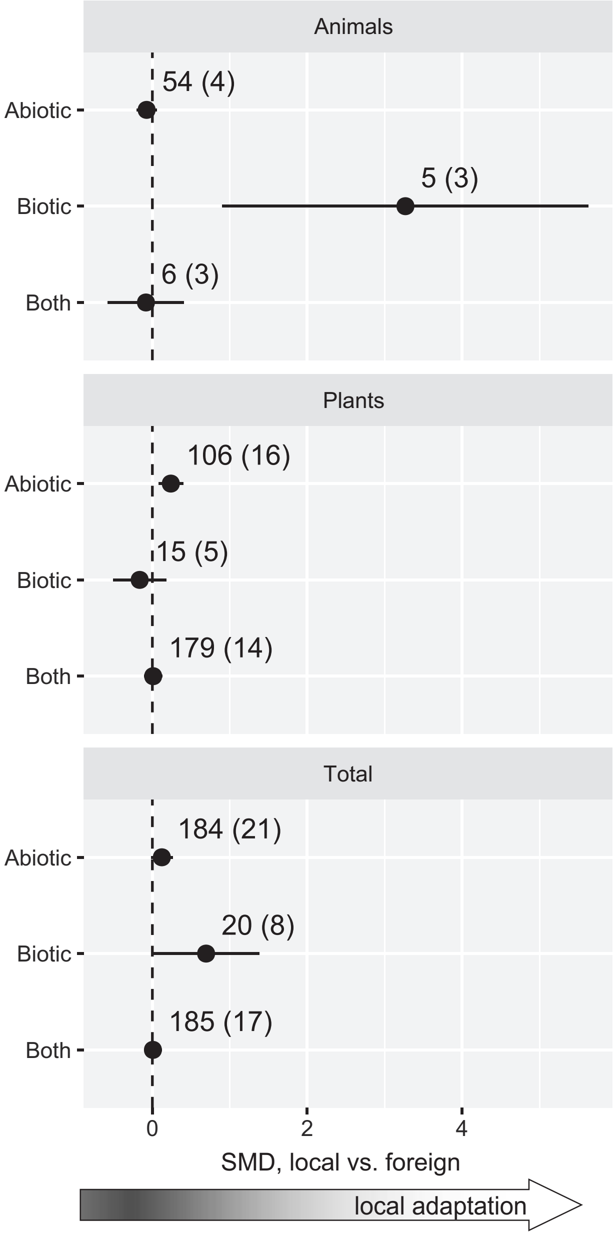

Figure 3: Local-foreign contrast values (mean ± SE) in relation to abiotic environments, biotic environments, or both abiotic and biotic environments identified as local, for animals, plants, and across the full data set. Positive values of standard mean difference (SMD) indicate local adaptation, and negative values of SMD indicate local maladaptation. Numbers adjacent to each point range indicate the number of contrasts and, in parentheses, the number of independent experiments. No pairwise differences were greater than what would be expected by chance (bootstrap $P > .05$ in all cases).

and biotic stress and the negative effects of abiotic conditions on foreign genotypes is manifest only in the presence of biotic factors. However, results differed for plants and animals. A model explaining variation in the magnitude of biotic influence contrasts with taxonomy (plant or animal) had marginally better fit than a model including only the random effect of experiment (for the full model, AICc = 701.6, $R^2 = .35$; for the simpler model, ΔAICc = .9, $R^2 = .33$; table S10). Mean biotic influence contrasts for plants and animals were greater than what would be expected by chance, based on the stratified bootstrap (bootstrap $P < .001$). For plants, the mean biotic influence contrast was significantly greater than zero (fig. 4*A*; mean ± SE: .51 ± .30; bootstrap $P = .001$), indicating that the local advantage was greater in the presence of a biotic interactor. For animals, however, the mean biotic influence contrast was significantly less than zero (fig. 4*A*; mean ± SE: −.80 ± .16; bootstrap $P <$ .001), indicating that the difference between local and foreign genotypes was less pronounced in the presence than in the absence of a biotic interactor. Only two experiments provided data for the calculation of biotic influence contrasts in animals—one on *Rana arvalis* (Egea-Serrano et al. 2014), the other on *Crassostea virginica* (Hughes et al. 2017). However, the biotic interaction in both of these studies was predation, so it is possible that this result reflects a general effect of predators reducing the advantage of otherwise locally adapted genotypes.

For plants, a model including life history had essentially the same fit to the data as a model including only the random effect of experiment identity (for the simpler model, AICc = 614.1, $R^2 = .30$; for the model including life history, ΔAICc = .8, $R^2 = .32$; table S11). For both annuals and perennials, the mean biotic influence contrast was significantly greater than zero (fig. 4*B*; bootstrap $P =$ .03 and .02 for annuals and perennials, respectively) but not significantly different from each other (fig. 4*B*; bootstrap $P = .20$).

Fitness Effects of Abiotic and Biotic Environments. Across the full data set, the fitness effects of biotic environments were greater than the fitness effects of abiotic environments (mean ± SE: for biotic environments, 1.30 ± .04; for abiotic environments, 1.07 ± .03; bootstrap $P < .001$). The best-fit model included the random effect of experiment, treatment type (abiotic or biotic environment), organism taxonomy (plant, animal, or bacteria), and an interaction between treatment type and taxonomy (AICc = 7,000.0, $R^2 = .48$; table S12); this was a better fit than the next-best model, which contained only the random effect of experiment (ΔAICc = 38.2, $R^2 = .43$). For both plants and bacteria, biotic environments had greater effects than abiotic environments; for animals, the reverse was true. For all three taxonomic groups, the differences between abiotic and biotic environments were greater than what would be expected by chance (fig. 5; bootstrap $P = .007$ for animals, bootstrap $P < .001$ for plants and bacteria).

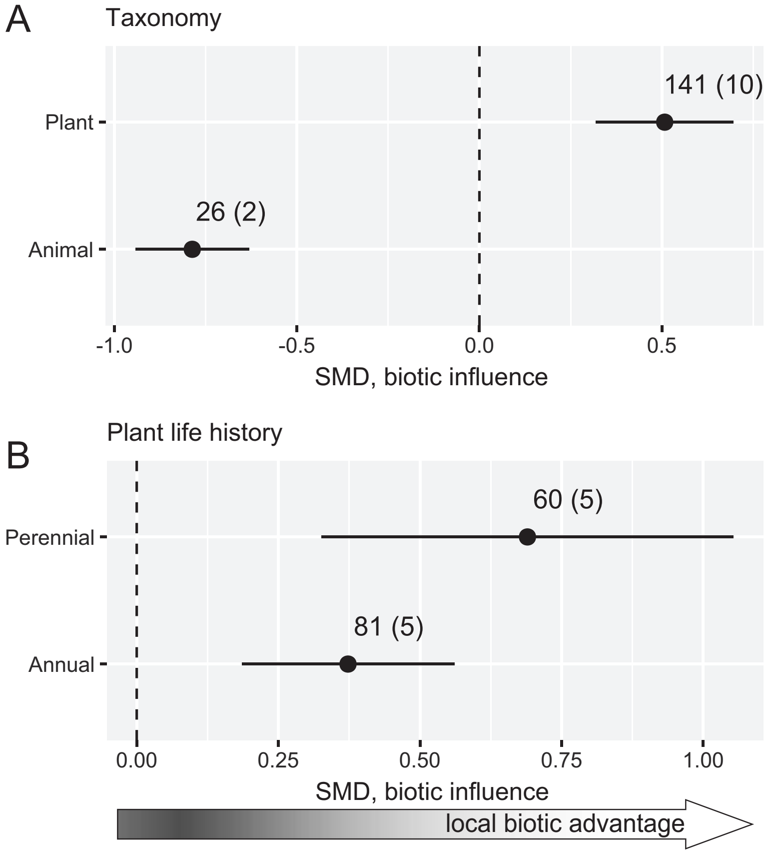

Figure 4: Biotic influence contrasts (mean ± SE) in plants or animals (*A*) and in perennial or annual plants (*B*). Positive values of standard mean difference (SMD) indicate that the local-foreign contrast was greater in the presence than in the absence of biotic interactors, and negative values of SMD indicate that the local-foreign contrast was greater in the absence than in the presence of biotic interactors. Numbers adjacent to each point range indicate the number of contrasts and, in parentheses, the number of independent experiments. Mean SMD is significantly different from zero for both plants and animals (bootstrap $P = .001$ for plants, $P < .001$ for animals), and the difference between groupings is greater than what would be expected by chance (bootstrap $P < .001$). Mean SMD is significantly greater than zero for both annuals and perennials (bootstrap $P = .03$ for annuals, .02 for perennials), but the difference between annuals and perennials is not greater than what would be expected by chance (bootstrap $P = .26$).

For plants, a model including treatment type, life history, and an interaction between them was the best fit and was better than the next best, which included only the random effect of experiment (AICc = 6,262.1, $R^2 = .19$; for the random-only model, ΔAICc = 15.7, $R^2 = .18$; table S13). Fitness effects of biotic environments were significantly greater than those of abiotic environments for annuals but not for perennials (fig. 6; bootstrap $P < .001$ for annuals, $P = .16$ for perennials).

Latitudinal Gradient. Latitude data were available for 275 local-foreign contrasts (from 23 experiments) and for 2,501 fitness contrasts in biotic and abiotic environments (from 44 experiments). Using all local-foreign contrasts, we found that local adaptation at high latitudes was significantly greater than that at low latitudes (Pearson's $r = .16$, bootstrap $P = .002$; fig. 7*A*). The strength of local adaptation (local-foreign contrasts) to abiotic factors was positively correlated with latitude (Pearson's $r = .20$, bootstrap $P = .005$), whereas for biotic factors the correlation with latitude was negative and near zero (Pearson's $r = -.015$, bootstrap $P = .55$; fig. 7*A*). These correlations were not significantly different from each other (Fisher *z*-transformation score = .77, one-tailed $P = .22$), although we note that the estimate of the correlation between latitude and the local adaptation to biotic factors was based on few contrasts.

The magnitude of fitness effects of biotic environments at low latitudes was significantly greater than that at high latitudes (Pearson's $r = -.08$, bootstrap $P < .001$; fig. 7*B*); fitness effects of abiotic environments were larger at high latitudes (Pearson's $r = .08$, bootstrap $P < .001$; fig. 7*B*).

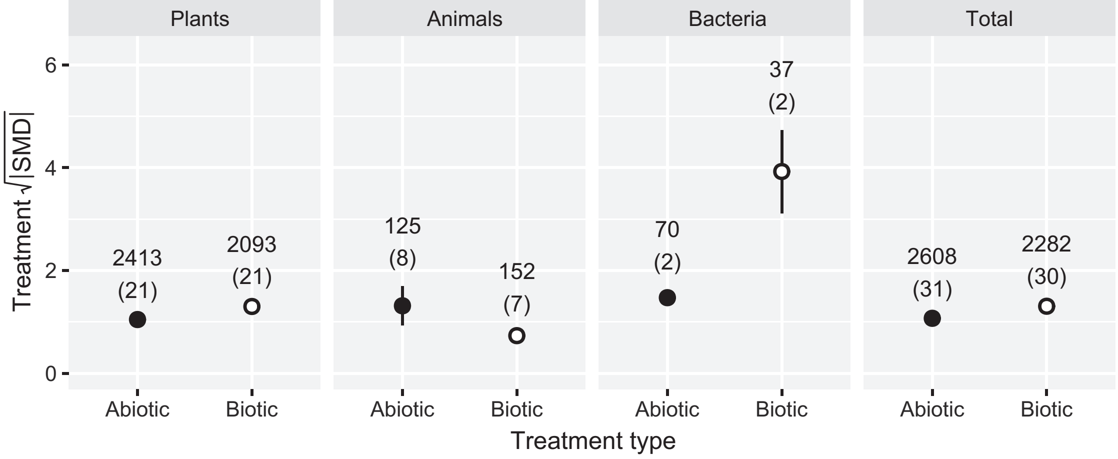

Figure 5: Absolute value of standard mean difference (SMD; mean ± SE) for fitness contrasts in biotic and abiotic environments, parsed by broad taxonomic group (plants, animals, bacteria) and across taxonomy (total). All values of SMD (and hence square-root-transformed SMD) are positive; larger values indicate larger effects on fitness due to the differences in environments. Numbers above each point range indicate the number of contrasts and, in parentheses, the number of independent experiments. Differences between the fitness effects of abiotic and biotic environments are greater than what would be expected by chance for all taxonomic groupings (bootstrap $P = .007$ for animals, $P < .0001$ for plants and bacteria) and overall (Wilcoxon sign-rank test $P = .006$).

This difference in correlations for abiotic versus biotic factors was greater than what would be expected by chance (Fisher z-transformation score $= 5.8$, one-tailed $P < .001$).

Qualitative Metasynthesis

The articles included in the metasynthesis encompassed the full set of 91 articles (fig. 1; table A1), of which 51 reported on field experiments, 23 reported on greenhouse experiments, and 17 reported on laboratory experiments. Plants were the focus of 62 articles, whereas invertebrates, vertebrates, and bacteria were the focus of 12, nine, and eight articles, respectively.

A qualitative synthesis involves discussion of key themes identified from the text of articles included in the analysis (Noblit and Hare 1988). We include a more thorough treatment of our results in the discussion section and here provide only a brief overview of the major findings of the qualitative synthesis. A table with the major themes identified from the synthesis and references to articles used in the analysis are provided in tables S6 and S7. The overarching result of our qualitative analysis is that researchers have clear differences in both their motivation for studying and how they manipulate abiotic and biotic treatments. We found that abiotic treatment levels tended to be continuous and were selected/motivated on the basis of natural gradients or strongly contrasting environments (e.g., serpentine soil, salinity). By contrast, biotic treatment levels were often discrete, reflecting a presence/absence design (e.g., presence/absence of herbivores, mycorrhizae, or competitors), and were often motivated by theory, including the stress-gradient hypothesis (Bertness and Callaway 1994) and coevolutionary theory (Van Valen 1973; Thompson 2005). The biotic interaction studies we analyzed could be grouped into three major categories of interactions: natural enemies, plant-plant interactions, and plant-microbe interactions. We also found that sessile, short-lived organisms were more commonly used as focal species and that many of those species had long historical bodies of literature. The greater

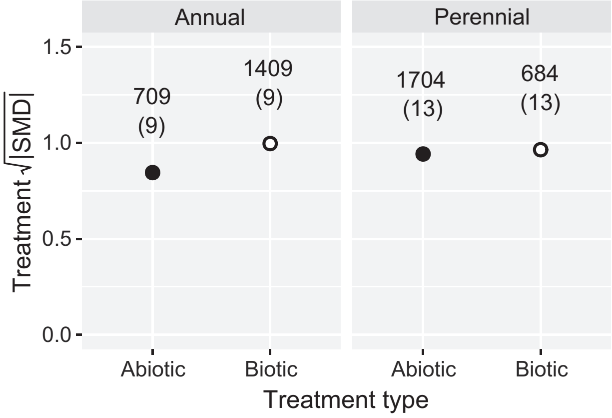

Figure 6: Absolute value of standard mean difference (SMD; mean ± SE) for fitness contrasts in biotic and abiotic environments in plants, aggregated by life-history types. All values of SMD (and hence square-root-transformed SMD) are positive; larger values indicate larger effects on fitness due to the differences in environments. Numbers above each point range indicate the number of contrast values and, in parentheses, the number of independent experiments aggregated.

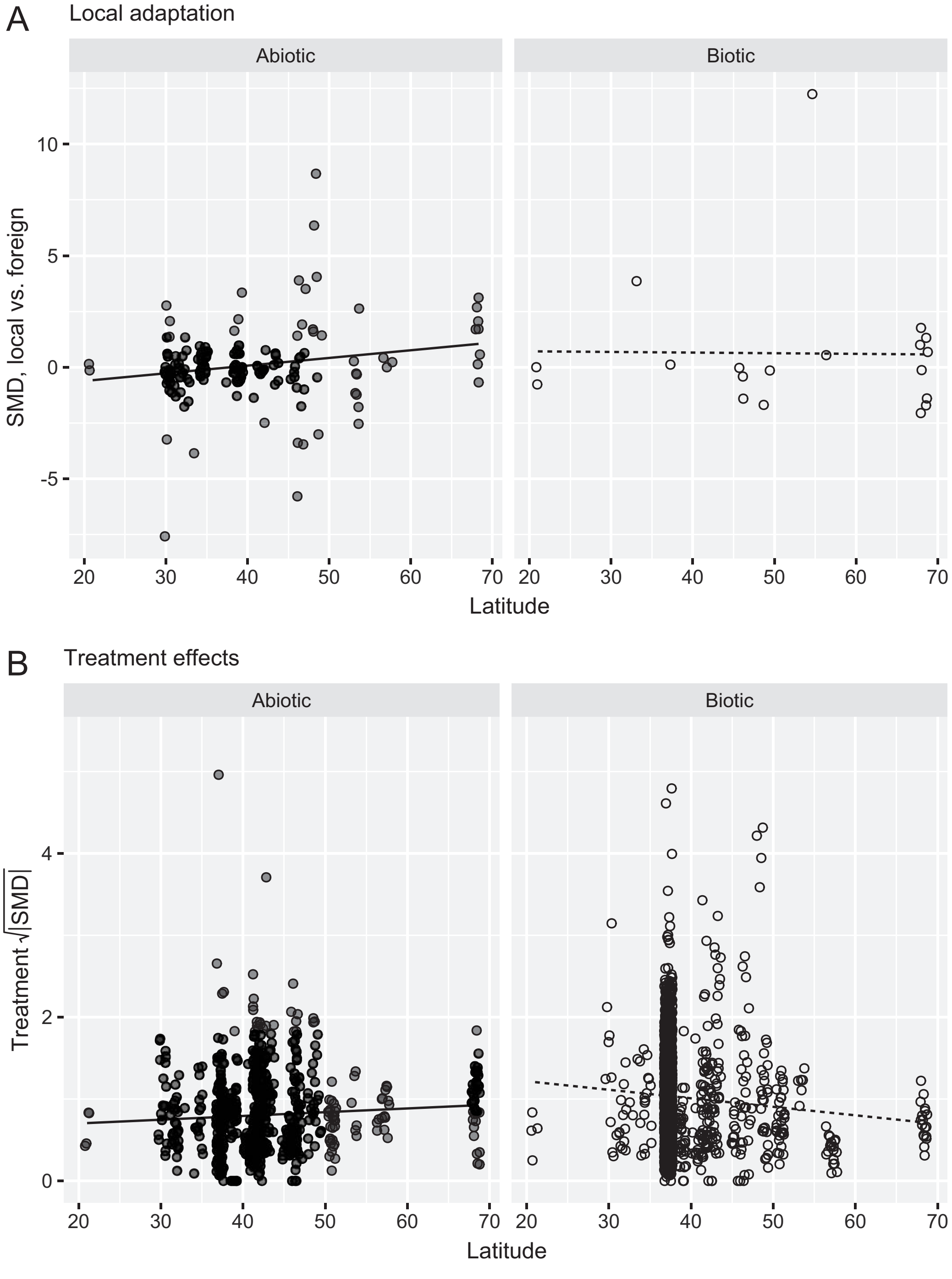

Figure 7: Scatterplots of standard mean difference (SMD) versus source population latitude for local-foreign contrasts (*A*) and for genotype-environment contrasts (*B*) with abiotic (gray-filled circles, *left panels*) and biotic (open circles, *right panels*) environments. Correlations with latitude are greater than expected by chance for local-foreign contrasts in abiotic environments (bootstrap $P = .007$) but not in biotic environments ($P = .53$), and correlations with latitude are greater than expected by chance for fitness effects of both abiotic and biotic environments (bootstrap $P < .001$ in both cases). Points have been jittered on the *X*-axis for greater clarity; in *B*, we eliminated one data point in the figure that had a very high SMD value to make the regression slopes more easily visible. For a version of the figure with all data points, see figure S5.

depth of knowledge available for those species provided substantially more detailed context for study design (e.g., population/genotype selection) and interpretation of experimental results. In addition, most studies were conducted in a single year, and field experiments were conducted at few field sites. Last, we found that many studies, in particular more recent studies, mentioned global change as a motivation for conducting experiments; however, studies rarely included realistic environmental manipulations that were justified on the basis of predictions about global change.

Discussion

We found that the degree of local adaptation (magnitude of local-foreign contrasts) to abiotic environments was modulated significantly by whether biotic interactions were present, and the direction of the effect depended on the focal taxa. This result suggests that local adaptation may often be context dependent due to interactions between abiotic and biotic environments. For example, in stressful abiotic environments, fitness may be considerably lower when competitors reduce available resources or considerably higher when co-occurring organisms ameliorate abiotic stresses. Similarly, Hargreaves et al. (2020) found that biotic manipulations that ameliorated negative biotic interactions put local genotypes at a disadvantage compared with foreign genotypes in a large subset of experiments. These results also indicate that researchers must be cautious when interpreting transplant experiments that simplify biotic aspects of the environment (e.g., eliminate surrounding neighbors). Our synthesis suggests that the most effective transplant experiments are those conducted in realistic environments where complex community interactions are intact or ones that involve manipulation of the biotic environment in order to quantify the extent to which the biotic environment modulates the outcome.

Overall, we did not find strong evidence for a difference in the magnitude of local adaptation to abiotic versus biotic environments. Nevertheless, we did find that the magnitude of fitness contrasts (i.e., fitness differences between the same population/genotype in different environments) differed for abiotic and biotic environments. While biotic environments had stronger fitness effects than abiotic environments overall, this pattern varied among taxonomic groups. The biotic environment had stronger fitness effects for plants and bacteria, but for animals abiotic environments had stronger fitness effects. We also found a significant relationship between latitude and the strength of the effect of the abiotic or biotic environment on fitness (absolute value of environmental effects). Abiotic fitness contrasts were greater in temperate regions; biotic fitness contrasts were greater in subtropical and tropical regions. Local adaptation to abiotic and biotic environments was in the same direction as environmental fitness contrasts, but only the abiotic relationship was significant. We suggest some caution in the interpretation of our results, since very few of the experiments in our meta-analysis were conducted in the arctic or tropics, which compromised our power to detect such a relationship.

These results are consistent with the hypothesis that biotic interactions are stronger at lower latitudes and abiotic selection is greater at higher latitudes, as proposed by Darwin (1859) and Wallace (1878) and formalized by Dobzhansky (1950) and others (Schemske et al. 2009). In a similar meta-analysis by Hargreaves et al. (2020), there was also some evidence that biotic interactions may promote local adaptation more often in the tropics than at high latitudes. Other evidence for such a latitudinal gradient has been found in a number of individual studies, but not others. For example, there is experimental evidence that predation of caterpillars and seeds is greater at low latitudes (Roslin et al. 2017; Hargreaves et al. 2019), but other studies have not found support for stronger biotic interactions at low latitudes (e.g., HilleRisLambers et al. 2002; Moles et al. 2011).

The Design of Local Adaptation Experiments Differs for Abiotic and Biotic Factors

The meta-analysis revealed that biotic environments had stronger fitness effects than abiotic environments, but the pattern was not consistent among taxonomic groups. This result may be interpreted as evidence of greater local adaptation to biotic factors. However, a key theme that emerged from our qualitative analysis was that researchers often chose abiotic and biotic factors to investigate for different reasons and manipulated them using very different approaches. These differences might mean that the results from abiotic- and biotic-focused experiments are not directly relatable. The choice of study system, central question, and experimental design were frequently motivated by prior observation of a natural abiotic gradient or an a priori expectation of local adaptation to a particular abiotic variable. By contrast, biotic factors were often added to make a study more biologically realistic rather than as a primary motivation and were often treated as presence/absence variables (e.g., Sambatti and Rice 2006; Compagnoni and Adler 2014). Only one study cited a naturally occurring biotic gradient as the motivation for an experiment (Abdala-Roberts 2007). Moreover, few investigations of local adaptation to abiotic gradients focused on environments where differences were subtle or not readily apparent. Rather, studies tended to focus on the extremes of abiotic gradients or examined relatively rare environments (table S7: site selection and experimental levels). For example, serpentine soils are relatively rare in nature but common in our data set; whereas some globally important abiotic factors (e.g., soil moisture, macronutrient levels) were the subject of fewer studies. Additionally, in many studies included in our analysis, "site" was considered as an abiotic factor; however, site variation often simultaneously involves both abiotic and biotic variation.

There were also important differences in the design of experimental treatments for abiotic and biotic factors. Abiotic variables were more commonly examined as continuously variable factors (or with multiple levels), whereas biotic variables were more commonly examined as presence versus absence (table S7: biotic interactions). For example, in studies of plants and their microbial symbionts, investigators usually considered the presence versus absence (or home vs. away) of the entire soil microbe community or some particular class of microbes (e.g., mycorrhizae). Similarly, when researchers examined plant-plant competition, they commonly manipulated density by either removing or allowing neighbors to grow in close proximity and less often manipulated multiple levels of density or the identity of the competitor. Last, herbivore and predator/prey interactions were most commonly manipulated using exclosures or by applying pesticides rather than by creating quantitative levels of antagonist density.

Although practical in application, all-or-nothing manipulations may fail to capture most of the variation found in nature. Furthermore, such manipulations do not directly inform our understanding of local adaptation to biotic factors because they often do not correspond with home/away or local/foreign conditions. We recommend that studies seeking to examine local adaptation to both environment types replicate the extent of natural variation of both abiotic and biotic factors in experimental settings. To do this, studies could include realistic, multilevel biotic treatments drawn from knowledge of natural variation. For example, in studies of host-parasite or host-symbiont interactions, including the use of multiple wild-collected strains (e.g., Laine 2008; Heath et al. 2010) is likely to be more informative than studies that use only laboratory-reared strains, especially if those samples represent true local versus foreign communities. Last, systems in which coevolution is important can be particularly challenging for studies of local adaptation. In a host-parasite system, for example, it can be difficult to interpret local adaptation of hosts or parasites because experiments may represent one moment in a continuous process of coevolution, in which local adaptation and maladaptation might both be expected (table S7: biotic interactions). Evaluating the extent of local adaptation in such systems will require multigenerational experiments that can determine whether interactions are stable or the fitness effects of the interacting species are changing through time (e.g., Koskella and Lively 2007; Lopez Pascua et al. 2012; Koskella and Brockhurst 2014).

The focus on extreme abiotic environments or the implementation of biotic factors in extreme treatments (presence/absence) may lead to biased estimates of local adaptation. By extension, our finding that fitness contrasts in biotic environments were greater than fitness contrasts in abiotic environments might reflect experimental bias. Robust comparisons of the relative importance of the abiotic and biotic environment will require additional experiments that use similar approaches to select abiotic and biotic treatment levels. Future experiments will be particularly valuable if they sample a greater range of natural abiotic and biotic environments, and not only where local adaptation is expected a priori. This is particularly important given that it is notoriously difficult to determine the agents of selection (Primack and Kang 1989; Kingsolver et al. 2001; Ridenhour 2005; Wadgymar et al. 2017), and the key selective agents may not be measured or immediately visible. For example, experiments could be designed on the basis of other criteria, such as different spatial scales or the dispersal neighborhood of the organism (Richardson et al. 2014). Environmental variation in abiotic and biotic factors could then be assessed following site selection. Experiments of this type will contribute to estimating the geographic scale at which local adaptation occurs (Richardson et al. 2014) and how such patterns vary from local to continental scales. Alternately, researchers could conduct multifactorial manipulations of the putative abiotic and biotic agents of selection in the field to provide a more robust understanding of the true drivers of local adaptation (Wadgymar et al. 2017).

Short-Lived Organisms and Single-Year Experiments Dominate the Literature and Influence Experimental Approaches

Our synthesis found that the literature is dominated by sessile, short-lived organisms (table S7: taxonomic biases), which is not surprising given the logistics of experiments testing for local adaptation. Because reciprocal transplant field studies require that organisms are tracked, our analyses were generally limited to studies that investigated plants, microbes, or animals that are largely sedentary. For long-lived species, where estimates of lifetime fitness are impractical to obtain, fitness was generally only assessed at early life stages. Experiments using short-lived organisms often provided more complete ecological and evolutionary context, including more detailed justifications for the selection of genotypes, generation of hypotheses, and interpretation of results (e.g., Rolán-Alverez et al. 1997; McCoy et al. 2002; Ortegón-Campos et al. 2012; Pánková et al. 2014). For experiments involving more challenging focal species (e.g., Schoebel et al. 2010; Fey and Cottingham 2011;

Scharf 2011; Echaubard et al. 2014), genotype sourcing was often not environment specific, and the interpretation of results was rarely grounded in a larger understanding of patterns of natural variation. The knowledge base inherent to well-studied systems may perpetuate the use of short-lived organisms and bias our understanding of how local adaptation occurs. Short-lived organisms tend to experience brief windows of the environment (e.g., via niche construction), whereas longer-lived organisms may experience continuous (or episodes of) exposure to environmental stressors across multiple years. The strong bias toward short-lived organisms limits the ability to understand how life history may modulate adaptation and affect the timing of the expression of adaptive genetic variation (Germino et al. 2019).

Finally, we found that few empirical studies included more than two or three study sites, and even fewer conducted experiments in multiple years. Adaptation occurs in the face of fluctuating environments over space and time; thus, results from single-year experiments may fail to identify key selective agents. Additionally, short-term studies may miss crucial phases of the life cycle where local adaptation becomes apparent, particularly for perennial organisms (e.g., Wright 2007; Germino et al. 2019). Although challenging and difficult to fund, long-term studies have proven invaluable because temporal fluctuations in population dynamics and selection are so common in nature (Clutton-Brock and Sheldon 2010). Aside from initiating new experiments, researchers may be able to take advantage of existing opportunities to examine adaptation over longer temporal scales. For example, restoration projects, long-term ecological studies, and provenance trials could be leveraged so long as initial genotypes are sampled or designed into the experiment (e.g., Wright 2007; Germino et al. 2019).

Choice and Manipulation of Biotic Factors Related to Tests of Ecological and Evolutionary Theories

Biotic interactions were frequently examined in the context of existing theory, especially coevolutionary theory on antagonistic interactions (table S7: theory). For example, articles in our data set often related their experiments to theory on predation (e.g., Reznick and Endler 1982; Rausher 2001), parasitism (e.g., Zuk et al. 2006), and host-pathogen interactions (e.g., Enard et al. 2016). In addition, articles in our data set were often focused on plant-plant interactions and were frequently motivated by the stress gradient hypothesis (SGH). The SGH posits that as abiotic stress increases, positive biotic interactions should become more important while negative interactions become less important (SGH; Bertness and Callaway 1994; table S7: theory). Some researchers sought to directly test the SGH, while others examined facilitation and competition across gradients of stress or explored local adaptation to density or identity of neighbors.

By contrast, studies driven primarily by interest in adaptation to abiotic variables often did not link explicitly to theory or functional aspects of organisms. The abiotic factors themselves tended to motivate experimental design and provide a convenient organizational scheme to test for local adaptation. Connecting chosen abiotic factors or levels in an experiment to a conceptual or theoretical framework would provide an explicit motivation for testing a greater range of abiotic factors (e.g., subtle or less readily apparent environmental differences). Although not an exhaustive list, we suggest researchers frame hypotheses regarding abiotic local adaptation in the light of theoretical predictions (e.g., interaction of selection and gene flow on range limits: Kirkpatrick and Barton 1997; Polechová 2018), physiological and functional mechanism underlying responses to stress (e.g., Dudley 1996; Schmitt et al. 1999; Storz et al. 2010), or the interplay of organism-environment feedbacks and life-history evolution (e.g., niche construction: Lewontin 2000, Donohue 2005).

Overall, we found that when researchers provided specific expectations and predictions about abiotic and biotic factors, the study results were more readily interpretable and added more contextual knowledge about local adaptation. In our set of literature, we saw this most clearly in studies that framed the relationship between abiotic and biotic interactions using the SGH or coevolutionary theory. The use of these frameworks provided a set of testable hypotheses and a lens for interpretation of results, and it allowed the integration of local adaptation to biotic and abiotic environments. The SGH and coevolutionary theory may not apply to all abiotic and biotic systems, but there is underlying value to explicitly formulating assumptions about relationships between abiotic and biotic factors within a system.

Global Change Is Often Cited as a Motivating Factor for Local Adaptation Experiments

We found that global change was frequently cited as both a motivating factor and a potential implication of results (table S7: global change). Some studies effectively used climate change to inform questions and experimental design (abiotic gradients: Landis et al. 2012; De Block et al. 2013; Muhamed et al. 2013; Compagnoni and Adler 2014; biotic interactions: Cunningham et al. 2009; Fey and Cottingham 2011; De Block et al. 2013; Liancourt et al. 2013; Alexander et al. 2015). The most integrated climate change applications came from studies specifically designed to understand assisted migration and restoration work (table S7:

global change). However, most studies did not simulate conditions under climate change, and most of the results from these studies would be difficult to extrapolate meaningfully to how populations will respond to global change. We see this as a missed opportunity; more studies that design treatments to simulate realistic future conditions, particularly in a multifactorial context, will better inform how local adaptation will affect or be affected by global change.

Benefits of Applying the Mixed-Methods Approach for Other Meta-analyses

We believe the combination of a quantitative meta-analysis and qualitative metasynthesis is a powerful approach that could be applied to other meta-analyses in evolution and ecology. This mixed-methods approach could be particularly useful for emerging fields that have not accumulated a large number of empirical studies and therefore may lack the statistical power to test specific hypotheses. It may also be useful for critical examinations of newer fields by revealing potential biases that can be investigated in the future. Furthermore, qualitative metasyntheses allow the retention of a greater number of studies because inclusion is not restricted to those studies that report particular numerical values.

Quantitative meta-analyses generally omit details of individual experiments in order to make consistent comparisons across studies. By contrast, qualitative metasyntheses retain the context in which each experiment was designed, which can illuminate the strengths and limitations of current approaches and identify potential differences in how researchers from different fields approach a given question. For example, a recent meta-analysis of phenotypic selection noted that the species used in experimental studies of selection (examined in their meta-analysis) differed from those used in observational studies (examined in other meta-analyses), preventing a quantitative comparison (Caruso et al. 2017). This suggests that there may be a fundamental difference in the perspective and motivation of researchers pursuing experimental versus observational studies of phenotypic selection, and a qualitative metasynthesis would allow this idea to be further examined. In a meta-analysis of local adaptation, Hereford (2009) observed that many experiments had a priori expectations of local adaptation because those experiments were conducted across strong environmental gradients; he suggested that this may lead to an overestimation of the magnitude of local adaptation. This observation is consistent with one of our major findings of a bias toward comparing highly divergent abiotic environments. However, since we used a formal textual analysis, we were able to conclude with more certainty that this was a truly pervasive source of bias.

Our mixed-methods approach highlights the complementary nature of these two analyses for emerging bodies of literature. While the quantitative meta-analysis provided a traditional understanding of the relative effect sizes in abiotic and biotic environments, it ignored much of the underlying information on experimental system and design. The qualitative metasynthesis is a powerful way to systematically capture this lost information. Gathering data on the framework of experiments can provide essential insights into historical patterns of analysis and design and can identify gaps and future opportunities. We suggest that the mixed-methods approach can be employed as a powerful method for providing both meaningful and nuanced syntheses of emerging topics and serve as a guide for future studies.

Acknowledgments

We thank the Community Genetics Discussion Group at the University of Minnesota, especially Ruth Shaw and Georgiana May, for lively discussion that helped begin this project; Chris Caruso for insightful comments on an early version of the manuscript; and Derek Nedveck for assistance collecting articles for the data set. The National Science Foundation provided generous support for R.D.B.R. and D.A.M. (DEB-1025004 and DEB-1255141) and for J.B.Y. and P.T. (IOS-1237993 and IOS-1724993), and the National Sciences and Engineering Research Council of Canada provided support for A.J.G. via the Alexander Graham Bell Graduate Scholarship. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

Literature Cited

Abdala-Roberts, L., and R. J. Marquis. 2007. Test of local adaptation to biotic interactions and soil abiotic conditions in the ant-tended *Chamaecrista fasciculata* (Fabaceae). Oecologia 154:315–326.

Alexander, J. M., J. M. Diez, and J. M. Levine. 2015. Novel competitors shape species' responses to climate change. Nature 525:515–518.

Anstett, D. N., K. A. Nunes, C. Baskett, and P. M. Kotanen. 2016. Sources of controversy surrounding latitudinal patterns in herbivory and defense. Trends in Ecology and Evolution 31:789–802.

Barton, K. 2009 Mu-MIn: multi-model inference. R package version 0.12.2/r18. http://R-Forge.R-project.org/projects/mumin/.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Benning, J. W., V. M. Eckhart, M. A. Geber, and D. A. Moeller. 2019. Biotic interactions contribute to the geographic range of an annual plant: herbivory and phenology mediate fitness beyond a range margin. American Naturalist 193:786–797.

Benning, J. W., and D. A. Moeller. 2019. Maladaptation beyond a geographic range limit driven by antagonistic and mutualistic biotic interactions across an abiotic gradient. Evolution 73:2044–2059.

Bertness, M. D., and R. Callaway. 1994. Positive interaction in communities. Trends in Ecology and Evolution 9:191–193.

Brady, S. P., D. I. Bolnick, R. D. H. Barrett, L. Chapman, E. Crispo, A. M. Derry, C. G. Eckert, et al. 2019. Understanding maladaptation by uniting ecological and evolutionary perspectives. American Naturalist 194:495–515.

Caruso, C. M., R. A. Martin, N. Sletvold, M. B. Morrissey, M. J. Wade, K. E. Augustine, S. M. Carlson, A. D. C. MacColl, A. M. Siepielski, and J. G. Kingsolver. 2017. What are the determinants of phenotypic selection? a meta-analysis of experimental studies. American Naturalist 190:363–376.

Cavanaugh, J. E. 1997. Unifying the derivations of the Akaike and corrected Akaike information criteria. Statistics and Probability Letters 31:201–208.

Clausen, J., D. D. Keck, and H. M. Hiesey. 1940. Experimental studies on the nature of species. I. Effects of varied environments on western North American plants. Carnegie Institute of Washington, Washington, DC.

Clutton-Brock, T., and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology and Evolution 25:562–573.

Compagnoni, A., and P. B. Adler. 2014. Warming, competition, and *Bromus tectorum* population growth across an elevation gradient. Ecosphere 5:1–34.

Côté, I. M., and J. D. Reynolds. 2012. Meta-analysis at the intersection of evolutionary ecology and conservation. Evolutionary Ecology 26:1237–1252.

Cunningham, H. R., L. J. Rissler, and J. J. Apodaca. 2009. Competition at the range boundary in the slimy salamander: using reciprocal transplants for studies on the role of biotic interactions in spatial distributions. Journal of Animal Ecology 78:52–62.

Darwin, C. 1859. On the origin of species. J. Murray, London.

De Block, M., K. Pauwels, M. Van Den Broeck, L. De Meester, and R. Stoks. 2013. Local genetic adaptation generates latitude-specific effects of warming on predator-prey interactions. Global Change Biology 19:689–696.

Dixon-Woods, M., S. Agarwal, D. Jones, B. Young, and A. Sutton. 2005. Synthesizing qualitative and quantitative evidence: a review of possible methods. Journal of Health Services Research and Policy 10:45–53.

Dobzhanksy, T. 1950. Evolution in the tropics. American Scientist 38:209–221.

Donohue, K. 2005. Niche construction through phenological plasticity: life history dynamics and ecological consequences. New Phytologist 166:83–92.

Dudley, S. A. 1996. The response to differing selection on plant physiological traits: evidence for local adaptation. Evolution 50:103–110.

Echaubard, P., J. Leduc, B. Pauli, V. G. Chinchar, J. Robert, and D. Lesbarrères. 2014. Environmental dependency of amphibian-ranavirus genotypic interactions: evolutionary perspectives on infectious diseases. Evolutionary Applications 7:723–733.

Egea-Serrano, A., S. Hangartner, A. Laurila, and K. Räsänen. 2014. Multifarious selection through environmental change: acidity and predator-mediated adaptive divergence in the moor frog (*Rana arvalis*). Proceedings of the Royal Society B 281:20133266.

Enard, D., L. Cai, C. Gwennap, and D. A. Petrov. 2016. Viruses are a dominant driver of protein adaptation in mammals. eLife 5:e12469.

Feeny, P. 1976. Plant apparency and chemical defense. Pages 1–40 *in* J. W. Wallace and R. L. Mansell, eds. Biochemical interaction between plants and insects. Springer, Boston.

Fey, S. B., and K. L. Cottingham. 2011. Linking biotic interactions and climate change to the success of the exotic *Daphnia lumholtzi*. Freshwater Biology 56:2196–2209.

Germino, M. J., A. M. Moser, and A. R. Sands. 2019. Adaptive variation, including local adaptation, requires decades to become evident in common gardens. Ecological Applications 29:e01842.

Godefroid, S., C. Piazza, G. Rossi, S. Buord, A.-D. Stevens, R. Aguraiuja, C. Cowell, et al. 2011. How successful are plant species reintroductions? Biological Conservation 144:672–682.

Greischar, M. A., and B. Koskella. 2007. A synthesis of experimental work on parasite local adaptation. Ecology Letters 10:418–434.

Guerrant, E. O. 2012. Characterizing two decades of rare plant reintroductions. Pages 9–29 *in* J. Maschinski, K. E. Haskins, and P. H. Raven, eds. Plant reintroduction in a changing climate: promises and perils. Island Press/Center for Resource Economics, Washington, DC.

Handel, S. N. 2012. The Red Queens of restoration. Ecological Restoration 30:3–4.

Hargreaves, A. L., R. M. Germain, M. Botranger, J. Persi, and A. L. Angert. 2020. Local adaptation to biotic interactions: a meta-analysis across latitude. American Naturalist 2020:XXX–XXX.

Hargreaves, A. L., E. Suárez, K. Mehltreter, I. Myers-Smith, S. E. Vanderplank, H. L. Slinn, Y. L. Vargas-Rodriguez, et al. 2019. Seed predation increases from the Arctic to the equator and from high to low elevations. Science Advances 5:eaau4403.

Heath, K. D., A. J. Stock, and J. R. Stinchcombe. 2010. Mutualism variation in the nodulation response to nitrate. Journal of Evolutionary Biology 23:2494–2500.

Hereford, J. 2009. A quantitative survey of local adaptation and fitness trade-offs. American Naturalist 173:579–588.

Hillebrand, H., and J. Gurevitch. 2016. Meta-analysis and systematic reviews in ecology. Pages 448–511 *in* Encyclopedia of life sciences. Wiley, London.

HilleRisLambers, J., J. S. Clark, and B. Beckage. 2002. Density-dependent mortality and the latitudinal gradient in species diversity. Nature 417:732–735.

Hoeksema, J. D., and S. E. Forde. 2008. A meta-analysis of factors affecting local adaptation between interacting species. American Naturalist 171:275–290.

Hughes, A. R., T. C. Hanley, J. E. Byers, J. H. Grabowski, J. C. Malek, M. F. Piehler, and D. L. Kimbro. 2017. Genetic by environmental variation but no local adaptation in oysters (*Crassostrea virginica*). Ecology and Evolution 7:697–709.

Janzen, D. 1973. Comments on host-specificity of tropical herbivores and its relevance to species richness. Pages 201–211 *in* V. Heywood, ed. Taxonomy and ecology. Academic Press, London.

Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters 7:1225–1241.

Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. American Naturalist 157:245–261.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. American Naturalist 150:1–23.

Koricheva, J., and J. Gurevitch. 2014. Uses and misuses of meta-analysis in plant ecology. Journal of Ecology 102:828–844.

Koskella, B., and M. A. Brockhurst. 2014. Bacteria-phage coevolution as a driver of ecological and evolutionary processes in microbial communities. FEMS Microbiology Reviews 38:916–931.

Koskella, B., and C. M. Lively. 2007. Advice of the rose: experimental coevolution of a trematode parasite and its snail host. American Naturalist 61:152–159.

Kuhn, M., and H. Wickham. 2017. rsample: general resampling infrastructure. R package version 0.0.2. https://CRAN.R-project.org/package = rsample.

Laine, A.-L. 2008. Temperature-mediated patterns of local adaptation in natural plant-pathogen metapopulation. Ecology Letters 11:327–337.

Lajeunesse, M. J., and M. R. Forbes. 2002. Host range and local parasite adaptation. Proceedings of the Royal Society B 269:703–710.

LaManna, J. A., S. A. Mangan, A. Alonso, N. A. Bourg, W. Y. Brockelman, S. Bunyavejchewin, L. W. Chang, et al. 2017. Plant diversity increases with the strength of negative density dependence at the global scale. Science 356:1389–1392.

Landis, S. H., M. Kalbe, T. B. H. Reusch, and O. Roth. 2012. Consistent pattern of local adaptation during an experimental heat wave in a pipefish-trematode host-parasite system. PLoS ONE 7:e30658.

Leimu, R., and M. Fischer. 2008. A meta-analysis of local adaptation in plants. PLoS ONE 3:e4010.

Lewontin, R. C. 2000. The triple helix: gene, organism, and environment. Harvard University Press, Cambridge, MA.

Liancourt, P., L. A. Spence, D. S. Song, A. Lkhagva, A. Sharkhuu, B. Boldgiv, B. R. Helliker, et al. 2013. Plant response to climate change varies with topography, interactions with neighbors, and ecotype. Ecology 94:444–453.

Lipsey, M. W., and D. B. Wilson. 2001. Practical meta-analysis. Applied Social Research Methods. Vol. 49. Sage, Thousand Oaks, CA.

Lopez Pascua, L., S. Gandon, and A. Buckling. 2012. Abiotic heterogeneity drives parasite local adaptation in coevolving bacteria and phages. Journal of Evolutionary Biology 25:187–195.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distributions of species. Princeton University Press, Princeton, NJ.

McCoy, K. D., T. Boulinier, S. Schjorring, and Y. Michalakis. 2002. Local adaptation of the ectoparasite *Ixodes uriae* to its seabird host. Evolutionary Ecology Research 4:441–456.

Moles, A. T., S. P. Bonser, A. G. Poore, I. R. Wallis, and W. J. Foley. 2011. Assessing the evidence for latitudinal gradients in plant defence and herbivory. Functional Ecology 25:380–388.

Muhamed, H., B. Touzard, Y. Le Bagousse-Pinguet, and R. Michalet. 2013. The role of biotic interactions for the early establishment of oak seedlings in coastal dune forest communities. Forest Ecology and Management 297:67–74.

Nakagawa, S., D. W. Noble, A. M. Senior, and M. Lagisz. 2017. Meta-evaluation of meta-analysis: ten appraisal questions for biologists. BMC Biology 15:18.

Noblit, G. W., and R. D. Hare. 1988. Meta-ethnography: synthesizing qualitative studies. Vol. 11. Sage, Thousand Oaks, CA.

Ortegón-Campos, I., L. Abdala-Roberts, V. Parra-Tabla, J. C. Cervera, D. Marrufo-Zapata, and C. M. Herrera. 2012. Influence of multiple factors on plant local adaptation: soil type and folivore effects in *Ruellia nudiflora* (Acanthaceae). Evolutionary Ecology 26:545–558.

Pánková, H., Z. Münzbergová, J. Rydlová, and M. Vosátka. 2014. Co-adaptation of plants and communities of arbuscular mycorrhizal fungi to their soil conditions. Folia Geobotanica 49:521–540.

Perring, M. P., R. J. Standish, J. N. Price, M. D. Craig, T. E. Erickson, K. X. Ruthrof, A. S. Whiteley, L. E. Valentine, and R. J. Hobbs. 2015. Advances in restoration ecology: rising to the challenges of the coming decades. Ecosphere 6:1–25.

Polechová, J. 2018. Is the sky the limit? on the expansion threshold of a species' range. PLoS Biology 16:e2005372.

Poulin, R., and M. R. Forbes. 2012. Meta-analysis and research on host-parasite interactions: past and future. Evolutionary Ecology 26:1169–1185.

Primack, R. B., and H. Kang. 1989. Measuring fitness and natural selection in wild plant populations. Annual Review of Ecology and Systematics 20:367–396.

R Core Team. 2016. R: a language and environment for statistical computing. Version 3.3.2.

Rausher, M. D. 2001. Coevolution and plant resistance to natural enemies. Nature 411:857–864.

Reznik, D., and J. A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution 36:160–177.

Richardson, J. L., M. C. Urban, D. I. Bolnick, and D. K. Skelly. 2014. Microgeographic adaptation and the spatial scale of evolution. Trends in Ecology and Evolution 29:165–176.

Ridenhour, B. J. 2005. Identification of selective sources: partitioning selection based on interactions. American Naturalist 166:12–25.

Rolán-Alvarez, E., K. Johannesson, and J. Erlandson. 1997. The maintenance of a cline in the marine snail *Littorina saxatalis*: the role of home site advantage and hybrid fitness. Evolution 51:1838–1847.

Roslin, T., B. Hardwick, V. Novotny, W. K. Petry, N. R. Andrew, A. Asmus, I. C. Barrio, Y. Basset, A. L. Boesing, T. C. Bonebrake, and E. K. Cameron. 2017. Higher predation risk for insect prey at low latitudes and elevations. Science 356:742–744.

Rúa, M. A., A. Antoninka, P. M. Antunes, V. B. Chaudhary, L. J. Lamit, J. D. Piculelll, J. D. Bever, et al. 2016. Home-field advantage? evidence of local adaptation among plants, soil, and arbuscular mycorrhizal fungi through meta-analysis. BMC Evolutionary Biology 10:122.

Sambatti, J. B. M., and K. J. Rice. 2006. Local adaptation, patterns of selection, and gene flow in the Californian serpentine sunflower (*Helianthus exilis*). Evolution 60:696–710.

Savolainen, O., M. Lascoux, and J. Merilä. 2013. Ecological genomics of local adaptation. Nature Reviews Genetics 14:807.

Scharf, I., S. Bauer, B. Fischer-Blass, and S. Foitzik. 2011. Impact of a social parasite on ant host populations depends on host species, habitat and year. Biological Journal of the Linnean Society 103:559–570.

Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? Annual Review of Ecology, Evolution, and Systematics 40:245–269.

Schmitt, J., S. A. Dudley, and M. Pigliucci. 1999. Manipulative approaches to testing adaptive plasticity: phytochrome-mediated shade-avoidance responses in plants. American Naturalist 154 (suppl.):S43–S54.

Schoebel, C. N., J. Wolinska, and P. Spaak. 2010. Higher parasite resistance in *Daphnia* populations with recent epidemics. Journal of Evolutionary Biology 23:2370–2376.

Siepielski, A. M., K. M. Gotanda, M. B. Morrissey, S. E. Diamond, J. D. DiBattista, and S. M. Carlson. 2013. The spatial patterns of directional phenotypic selection. Ecology Letters 16:1382–1392.

Smilanich, A. M., R. M. Fincher, and L. A. Dyer. 2016. Does plant apparency matter? thirty years of data provide limited support but reveal clear patterns of the effects of plant chemistry on herbivores. New Phytologist 210:1044–1057.

Storz, J. F., G. R. Scott, and Z. A. Cheviron. 2010. Phenotypic plasticity and genetic adaptation to high-altitude hypoxia in vertebrates. Journal of Experimental Biology 213:4125–4136.

Thompson, J. N. 2005. Geographic mosaic of coevolution. University of Chicago Press, Chicago.

Thuiller, W., C. Albert, M. B. Araújo, and P. M. Berry. 2008. Predicting global change impacts on plant species' distributions: future challenges. Perspectives in Plant Ecology, Evolution, and Systematics 9:137–152.

Tiffin, P., and J. Ross-Ibarra. 2014. Advances and limits of using population genetics to understand local adaptation. Trends in Ecology and Evolution 29:673–680.

Turesson, G. 1922. The genotypical responses of plant species to habitat. Hereditas 3:211–350.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

Valladares, F., S. Matesanz, F. Duilhaumon, M. B. Araújo, L. Balaguer, M. Benito-Garzón, W. Cornwell, et al. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecology Letters 17:1351–1364.

Van Valen, L. 1973. A new evolutionary law. Evolutionary Theory 1:1–30.

Vetter, D., G. Rücker, and I. Storch. 2013. Meta-analysis: a need for well-defined usage in ecology and conservation biology. Ecosphere 4:1–24.

Wadgymar, S. M., D. B. Lowry, B. A. Gould, C. N. Byron, R. M. Mactavish, and J. T. Anderson. 2017. Identifying targets and agents of selection: innovative methods to evaluate the processes that contribute to local adaptation. Methods in Ecology and Evolution 8:738–749.

Wallace, A. R. 1878. Tropical nature, and other essays. Macmillan, London.

Wolf, J. B., E. D. Brodie III, J. M. Cheverud, A. J. Moore, and M. J. Wade. 1998. Evolutionary consequences of indirect genetic effects. Trends in Ecology and Evolution 13:64–69.

Wright, J. W. 2007. Local adaptation to serpentine soils in *Pinus ponderosa*. Plant and Soil 293:209–217.

Yates, C. J., J. Elith, A. M. Latimer, D. Le Maitre, G. F. Midgley, F. M. Schurr, and A. G. West. 2010. Projecting climate change impacts on species distributions in megadiverse South African Cape and Southwest Australian Floristic Regions: opportunities and challenges. Austral Ecology 35:374–391.

Zuk, M., J. T. Rotenberry, and R. M. Tinghitella. 2006. Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. Biology Letters 2:521–524.

References Cited Only in the Online Enhancements

Antunes, P. M., A. M. Koch, J. B. Morton, M. C. Rillig, and J. N. Klironomos. 2011. Evidence for functional divergence in arbuscular mycorrhizal fungi from contrasting climatic origins. New Phytologist 189:507–514.

Ariza, C., and K. Tielbörger. 2011. An evolutionary approach to studying the relative importance of plant-plant interactions along environmental gradients: evolutionary approach to interactions in gradients. Functional Ecology 25:932–942.

Ayres, E., H. Steltzer, S. Berg, and D. H. Wall. 2009. Soil biota accelerate decomposition in high-elevation forests by specializing in the breakdown of litter produced by the plant species above them. Journal of Ecology 97:901–912.

Bankier, C. 2016. Coevolutionary interactions between bacteria and phage in natural environments. PhD diss. Imperial College London.

Barton, A. M. 1993. Factors controlling plant distributions: drought, competition, and fire in montane pines in Arizona. Ecological Monographs 63:367–397.

Bischoff, A., L. Crémieux, M. Smilauerova, C. S. Lawson, S. R. Mortimer, J. Dolezal, V. Lanta, et al. 2006. Detecting local adaptation in widespread grassland species? the importance of scale and local plant community. Journal of Ecology 94:1130–1142.

Bohrer, G., V. Kagan-Zur, N. Roth-Bejerano, D. Ward, G. Beck, and E. Bonifacio. 2003. Effects of different Kalahari-desert VA mycorrhizal communities on mineral acquisition and depletion from the soil by host plants. Journal of Arid Environments 2:193–208.

Braco, S. 2009. Are oaks locally adapted to serpentine soils? Northeastern Naturalist 16:329–340.

Bray, J. P., J. Reich, S. J. Nichols, G. Kon Kam King, R. Mac Nally, R. Thompson, A. O'Reilly-Nugent, and B. J. Kefford. 2018. Biological interactions mediate context and species-specific sensitivities to salinity. Philosophical Transactions of the Royal Society B 374:20180020.

Bryner, S. F., and D. Rigling. 2011. Temperature-dependent genotype-by-genotype interaction between a pathogenic fungus and its hyperparasitic virus. American Naturalist 177:65–74.

Buser, C. C., M. Jansen, K. Pauwels, L. De Meester, and P. Spaak. 2012. Combined exposure to parasite and pesticide causes increased mortality in the water flea *Daphnia*. Aquatic Ecology 46:261–268.

Castro, B. M., K. S. Moriuchi, M. L. Friesen, M. Badri, S. V. Nuzhdin, S. Y. Strauss, D. R. Cook, and E. von Wettberg. 2013. Parental environments and interactions with conspecifics alter salinity tolerance of offspring in the annual *Medicago truncatula*. Journal of Ecology 101:1281–1287.

Colautti, R. I., and S. C. Barrett. 2013. Rapid adaptation to climate facilitates range expansion of an invasive plant. Science 342:364–366.

Crémieux, L., A. Bischoff, M. Šmilauerová, C. S. Lawson, S. R. Mortimer, J. Doležal, V. Lanta, et al. 2008. Potential contribution of natural enemies to patterns of local adaptation in plants. New Phytologist 180:524–533.

Donohue, K., D. Messiqua, E. H. Pyle, M. S. Heschel, and J. Schmitt. 2000. Evidence of adaptive divergence in plasticity: density- and site-dependent selection on shade-avoidance responses in *Impatiens capensis*. Evolution 54:1956–1968.

Donohue, K., E. H. Pyle, D. Messiqua, M. S. Heschel, and J. Schmitt. 2001. Adaptive divergence in plasticity in natural population of *Impatiens capensis* and its consequences for performance in novel habitats. Evolution 55:692–702.

Doubková, P., J. Suda, and R. Sudová. 2012. The symbiosis with arbuscular mycorrhizal fungi contributes to plant tolerance to serpentine edaphic stress. Soil Biology and Biochemistry 44:56–64.

Ehlers, B. K., E. Grøndahl, J. Ronfort, and T. Bataillon. 2012. “Ménage à trois”: the presence/absence of thyme shapes the mutualistic interaction between the host plant *Medicago truncatula* (Fabaceae) and its symbiotic bacterium *Sinorhizobium meliloti*. Ecology and Evolution 2:1676–1681.

Ehlers, B. K., and J. Thompson. 2004. Do co-occurring plant species adapt to one another? the response of *Bromus erectus* to the presence of different *Thymus vulgaris* chemotypes. Oecologia 141:511–518.

Eränen, J., and M. Kozlov. 2009. Interactions between mountain birch seedlings from differentiated populations in contrasting environments of subarctic Russia. Plant Ecology 200:167–177.

Espeland, E. K., and K. J. Rice. 2007. Facilitation across stress gradients: the importance of local adaptation. Ecology 88:2404–2409.

Fine, P. V. A., I. Mesones, and P. D. Coley. 2004. Herbivores promote habitat specialization by trees in Amazonian forests. Science 305:663–665.

Germain, R. M., M. M. Mayfield, and B. Gilbert. 2018. The “filtering” metaphor revisited: competition and environment jointly structure invasibility and coexistence. Biology Letters 14:20180460.

Germain, R. M., J. T. Weir, and B. Gilbert. 2016. Species coexistence: macroevolutionary relationships and the contingency of historical interactions. Proceedings of the Royal Society B 283:20160047.

Gómez-Mestre, I., and M. Tejedo. 2002. Geographic variation in asymmetric competition: a case study with two larval anuran species. Ecology 83:2102–2111.

Gorter, F. A., P. D. Scanlan, and A. Buckling. 2016. Adaptation to abiotic conditions drives local adaptation in bacteria and viruses coevolving in heterogeneous environments. Biology Letters 12:20150879.

Grassein, F., S. Lavorel, and I. Till-Bottraud. 2014. The importance of biotic interactions and local adaptation for plant response to environmental changes: field evidence along an elevational gradient. Global Change Biology 20:1452–1460.

Hufford, K. M., and S. J. Mazer. 2012. Local adaptation and the effects of grazing on the performance of *Nassella pulchra*: implications for seed sourcing in restoration. Restoration Ecology 20:688–695.

Hufford, K. M., S. J. Mazer, and M. D. Camara. 2008. Local adaptation and effects of grazing among seedlings of two native California bunchgrass species: implications for restoration. Restoration Ecology 16:59–69.

Johnson, N. C., G. W. T. Wilson, M. A. Bowker, J. A. Wilson, and R. M. Miller. 2010. Resource limitation is a driver of local adaptation in mycorrhizal symbioses. Proceedings of the National Academy of Sciences of the USA 107:2093–2098.

Jurjavcic, N., S. Harrison, and A. Wolf. 2002. Abiotic stress, competition, and the distribution of the native annual grass *Vulpia microstachys* in a mosaic environment. Oecologia 130:555–562.

Kardol, P., J. R. De Long, and D. A. Wardle. 2014. Local plant adaptation across a subarctic elevational gradient. Open Science 1:140141.

Kindell, C. E., A. A. Winn, and T. E. Miller. 1996. The effects of surrounding vegetation and transplant age on the detection of local adaptation in the perennial grass *Aristida stricta*. Journal of Ecology 84:745–754.

King, K. C., L. F. Delph, J. Jokela, and C. M. Lively. 2011. Coevolutionary hotspots and coldspots for host sex and parasite local adaptation in a snail-trematode interaction. Oikos 120:1335–1340.

Knight, T. M., and T. E. Miller. 2004. Local adaptation within a population of *Hydrocotyle bonariensis*. Evolutionary Ecology Research 6:103–114.

Koutecká, E., and J. Lepš. 2013. The growth and survival of three closely related *Myosotis* species in a 3-year transplant experiment. Botany 91:209–217.

Lankau, R. A. 2013. Species invasion alters local adaptation to soil communities in a native plant. Ecology 94:32–40.

Lehndal, L., and J. Ågren. 2015. Herbivory differentially affects plant fitness in three populations of the perennial herb *Lythrum salicaria* along a latitudinal gradient. PLoS ONE 10:e0135939.

Liancourt, P., and K. Tielbörger. 2009. Competition and a short growing season lead to ecotypic differentiation at the two extremes of the ecological range. Functional Ecology 23:397–404.

Menke, S. B., R. N. Fisher, W. Jetz, and D. A. Holway. 2007. Biotic and abiotic controls of Argentine ant invasion success at local and landscape scales. Ecology 88:3164–3173.

Mitchell, S. E., E. S. Rogers, T. J. Little, and A. F. Read. 2005. Host-parasite and genotype-by-environment interactions: temperature modifies potential for selection by a sterilizing pathogen. Evolution 59:70–80.

Molina-Montenegro, M. A., C. Palma-Rojas, Y. Alcayaga-Olivares, R. Oses, L. J. Corcuera, L. A. Cavieres, and E. Gianoli. 2013. Ecophysiological plasticity and local differentiation help explain the invasion success of *Taraxacum officinale* (dandelion) in South America. Ecography 36:718–730.

O’Brien, E. K., M. Higgie, C. T. Jeffs, A. A. Hoffmann, J. Hrcek, O. T. Lewis, and J. R. Bridle. 2018. Interacting effects of the abiotic and biotic environment on fitness of rainforest *Drosophila*. bioRxiv, https://doi.org/10.1101/395624.

Padfield, D., M. Castledine, and A. Buckling. 2019. Temperature-dependent changes to host-parasite interactions alter the thermal performance of a bacterial host. ISME Journal, https://doi.org/10.1038/s41396-019-0526-5.

Pahl, A. T., J. Kollmann, A. Mayer, and S. Haider. 2013. No evidence for local adaptation in an invasive alien plant: field and greenhouse experiments tracing a colonization sequence. Annals of Botany 112:1921–1930.

Parain, E. C., D. Gravel, R. P. Rohr, L. F. Bersier, and S. M. Gray. 2016. Mismatch in microbial food webs: predators but not prey perform better in their local biotic and abiotic conditions. Ecology and Evolution 6:4885–4897.

Pellissier, L., A. Roger, J. Bilat, and S. Rasmann. 2014. High elevation *Plantago lanceolata* plants are less resistant to herbivory than their low elevation conspecifics: is it just temperature? Ecography 37:950–959.

Pickles, B. J., B. D. Twieg, G. A. O’Neill, W. W. Mohn, and S. W. Simard. 2015. Local adaptation in migrated interior Douglas-fir seedlings is mediated by ectomycorrhizas and other soil factors. New Phytologist 207:858–871.

Poisot, T., G. Lepennetier, E. Martinez, J. Ramsayer, and M. E. Hochberg. 2011. Resource availability affects the structure of a natural bacteria-bacteriophage community. Biology Letters 7:201–204.

Rice, K. J., and E. E. Knapp. 2008. Effects of competition and life history stage on the expression of local adaptation in two native bunchgrasses. Restoration Ecology 16:12–23.

Rodl, T., and D. Ward. 2002. Host recognition in a desert mistletoe: early stages of development are influenced by substrate and host origin. Functional Ecology 16:128–134.

Schoen, D. J., S. C. Stewart, M. J. Lechowicz, and G. Bell. 1986. Partitioning the transplant site effect in reciprocal transplant experiments with *Impatiens capensis* and *Impatiens pallida*. Oecologia 70:149–154.

Schwarzer, C., and J. Joshi. 2017. Parallel adaptive responses to abiotic but not biotic conditions after cryptic speciation in European peat moss *Sphagnum magellanicum* Brid. Perspectives in Plant Ecology, Evolution, and Systematics 26:14–27.

Sherrard, M. E., and H. Maherali. 2012. Local adaptation across a fertility gradient is influenced by soil biota in the invasive grass, *Bromus inermis*. Evolutionary Ecology 26:529–544.

Sikes, B. A., H. Maherali, and J. N. Klironomos. 2014. Mycorrhizal fungal growth responds to soil characteristics, but not host plant identity, during a primary lacustrine dune succession. Mycorrhiza 24:219–226.

Skelly, D. K. 1995. A behavioral trade-off and its consequences for the distribution of *Pseudacris* treefrog larvae. Ecology 76:150–164.

Smith, N. F., and G. M. Ruiz. 2004. Phenotypic plasticity in the life history of the mangrove snail *Cerithidea scalariformis*. Marine Ecology Progress Series 284:195–209.

Stanton-Geddes, J., P. Tiffin, and R. G. Shaw. 2012. Role of climate and competitors in limiting fitness across range edges of an annual plant. Ecology 93:1604–1613.

Sullivan, T. J., and S. H. Faeth. 2008. Local adaptation in *Festuca arizonica* infected by hybrid and nonhybrid *Neotyphodium* endophytes. Microbial Ecology 55:697–704.

Taheri, W. I., and J. D. Bever. 2010. Adaptation of plants and arbuscular mycorrhizal fungi to coal tailings in Indiana. Applied Soil Ecology 45:138–143.

Thompson, J. D., T. McNeilly, and A. J. Gray. 1991. Population variation in *Spartina anglica* CE Hubbard. II. Reciprocal transplants among three successional populations. New Phytologist 117:129–139.

Thrall, P. H., J. D. Bever, and J. F. Slattery. 2008. Rhizobial mediation of *Acacia* adaptation to soil salinity: evidence of underlying trade-offs and tests of expected patterns. Journal of Ecology 96:746–755.

Tomiolo, S., W. H. van der Putten, and K. Tielbörger. 2015. Separating the role of biotic interactions and climate in determining adaptive response of plants to climate change. Ecology 96:1298–1308.

Traxler, M. A., and A. Joern. 1999. Performance tradeoffs for two hosts within and between populations of the oligophagous grasshopper *Hesperotettix viridis* (Acrididae). Oikos 87:239–250.

Vinebrooke, R. D. 1996. Abiotic and biotic regulation of periphyton in recovering acidified lakes. Journal of the North American Benthological Society 15:318–331.

Volis, S., S. Mendlinger, and D. Ward. 2002. Adaptive traits of wild barley plants of Mediterranean and desert origin. Oecologia 133:131–138.

Welk, A., E. Welk, and H. Bruelheide. 2014. Biotic interactions overrule plant responses to climate, depending on the species' biogeography. PLoS ONE 9:e111023.

Wendling, C. C., and K. M. Wegner. 2015. Adaptation to enemy shifts: rapid resistance evolution to local *Vibrio* spp. in invasive Pacific oysters. Proceedings of the Royal Society B 282:20142244.

Yang, R., S. Li, X. Cai, X. Li, P. Christie, J. Zhang, and J. Gai. 2016. Responses of arbuscular mycorrhizal symbionts to contrasting environments: field evidence along a Tibetan elevation gradient. Mycorrhiza 26:623–632.

Associate Editor: Jill T. Anderson
Editor: Daniel I. Bolnick

Environmental variation in the southern Sierra Nevada, Kern County, California. Photo credit: David A. Moeller.