

Local Adaptation to Biotic Interactions: A Meta-analysis across Latitudes

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ABSTRACT: Adaptation to local conditions can increase species' geographic distributions and rates of diversification, but which components of the environment commonly drive local adaptation—particularly the importance of biotic interactions—is unclear. Biotic interactions should drive local adaptation when they impose consistent divergent selection; if this is common, we expect transplant experiments to detect more frequent and stronger local adaptation when biotic interactions are left intact. We tested this hypothesis using a meta-analysis of transplant experiments from >125 studies (mostly of plants). Overall, local adaptation was common, and biotic interactions affected fitness. Nevertheless, local adaptation was neither more common nor stronger when biotic interactions were left intact, either between experimental treatments within studies (control vs. biotic interactions experimentally manipulated) or between studies that used natural versus biotically altered transplant environments. However, the effect of ameliorating negative interactions varied with latitude, suggesting that interactions may promote local adaptation more often in tropical than in temperate ecosystems, although few tropical studies were available to test this. Our results suggest that biotic interactions often fail to drive local adaptation even though they strongly affect fitness, perhaps because temperate biotic environments are unpredictable at the spatiotemporal scales required for local adaptation.

Keywords: local adaptation, species interactions, transplant experiments, translocation experiments, meta-analysis, competition.

Introduction

Adaptation to local conditions is fundamental to species' evolutionary and biogeographic dynamics. Local adaptation among populations, where local individuals outperform foreign individuals, can significantly improve mean population fitness (Griffith and Watson 2005), lead to population differentiation that contributes to ecological speciation (Reznick and Ghalambor 2001), and promote range expansions by enabling colonization of previously uninhabitable locations (Holt 1996; Levin 2000; Hargreaves and Eckert 2019). Local adaptation is equally important for management: foresters seek genotypes best suited to planting sites (Liepe et al. 2016), locally adapted populations are prioritized in restoration and conservation (McKay et al. 2005; Bonin et al. 2007), and biologists increasingly recognize local adaptation's role in the spread of invasive species (Colautti and Barrett 2013; Oduor et al. 2016).

While the importance of local adaptation is well recognized and its prevalence has been tested for decades (Clausen et al. 1940), it remains unclear which environmental factors most commonly drive it, particularly the importance of interactions among species (Parachnowitsch and Lajeunesse 2012). Seminal tests of local adaptation have traditionally focused on abiotic factors (e.g., climate [Bateman 1967], soil [Antonovics 1975], photoperiod [Griffith and Watson 2005]). Yet all environments include other species, and species composition often shifts predictably along abiotic gradients (Maron et al. 2014). A handful of case studies show that biotic interactions can promote local adaptation among populations (e.g., Rice and Knapp 2008; Garrido et al. 2012), but how commonly this occurs is unknown. This uncertainty impedes our understanding of the dominant agents of diversification and ability to predict when local adaptation will facilitate success

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in environments with novel biotic conditions (Aitken and Whitlock 2013; Alexander et al. 2015).

To drive local adaptation, biotic interactions must affect fitness, fitness effects must promote divergent selection among populations, and divergent selection must be consistent across generations (Levins 1968). Studies of species distributions suggest that biotic interactions often meet the first two criteria; interactions commonly affect fitness at geographic scales (Wisz et al. 2013) and can have different fitness consequences among sites. For example, negative interactions like competition and herbivory can limit one end of a species' range with little impact at the other (Barton 1993; Scheidel and Bruelheide 2001) and are more often involved in limiting the low-elevation and latitude ends of species distributions (Hargreaves et al. 2014). How often such spatial variation in fitness effects leads to consistent divergent selection is less clear given that biotic interactions can be highly dynamic (Schemske 2009). If biotic interactions vary unpredictably relative to the speed of adaptation or scale of gene flow, they are unlikely to drive local adaptation even if they strongly affect fitness.

Given the rich experimental literature on local adaptation, why is the importance of biotic interactions in driving it still unresolved? First, meta-analyses have focused on the frequency of local adaptation more than its selective agents (Leimu and Fischer 2008; Hereford 2009)—a gap our study aims to fill. Second, we suspected that common features of reciprocal transplant experiments—the gold standard for testing local adaptation (Kawecki and Ebert 2004)—may obscure the effect of biotic interactions. For example, while empirical evidence suggests that interactions most strongly affect early life stages (e.g., competition; Goldberg et al. 2001), many studies transplant older juveniles or adults. Furthermore, a meta-analysis of transplants across species range edges found that 42% altered the transplant sites (e.g., by mowing all plots) in ways that disproportionately affected biotic interactions compared with the abiotic environment (Hargreaves et al. 2014). If the same is true of local adaptation experiments, they may miss the full effect of biotic interactions and could erroneously detect “maladaptation,” where foreign populations outperform the local population. For example, when anti-herbivore defense involves a trade-off with growth (Züst and Agrawal 2017), plants from high-herbivory sites may be locally adapted to natural conditions yet be outperformed by poorly defended but fast-growing foreign plants if herbivory is artificially reduced (for a species-level example, see Fine et al. 2004).

Here we test how biotic interactions affect local adaptation using a quantitative meta-analysis. We synthesize experiments that transplanted individuals from local and foreign populations into a common field site (i.e., common-

garden and reciprocal transplant studies) and reported at least one component of lifetime fitness (emergence, survival, reproduction; >125 studies of >125 taxa, mostly vascular plants; fig. 1). From these we constructed two data sets (table 1). Data set 1 (controlled manipulations within studies) is the subset of studies that experimentally manipulated the environment—for example, a competition-reduction treatment in weeded plots with a paired control treatment in natural vegetation, enabling direct tests of treatment effects. Data set 2 (uncontrolled manipulations across studies) includes the most natural transplant conditions from all studies, including many that altered the environment of all plots without a control treatment, for example, by weeding all plots. Although uncontrolled manipulations often obscure the effect of biotic interactions within studies, they enable among-study comparisons of local adaptation in natural versus biotically altered environments with a larger and more diverse data set. Few studies manipulated only the abiotic environment (with a control treatment or otherwise), so we focus on how manipulating biotic interactions affects local adaptation. Section A of the supplemental PDF (available online) gives results from both biotic and abiotic manipulations, which are generally consistent with each other.

First, we use these data sets to investigate the overall importance of biotic interactions in local adaptation and fitness (questions 1–4). We ask, Does the frequency (question 1) or strength (question 2) of local adaptation vary with whether biotic interactions are left intact (both data sets)? If local adaptation to biotic interactions is common, we should detect more frequent and stronger local adaptation when interactions are left intact. Since affecting fitness is a prerequisite for inducing local adaptation, we use the subset of studies that experimentally manipulated biotic interactions (data set 1) to ask, Do biotic interactions affect fitness (question 3)? We also use data set 1 to ask, How often does manipulating biotic interactions generate “false maladaptation,” where local adaptation is detected under control conditions but foreign advantage is detected when interactions were ameliorated (question 4)?

Second, we test predictions that biotic interactions are especially likely to select for local adaptation at some stages or places (questions 5 and 6). Using both data sets we ask, Do the effects of biotic interactions on local adaptation differ among life stages (question 5)? If biotic interactions are most important at early life stages, we expect that manipulating interactions will affect local adaptation in emergence more than survival or reproduction. Next, because biologists have long speculated that biotic interactions are more evolutionarily important in the tropics (Dobzhansky 1950; Schemske 2009), we ask, Is there a stronger signal of local adaptation to biotic interactions in the tropics (question 6)? We use data set 2 because too few tropical

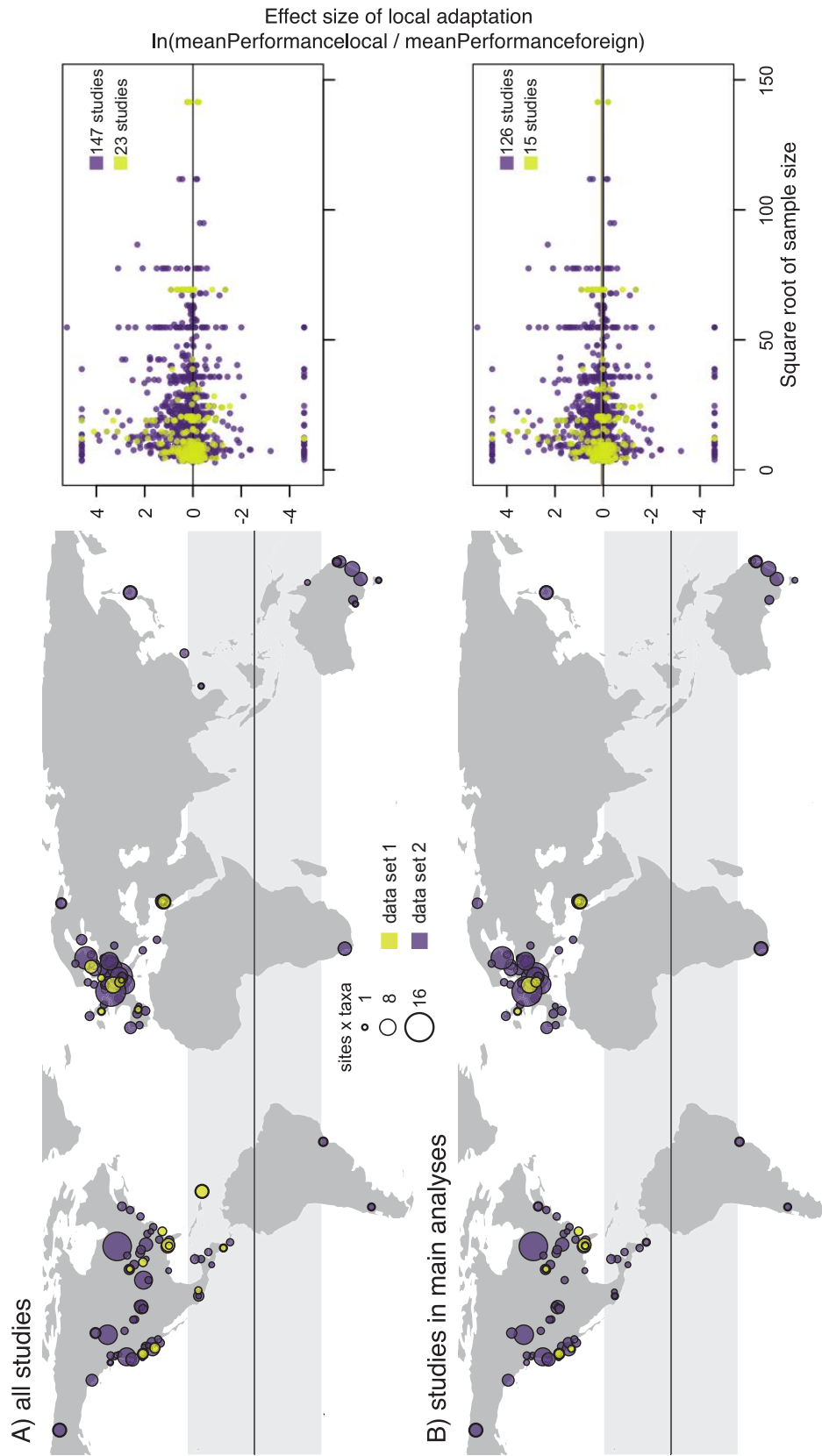


Figure 1: Distribution of transplant experiments regarding geography and sample size. A, One hundred forty-seven studies transplanted local and foreign sources to a common field site (purple), of which 23 studies also experimentally manipulated transplants' biotic or abiotic environment with an appropriate control (yellow; analyses of full data are shown in the supplemental PDF). B, Main analyses on the effects of ameliorating the biotic environment: 126 studies used unaltered environments or universally ameliorated negative biotic interactions (purple), and 15 ameliorated negative biotic interactions with an experimental control (yellow). Maps show one point per study; when studies included multiple sites, we used their average latitude and longitude. Point size reflects the total number of sites \times taxa per study. Shaded rectangles indicate the tropics (-23.5° to 23.5° latitude). Funnel plots show the relatively symmetrical distributions of effect size versus sample size (local + foreign individuals); one point per taxon \times site \times source population \times temporal replicate \times fitness component (and treatment for data set 1).

studies performed a controlled manipulation of transplants' biotic environment (fig. 1).

Methods

Literature Search

Our study leveraged a database of transplant experiments compiled to test the effects of climate anomalies on local adaptation (M. Bontrager, C. D. Muir, C. Mahony, et al., unpublished manuscript). This database compiled previous meta-analyses of local adaptation (Leimu and Fischer 2008; Hereford 2009; Gibson et al. 2016; Oduor et al. 2016) and transplant experiments (Hargreaves et al. 2014; Lee-Yaw et al. 2016) and added studies found in a March 19, 2017, Web of Science search for transplant/translocation/common-garden/provenance trial experiments or encountered while gathering data. The resulting studies were heavily biased toward temperate latitudes, so we added targeted searches for tropical studies, including appeals to colleagues working in the tropics, expanding the search date to March 2019, and searching in Spanish. Full search terms are provided in section B of the supplemental PDF.

We discarded studies that pooled results across transplant sites or source populations unless authors could provide unpooled data.

From >2,000 studies initially found, we discarded those that did not meet the following criteria (the exclusion criteria given below were not used in a concurrent meta-analysis of local adaptation [Briscoe Runquist et al. 2020], which partly explains why some conclusions differ between our studies). We retained only experiments that measured fitness or fitness components (emergence, survival, reproduction), as growth alone is an unreliable indicator of relative fitness in contrasting environments (Hargreaves et al. 2014). We discarded nonnative species, as they have had less time to adapt to conditions in their introduced range, and indoor studies (e.g., growth chambers, greenhouses), as they cannot replicate the suite of diverse, correlated conditions to which populations would adapt in nature.

We defined local adaptation as a local source population outperforming foreign sources at its home site (Kawecki and Ebert 2004) and therefore excluded data from sites that lacked a local source (no sites lacked a foreign source). For each transplant site, we categorized each source

Table 1: Summary of the literature

	Biotic environment manipulated		Abiotic environment manipulated		Both environments manipulated	No environments manipulated ^f
	Expected effect: increase transplant fitness ^a	Expected effect: decrease transplant fitness ^b	Expected effect: increase transplant fitness ^c	Expected effect: decrease transplant fitness ^d	Expected effect: increase transplant fitness ^e	
Data set 1 (23 studies):						
Studies	15	2	4	2	0	23
Taxa	22	2	6	2	0	31
Data set 2 (147 studies):						
Studies	67	0	2	0	22	63
Taxa	76	0	2	0	33	66

Note: For each of 147 studies that transplanted 159 taxa, we noted whether authors manipulated components of the biotic or abiotic environment. Data were grouped into two data sets: data set 1 included all treatments from studies that conducted controlled manipulations (23 studies, 31 taxa), and data set 2 included the most natural conditions from all 147 studies, some of which manipulated the environment without a control treatment. Controlled experiments included manipulations expected to increase or decrease transplant fitness, whereas uncontrolled manipulations were always expected to increase fitness. Study sample sizes for data set 2 sum to >147 because some studies applied different manipulations to different life stages. Main analyses compare the first and last columns, paired within studies for data set 1 ($n = 15$ studies) and across studies for data set 2 ($n = 130$ studies).

^a Manipulations: fencing, caging, insecticide, molluscicide, weeding, mowing, tilling soil, planting in pots using local soil (i.e., microorganisms still present).

^b Manipulations: reducing ant mutualists, planting without nurse plants.

^c Manipulations: irrigation in dry environments, shading seeds to reduce photoinhibition of germination, warming in cold environments, wind barriers, fertilizing.

^d Manipulations: warming in hot environments, exposing seeds to full sunlight (increasing potential photoinhibition).

^e Manipulations: planting in gardening soil, planting in old agricultural fields (presumably enriched soil and reduced canopy height), combinations of individual biotic and abiotic manipulations (e.g., weeding plus irrigation).

^f Note: "Manipulation" refers to controlled experimental manipulations in data set 1 and uncontrolled manipulations in data set 2. Thus, individuals in "No environments manipulated" (i.e., control treatment) for data set 1 are not necessarily in "No environments manipulated" in data set 2, as they may have been subject to an uncontrolled manipulation.

as “local” or “foreign” using the designations given by the authors; if no source was specified as local, we designated the closest source as local. However, in some cases the local source (even as defined by the authors) came from a considerable distance from the transplant site. We therefore imposed a cutoff that local sources must originate from <100 km and <100 m elevation of the transplant site; those from farther away were redesignated as foreign. Median (mean) distance between source origin and transplant site was 0 km (5.0 km) for local sources and 230 km (584 km) for foreign sources (fig. S1; figs. S1–S4 are available online). The threshold for local is necessarily arbitrary, so we explored it in supplemental analyses, first including the distance between local source origin and transplant site as a random covariate, then using a more restrictive definition of local (<50 km and <100 m asl; supplemental PDF, sec. A.2). Conclusions were unchanged in 10 of 11 alternate models, but in one analysis (question 2, data set 2, effect size of local adaptation) the effect of biotic amelioration on local adaptation became nonsignificant ($P = .043$ to $P = .10$) under a stricter definition of local (table S1; tables S1, S2 are available online).

These refinements yielded a data set of 147 studies of 159 taxa (usually species but occasionally subspecies or ploidy levels), of which 23 also conducted controlled manipulations of the biotic or abiotic environment (fig. 1; table 1).

Data Collection

Data were sourced from tables and figures using WebPlot Digitizer (Rohatgi 2018) or from authors. For each study, we collected mean fitness for each combination of taxon, source population, transplant site, life stage at which the source was transplanted (seeds/eggs, seedlings/juveniles, or adults), temporal replicate (e.g., if transplants were replicated in multiple years), fitness component (germination/emergence, survival, reproduction, or composites of these), and experimental treatment if studies experimentally manipulated the environment; hereafter, each taxon \times source population \times transplant site \times life stage \times temporal replicate \times fitness component \times treatment combination is referred to as a “data point.” When multiple variables could be used for a single fitness component (e.g., both flower counts and total seed weight reported as “reproductive output”), we used the one that most closely represented fitness. If germination or survival was reported multiple times for the same temporal replicate (e.g., first- and second-season survival for a perennial plant), only the final estimates were recorded as a proportion of the initial number of individuals. If multiple estimates of reproductive output were reported for a single temporal replicate (e.g., first- and second-season fruit production), we summed

these to calculate cumulative reproduction. For studies that did not report composite fitness but did report at least two of emergence rate, survival rate, and reproductive output, we calculated composite fitness as their product (e.g., emergence of seedlings/seed \times survival of juveniles/seedling = juveniles/seed).

For each mean fitness value we extracted the associated sample size and variation. Many studies used blocked designs, sometimes with multiple block levels, such that n was not always clear in every analysis; we therefore extracted the total n individuals across blocks. We extracted whatever measure of variation was provided and noted the type of measure (e.g., standard error, standard deviation, variance).

We recorded whether and how the biotic or abiotic environment was manipulated for each data point (possible manipulations are listed in the footnotes of table 1). We did not count manipulations intended to mimic the natural environment (e.g., irrigation for riparian species planted outside riparian habitat; Angert and Schemske 2005). We categorized whether each data point was part of an experimental treatment testing the effect of biotic or abiotic factors (i.e., experimentally applied manipulations or their concurrent control treatments). Note that even the control treatment of an experiment can be subject to an uncontrolled environmental manipulation. For example, a study might grow all transplants in a herbivore enclosure and then apply an irrigation treatment to half (an uncontrolled biotic manipulation with a controlled abiotic manipulation; Center et al. 2016). Based on whether studies included controlled experimental manipulations, we created two data sets as described below.

Data Set 1: Studies with Controlled Experimental Manipulations of the Biotic or Abiotic Environment

Data set 1 includes only transplant experiments that also experimentally manipulated (i.e., with an appropriate control treatment) the biotic or abiotic environment. We categorized the most natural treatment as the control and categorized manipulative treatments based on (a) whether they directly affected biotic interactions, the abiotic environment, or both and (b) whether authors expected treatments to increase or decrease transplant performance (table 1). While we found 23 studies that experimentally manipulated the environment, because of the low sample size of abiotic treatments and treatments expected to decrease performance we focus on control treatments and biotic treatments that increase performance ($n = 15$ studies including 22 taxa: 14 herbaceous perennials, 7 annuals, 1 mollusk). Figure S1 shows results from all 23 studies and all treatment categories.

Data Set 2: Most Natural Treatment from All Studies

Data set 2 includes the most natural treatment from all transplant experiments, including the control treatment from studies in data set 1 (full data set 2: 147 studies of 159 taxa). Even the most natural conditions of each study were often subject to procedures that altered the biotic and/or abiotic environment. We categorized each data point based on whether it was subject to manipulations that directly affected biotic interactions, the abiotic environment, both, or neither. Unlike experimental treatments, all uncontrolled manipulations were expected to improve transplant success (table 1). Because of the low sample size of uncontrolled manipulations that affected only abiotic factors and the difficulty disentangling the roles of biotic and abiotic factors when they are altered simultaneously, we focus on transplants where conditions were entirely natural versus those where only biotic interactions were directly altered (main analyses data set 2 = 126 studies of 130 taxa: 65 herbaceous perennials, 34 woody perennials, 18 annuals, 5 arthropods, 4 mollusks, 2 fish, 1 fungus, 1 coral). Results from all 149 studies comparing all alterations are shown in figure S1.

Calculation of Local Adaptation Metrics

For each data set, we calculated three metrics of local adaptation: probability of local adaptation, effect size of local adaptation, and standardized fitness. The first two (probability and effect size) directly compare performance of local versus foreign source populations at each site. First, for each site we averaged across data points to get mean(fitness_{local}) and mean(fitness_{foreign}) for each taxon × treatment × life stage × temporal replicate × fitness component combination (Blanquart et al. 2013; experimental treatment is relevant only for data set 1). To assess the probability of local adaptation (question 1), we calculated a binary variable (yes if mean(fitness_{local}) > mean(fitness_{foreign}), otherwise no) to qualitatively assess the direction of differences given that statistical significance was not always reported.

Second, to assess the strength of local adaptation (question 2) at each site, we calculated a quantitative effect size for each taxon × treatment × life stage × temporal replicate × fitness component combination (as for the probability of local adaptation, only control treatments are included in calculations for data set 2) as a classic response ratio (Hedges et al. 1999; Nakagawa and Santos 2012): $\ln(\text{mean}(\text{fitness}_{\text{local}})/\text{mean}(\text{fitness}_{\text{foreign}}))$. Positive effect sizes indicate local adaptation while negative values indicate foreign advantage, and the metric is proportional; for example, a doubling of the effect size represents a doubling of the magnitude of local adaptation (Hedges et al. 1999). In the few cases when mean(fitness_{foreign}) or mean(fitness_{local}) =

0, this ratio yields +infinity or -infinity, respectively. We reasoned that these are instances of strong adaptation or maladaptation, but because of finite sample sizes zeros are more likely than very small values. We handled this by replacing 0 foreign fitness with 1% of the mean local fitness at the site and replacing 0 local fitness with 1% of the mean foreign fitness at the site. Cases where fitness = 0 for all sources were excluded from both binary and response ratio metrics. We did not calculate a standard meta-analytic effect size that incorporates variance (e.g., Hedges' *d*), as a quarter of studies did not quantify variation. Instead, we accounted for variation in sampling effort across studies by weighting each effect size by the square root of the combined sample size across sources (details are provided in "Analyses").

Third, to compare performance without reducing the data to mean local versus mean foreign performance and without having to adjust zero values, for each data set we calculated a standardized fitness metric for each source at each site. We used this metric to compare local versus foreign sources (strength of local adaptation; question 2, both data sets) and control versus biotically altered environments (fitness effect of biotic interactions; question 3, data set 1). For each taxon × life stage × temporal replicate × fitness component combination, we divided the fitness of each data point by the maximum fitness achieved by any source at that site in that data set. This removes the effect of site quality and transforms different response scales to values between 0 and 1, similar to the local adaptation meta-analysis of Halbritter et al. (2013). For data set 1, the maximum fitness can be from any treatment. For data set 2, which excludes experimental manipulations, the maximum fitness is from the most natural treatment, so standardized fitness can vary for studies that occur in both data sets. Note that for any analysis, standardized fitness has a bigger *n* than the equivalent analysis of probability or effect size (compare *n* in fig. 2 [probability] and fig. 3A and 3B [effect size] with that in fig. 3C and 3D [standardized fitness], and compare *n* in fig. S1C and S1D with that in fig. S1E and S1F), as each source population at a transplant site contributes data rather than being combined into one local-foreign comparison per site.

Analyses

Analyses were performed in R version 3.3.3 (R Core Team 2017). Data sets 1 and 2 were analyzed using separate mixed effects models (lmer and glmer functions, lme4 package; Bates et al. 2015). As data points from the same study or taxon are not independent and fitness components could vary in their ability to reveal local adaptation, we included random intercepts for study, taxon, and fitness metric (Bolker et al. 2009; Nakagawa and Santos 2012). Rerunning

models using only the fitness component that most closely approximated lifetime fitness did not alter conclusions (table S2); thus, studies that measured multiple fitness components did not overinfluence our results. To account for phylogenetic relatedness across studies (Nakagawa and Santos 2012), we included a nested taxonomic random effect (as per Pinsky et al. 2019) up to the highest taxonomic grouping with at least five levels: genus to order for data set 1, and genus to phylum for data set 2. We also ran a formal phylogenetically controlled analysis but could only do this for plants (92% of our data), as an equivalent full eukaryotic tree was not available (supplemental PDF, sec. A.4). Neither the nested taxonomic random effects compared with a simpler “species” random effect nor the full phylogenetic analysis compared with the equivalent (plant-only) model without accounting for the tree altered results; therefore, we did not detect a phylogenetic signal of local adaptation.

Formal meta-analyses weight effect sizes by their pooled variance, but >25% of our data points lacked variance estimates and response ratios included binomial and Poisson-distributed data, violating assumptions for calculating pooled variance for response ratios (Hedges et al. 1999). Rather, for analyses of effect size we accounted for variation in sampling effort by weighting each response ratio by the square root of the corresponding sample size, the sum of local and foreign individuals from which the response was obtained. This downweights effect sizes from fewer source populations or fewer individuals per source but not effect sizes with higher variance for a given n . Funnel plots show a relatively symmetrical distribution of effect size versus n , suggesting that publication bias did not strongly influence results (fig. 1). Analyses of the probability of local adaptation and standardized fitness were left unweighted, because weights cannot be incorporated as flexibly into binomial models (weights are the number of binomial trials that produces a proportional response; binary local adaptation is not a proportional response, and standardized fitness includes nonbinomial data). As neither the probability of local adaptation nor standardized fitness are effect sizes, they should be less affected by publication bias.

For questions 1–3, 5, and 6 we tested the importance of fixed effects (including interactions) by comparing models with and without the effect of interest using likelihood ratio tests and a χ^2 distribution (anova function, base R). Differences among factor levels within significant fixed effects or between fixed effects and zero were assessed using the lsmeans function from the lsmeans package (Lenth 2016). Figures present means and residuals after partialing out variance attributable to random factors (visreg package; Breheny and Burchett 2017); 95% confidence intervals were extracted via lsmeans.

Question 1: Is Local Adaptation More Common When Biotic Interactions Are Left Intact? Using the binary local adaptation metric and binomial generalized linear mixed models (GLMMs; log link function), we tested whether ameliorating negative interactions affects the probability of detecting local adaptation (i.e., control vs. biotically ameliorated treatments in data set 1, natural vs. biotically ameliorated transplant conditions in data set 2). Biotic amelioration affects local adaptation if the effect of manipulation is significant. An overall signal of local adaptation exists if the mean frequency of local adaptation is >0 (lower 95% confidence limit >0), which is a 50% probability on the logit scale.

Question 2: Is Local Adaptation Stronger When Biotic Interactions Are Left Intact? We compared the strength of local adaptation among control/natural versus biotically ameliorated environments using two metrics, effect size of local adaptation (direct local-foreign comparison) and standardized fitness (larger data set). Effect sizes were analyzed using a Gaussian error distribution, weighted by the square root of n . As response ratios already incorporate the difference between local and foreign source populations, the only fixed effect in these models was whether biotic interactions had been ameliorated (“manipulation”). Biotic amelioration affects local adaptation if the effect of amelioration is significant, and an overall signal of local adaptation exists if the mean effect size exceeds a null expectation of zero (i.e., no difference in performance between local and foreign sources). Standardized fitness is bounded between 0 and 1, so we used a binomial GLMM and logit link function with manipulation (control/natural vs. biotically ameliorated) and source (local vs. foreign) as interacting fixed effects. Biotic amelioration affects the strength of local adaptation if the fitness difference between local and foreign sources depends on the biotic environment (i.e., significant source \times manipulation interaction). When this was the case, we tested whether local and foreign fitness differed within each environment using least square means contrasts and a Tukey correction for multiple comparisons to maintain $\alpha = .05$; overall local adaptation was detected if local sources had greater mean fitness than foreign sources.

Question 3: Do Biotic Interactions Affect Fitness? For biotic interactions to generate local adaptation, they must affect fitness. We tested whether this was the case by comparing standardized fitness in control versus biotically ameliorated treatments in data set 1 (we did not use data set 2, as the effect of biotic amelioration is confounded with study; note that all data set 1 studies in the main analyses come from temperate zones; fig. 1B). This was equivalent to the reduced model from question 2; that is, treatment

and source (local vs. foreign) were noninteracting fixed effects.

Question 4: Does Manipulating Biotic Interactions Lead to False Detections of “Maladaptation”? First, we asked how often ameliorating biotic interactions changed the qualitative conclusion about local adaptation. We assessed this question using 74 taxon \times site \times life stage \times temporal replicate \times fitness component combinations from data set 1 with both a control and a biotically ameliorated treatment. For each of the 74 comparisons, we determined whether both treatments yielded the same qualitative conclusion about mean(fitness_{local}) versus mean(fitness_{foreign}) (i.e., both find local > foreign, both find local < foreign, or both find local = foreign) or different conclusions (table 2). We assessed qualitative differences, as authors did not always test these contrasts statistically; we tally these results but do not perform a statistical test because we do not have a null hypothesis to compare to.

Second, we asked whether ameliorating biotic interactions led to false detections of maladaptation more often than expected by chance (i.e., if local adaptation to biotic interactions was common and reduced relative fitness in environments where biotic interactions were ameliorated). We define false maladaptation as cases where local adaptation (local > foreign) was detected under control conditions but foreign advantage (foreign > local) was detected when biotic interactions were experimentally ameliorated (table 2, G). We tallied such cases from the 74 comparisons described above. To assess whether biotic amelioration leads to false detections of maladaptation more often than expected by chance, we also tallied cases of the opposite pattern (foreign advantage in the control and local adaptation under biotic amelioration; table 2, C). For two taxa \times site combinations that contributed comparisons for more than one fitness component, we retained only composite fitness to avoid pseudoreplication. This yielded $n = 19$ unique taxa \times site comparisons where local adaptation was detected in one treatment and foreign advantage in the other (table 2, C + G). We compared the detections of false maladaptation versus the opposite pattern to a null expecta-

tion of 50:50 using a one-tail binomial test (binom.test function, base R).

Question 5: Do Biotic Interactions Affect Local Adaptation Most Strongly at Early Life Stages? If biotic interactions are most important at early life-history stages, we expect the greatest difference in local adaptation between natural versus biotically ameliorated environments to be detected in measurements of emergence versus survival or reproduction. Using both data sets, we tested whether the effect of biotic amelioration on the frequency and effect size of local adaptation differed among fitness components (i.e., a manipulation \times fitness component interaction). We excluded composite measures, as these confound multiple life stages.

Question 6: Is There More Local Adaptation to Biotic Interactions in the Tropics? Whereas most transplant experiments come from the temperate zone, biologists have long speculated that biotic interactions may be more evolutionarily important in the tropics. We tested this by re-running models from questions 1 and 2 with an additional interacting fixed effect, “latitudinal zone,” classifying data from sites between 23.5°N and 23.5°S as tropical and those closer to the poles as temperate. We used categorical latitude to be consistent with seminal work postulating differences between latitudinal zones rather than continuous latitudinal gradients (Dobzhansky 1950). We used data set 2, as the only tropical studies in data set 1 experimentally manipulated the abiotic environment (Fetcher et al. 2000; Center et al. 2016), which also meant we were unable to test latitudinal patterns associated with question 3. We excluded phylum, class, and genus from the nested random effect, as less than three levels overlapped between latitudinal zones (final random effect (1 | order/family)).

Results

Of the 147 studies that measured fitness components of local and foreign sources in a common field site, less than half (43%, i.e., 63 studies) had at least some transplants

Table 2: Comparisons in question 4

Biotic amelioration treatment	Control treatment		
	Local > foreign (local adaptation)	Local = foreign	Local < foreign (foreign advantage)
Local > foreign (local adaptation)	A	B	C
Local = foreign	D	E	F
Local < foreign (foreign advantage)	G	H	I

Note: Using data set 1, we compared the relative fitness of local versus foreign sources between control treatments and paired treatments that ameliorated the biotic environment. We asked how often ameliorating biotic interactions changed the conclusion about local adaptation by tallying cases where treatments reached the same conclusion (bold type) versus different conclusions (roman type). We tested whether ameliorating interactions led to false detections of maladaptation (G) more often than the reverse (C).

in unaltered natural environments (table 1). Sixty percent universally altered the biotic environment for at least one life stage (numbers sum to >100%, as some studies alter the environment of some life stages but not others). Most studies (92%) used plants, and by far the most frequently altered components of the environment were biotic: competition (63 studies via herbicide, weeding, clipping, or planting in tilled gardens or pots) and herbivory/predation (45 studies via fences, cages, and poisons). Only 23 studies paired transplants with experimental manipulations of biotic or abiotic factors that might cause local adaptation, of which only 10 included a control treatment in a natural, unaltered environment (Thompson et al. 1991; Kindell et al. 1996; Knight and Miller 2004; Sambatti and Rice 2006; Abdala-Roberts and Marquis 2007; Ariza and Tielbörger 2011; Hufford and Mazer 2012; Stanton-Geddes et al. 2012; Tomiolo et al. 2015; Hughes et al. 2017).

Question 1: Is Local Adaptation More Common When Biotic Interactions Are Left Intact?

No—ameliorating negative biotic interactions (i.e., reducing competition, herbivory, or predation) did not affect the probability of detecting local adaptation (fig. 2). Local adaptation was equally probable in control and biotically ameliorated treatments within experimental stud-

ies (fig. 2A) and between studies using natural versus biotically ameliorated environments (fig. 2B). Local adaptation was detected more often than what would be expected by chance across studies in the larger data set 2 but not in data set 1 (fig. 2).

Question 2: Is Local Adaptation Stronger When Biotic Interactions Are Left Intact?

No—the strength of local adaptation was either unaffected by biotic amelioration or stronger when interactions were ameliorated (i.e., opposite of predictions; table 3). When studies experimentally tested the effect of biotic interactions on local adaptation (data set 1), ameliorating biotic interactions did not alter the effect size of local adaptation (fig. 3A) or the fitness advantage of local sources (fig. 3C). Furthermore and contrary to our predictions if local adaptation to biotic interactions was common, studies that universally ameliorated biotic interactions detected stronger local adaptation than studies that used natural environments (data set 2: fig. 3B, 3D). We did not detect an overall signal of local adaptation measured as effect size (fig. 3A, 3B) but did when local adaptation was measured as the fitness advantage of all local sources versus all foreign sources (fig. 3C, 3D). This discrepancy is likely due to

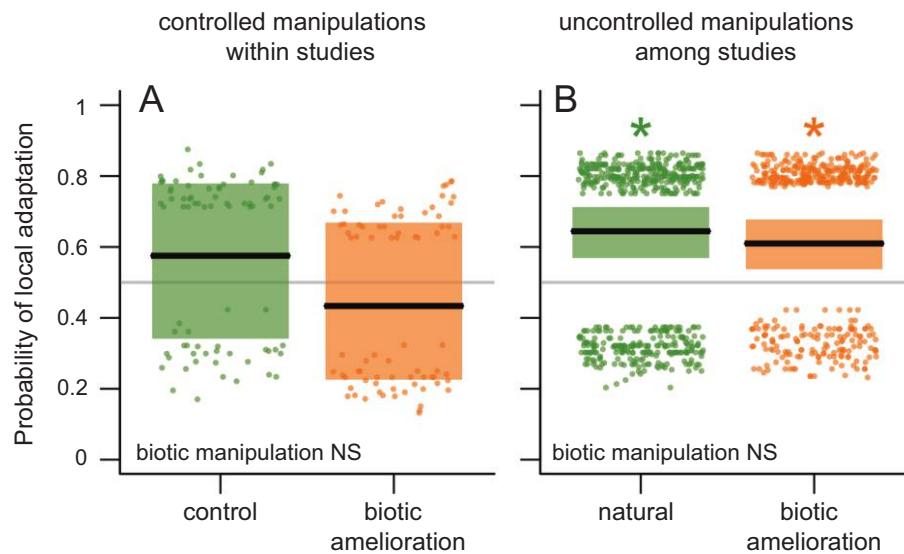


Figure 2: Local adaptation was not detected more often when biotic interactions were left intact (question 1). Local adaptation was scored as detected if the mean fitness of local sources was greater than the mean fitness of foreign sources. Central lines, points, and rectangles respectively show means, partial residuals, and 95% confidence intervals extracted from models and back transformed from the logit scale; scatter on the Y-axis is residual variation after accounting for random effects of study, taxon, and fitness component. Green = control or natural transplant environments; orange = biotically ameliorated environments. A, Studies that experimentally ameliorated biotic interactions with a control treatment ($n = 155$ data points from 15 studies; data set 1). B, Most natural conditions from all studies ($n = 958$ data points from 126 studies; data set 2). Asterisks indicate that local adaptation was detected more often than what would be expected by chance (i.e., probability >0.5). Full statistical results are shown in table 3. NS = not significant.

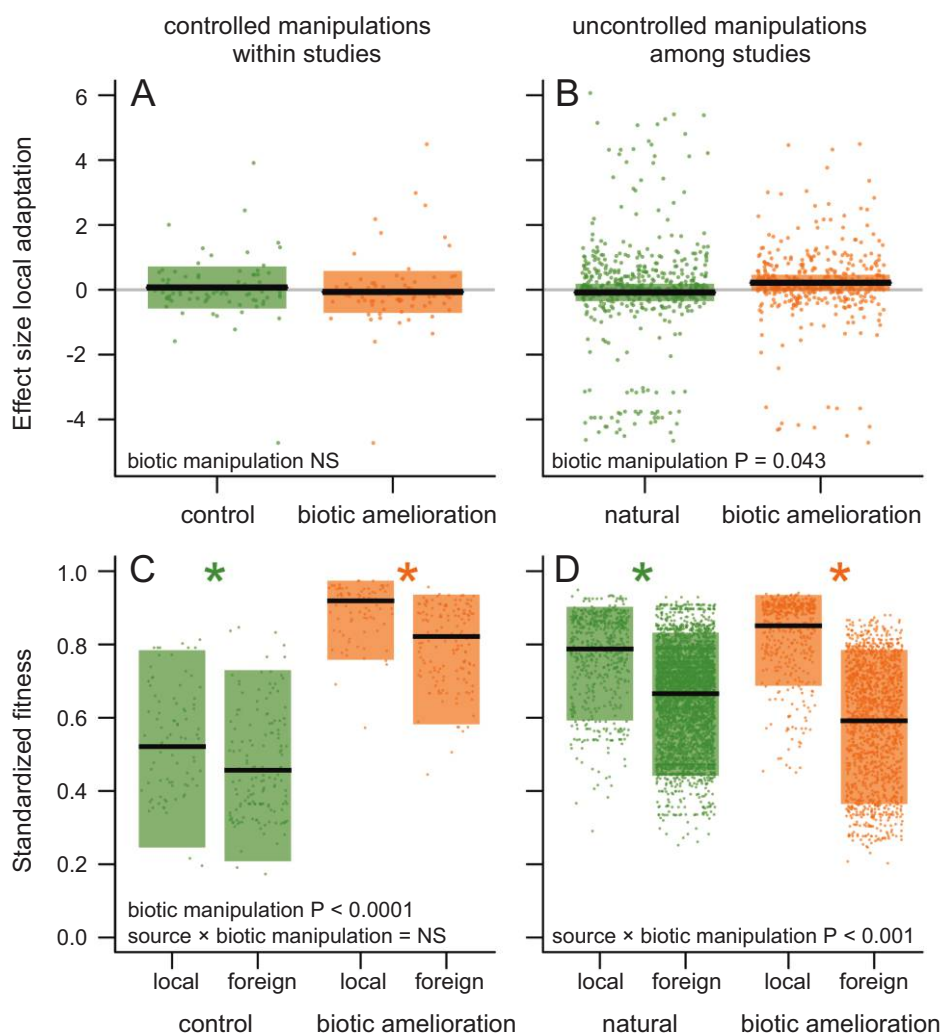


Figure 3: Local adaptation was not stronger when biotic interactions were left intact. The strength of local adaptation was assessed directly as an effect size (A, B; $\ln(\text{mean local fitness}/\text{mean foreign fitness})$; significant local adaptation if confidence intervals do not overlap zero) and indirectly but with a larger n using the standardized fitness of local versus foreign source populations (C, D; significant local adaptation if local fitness is greater than foreign fitness). Bottom left text indicates whether manipulating biotic interactions affected the strength of local adaptation (question 2, all panels) and/or fitness (question 3; C, biotic manipulation). Asterisks indicate significant local adaptation in a given data set—manipulation group. A, C, Within studies that experimentally manipulated biotic interactions (data set 1), local adaptation was not stronger in the control treatment, even though biotic interactions affected fitness (C). B, D, Across all studies (data set 2), biotic amelioration did not affect the effect size of local adaptation (B) but increased the difference in standardized fitness of local versus foreign sources (D). n data points (studies): for A, 155 (15); for B, 958 (126); for C, 456 (15); for D, 6,688 (126). Colors are as in figure 2. NS = not significant.

the much larger n for standardized fitness versus effect size (fig. 3).

Question 3: Do Biotic Interactions Affect Fitness?

Yes—transplant fitness was almost twice as high when negative biotic interactions were experimentally ameliorated (i.e., reduced herbivores, competitors, or predators) compared with when they were left intact (least square mean \pm SE across studies and sources: control, 0.50 ± 0.14 ; biotically ameliorated, 0.87 ± 0.07 ; fig. 3C; table 3).

Question 4: Does Manipulating Biotic Interactions Lead to False Detections of “Maladaptation”?

Among studies that experimentally ameliorated interactions (data set 1), manipulating the biotic environment changed the qualitative signal of local adaptation in 22 (30%) of 74 comparisons (each comparison is local vs. foreign fitness per taxon \times site \times life stage \times temporal replicate). Of 19 taxon \times site comparisons where the signal changed from local adaptation in one treatment to foreign advantage in the other, ameliorating interactions

Table 3: Analyses for questions 1–3: biotic interactions versus local adaptation (LA) and fitness

	Response	Fixed effect	Do biotic interactions affect LA (questions 1 and 2) or fitness (question 3)?	Overall local adaptation?	Figure
Question 1: Is LA more common when biotic interactions are left intact?					
Data set 1	Binary LA	Manipulation	No: manipulation not significant $\chi^2_1 = 2.5, P = .11$	No	2A
Data set 2	Binary LA	Manipulation	No: manipulation not significant $\chi^2_1 = .5, P = .47$	Yes	2B
Question 2: Is LA stronger when biotic interactions are left intact or ameliorated?					
Data set 1	Effect size LA	Manipulation	No: manipulation not significant $\chi^2_1 = .8, P = .38$	No	3A
Data set 1	Standardized fitness	Manipulation × source	No: interaction not significant $\chi^2_1 = 1.8, P = .18$	Yes: local/foreign significant $\chi^2_2 = 5.1, P = .025$ Local > foreign	3C
Data set 2	Effect size LA	Manipulation	Yes: manipulation significant $\chi^2_1 = 4.1, P = .043$ Bio.amel > control	Natural: no Bio.amel: no	3B
Data set 2	Standardized fitness	Manipulation × source	Yes: interaction significant $\chi^2_1 = 13.7, P = .0002$	Natural: yes (local > foreign: $P < .0001$) Bio.amel: yes (local ≫ foreign: $P < .0001$)	3D
Question 3: Do biotic interactions affect fitness?					
Data set 1	Standardized fitness	Manipulation + source ^a	Yes: manipulation significant $\chi^2_1 = 70.5, P < .0001$ Bio.amel > control	Yes: local/foreign significant $\chi^2_1 = 5.1, P = .025$ Local > foreign	3C

Note: We tested whether local sources outperformed foreign sources more frequently (binary LA) or more strongly (effect size LA or standardized fitness) in control treatments versus treatments that experimentally ameliorated biotic interactions (“bio.amel”; data set 1) or between studies that transplanted into natural, unaltered environments versus those that ameliorated biotic interactions without a control treatment (data set 2). Binary (yes if $\text{mean}(\text{fitness}_{\text{local}}) > \text{mean}(\text{fitness}_{\text{foreign}})$) and effect size ($\ln(\text{mean}(\text{fitness}_{\text{local}})/\text{mean}(\text{fitness}_{\text{foreign}}))$) responses explicitly compare local versus foreign sources; biotic interactions affect local adaptation if “manipulation” is significant. For standardized fitness, biotic interactions affect local adaptation if the effect of being local differs between natural versus biotically ameliorated environments (source × manipulation interaction). Local adaptation is detected overall if confidence intervals do not overlap zero (binary LA and effect size LA) or if local standard fitness is greater than foreign standard fitness (tested against the no-interaction model if the interaction was not significant). Significant effects are in bold. The column labeled “Figure” indicates where data are shown. All models include random intercepts for taxonomy, study, and fitness component.

^a The model in question 3 is the reduced form of the second model from question 2 (standardized fitness, data set 1) with the nonsignificant interaction removed.

led to false detections of maladaptation (local adaptation in the control but foreign advantage in the biotic amelioration treatment), twice as often as the reverse pattern (13 vs. 6 comparisons; $P = .08$ in binomial test compared with null expectation of 50:50).

Question 5: Do Biotic Interactions Affect Local Adaptation Most Strongly at Early Life Stages?

No—biotic interactions did not affect local adaptation more strongly at emergence versus later life stages (table 4). In the only analysis in which local adaptation varied among fitness components (binary local adaptation, data set 2; table 4), biotic amelioration did not affect the probability

of local adaptation in emergence or survival but increased the detection of local adaptation for reproduction (i.e., the latest life stage), opposite of our predictions.

Question 6: Is There More Local Adaptation to Biotic Interactions in the Tropics?

With the admittedly few tropical studies available to test the question, the answer from the best available data is mixed: yes for the probability of local adaptation, no for the strength of local adaptation. Latitude interacted significantly with biotic amelioration to affect the probability of local adaptation (latitudinal zone × biotic amelioration: $\chi^2_1 = 4.3, P = .038$; fig. 4). Whereas temperate studies

Table 4: Local adaptation not affected more strongly by biotic interactions at early life stages (question 5)

Response	Initial fixed effects	Significance of fixed effects			Overall local adaptation in any manipulation × fitness component combination?
		Interaction	Manipulation ^a	Fitness component ^b	
Data set 1: Studies with controlled manipulations of biotic interactions					
Binary LA	Manipulation × fitness component	$\chi^2_1 = 4.4$ $P = .11$...	$\chi^2_2 = 2.0$ $P = .36$	No
Effect size LA	Manipulation × fitness component	$\chi^2_1 = .3$ $P = .86$...	$\chi^2_2 = 3.7$ $P = .16$	No
Data set 2: Most natural conditions from all studies					
Binary LA	Manipulation × fitness component	$\chi^2_1 = 6.6$ $P = .037$	For emergence: manipulation not significant For survival: manipulation not significant For reproduction: $P = .032$ (LA more common in bio.amel)	Natural: fitness component not significant Bio.amel: LA approximately more common in reproduction than emergence ($P = .050$)	Natural: LA in survival and reproduction Bio.amel: LA in survival and reproduction
Effect size LA	Manipulation × fitness component	$\chi^2_1 = 1.9$ $P = .39$...	$\chi^2_2 = 3.2$ $P = .21$	No

Note: “Manipulation” compares the probability of local adaptation (binary LA) or the strength of local adaptation (effect size LA) under ameliorated biotic interactions (“bio.amel”) to more natural conditions in either a concurrent control treatment (“control”; data set 1) or treatments from other studies (“natural”; data set 2). “Fitness component” is emergence, survival, or reproduction. A significant manipulation × fitness component interaction means the effect of biotic interactions on local adaptation differs among fitness components. If the interaction was not significant, it was removed and the effect of fitness component was assessed to test whether local adaptation varied among life stages (the effect of biotic amelioration is tested with the full data set; table 3). When the interaction was significant, we assessed how the effect of biotic amelioration on local adaptation differed among life stages (“Manipulation”) and whether local adaptation was stronger for some life stages within each treatment (“Fitness component”). Data differ from questions 1 and 2, as composite fitness metrics are excluded. Responses and significance testing are as in table 3.

^a Comparing model with manipulation + fitness component to a model without manipulation.

^b Comparing model with manipulation + fitness component to a model without fitness component.

did not detect local adaptation more often in natural conditions (least square mean effect of biotic amelioration in temperate zones: $P = .32$), tropical studies did tend to detect local adaptation more often in natural environments (least square mean effect of biotic amelioration in tropics: $P = .086$): 89% of tropical data points in natural environments detected local adaptation ($n = 9$ data points from four studies), compared with only 50% of tropical data points in biotically ameliorated environments ($n = 26$ data points from nine studies; fig. 4).

The strength of local adaptation also varied as expected if local adaptation to biotic interactions was stronger in the tropics, but statistical support was low. The effect size of local adaptation was greater in natural versus biotically ameliorated environments in the tropics, whereas the opposite was true in the temperate zone, but the interaction was not significant (amelioration × latitudinal zone: $\chi^2_1 =$

0.44, $P = .51$). Similarly, in the tropics local sources had the greatest advantage in natural environments, whereas in the temperate zone local sources had the greatest advantage in biotically ameliorated environments, but the interaction was not significant (amelioration × local/foreign × latitudinal zone: $\chi^2_1 = 2.9$, $P = .088$).

Discussion

Across studies (which were dominated by vascular plants in temperate latitudes), we found little evidence that biotic interactions are broadly important in driving local adaptation. Local adaptation was not more common or stronger in control treatments than in treatments that experimentally ameliorated negative interactions (competition, herbivory, predation), nor was it more common or stronger in studies that used intact transplant environments versus

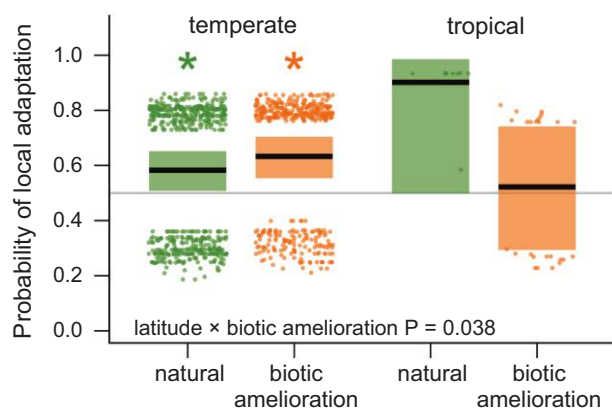


Figure 4: The effect of biotic amelioration on local adaptation varies between the temperate and tropical zones (question 6). In the temperate zone, local adaptation (scored as yes if local fitness was greater than foreign fitness) was more common across studies that ameliorated biotic interactions than studies that used natural conditions, whereas in the tropics local adaptation was more common when biotic interactions were left intact (data set 2). However, least square mean contrasts comparing the probability of local adaptation among environments (green vs. orange bars) were not significant for either latitudinal zone. Asterisks indicate significant local adaptation for a given manipulation-latitude combination (local adaptation was not quite significant under natural conditions in the tropics, as the lower confidence interval bound overlapped zero [-0.017]). Formatting is as in figure 2. Sample sizes: temperate, $n = 938$ data points from 119 studies; tropical, $n = 35$ data points from 13 studies).

studies that ameliorated negative interactions for all transplants (figs. 2, 3). Importantly, the apparent lack of overall local adaptation to biotic interactions did not occur because interactions did not affect fitness, as experimental alleviation of negative interactions significantly improved fitness across studies (fig. 3C), an effect also found across studies that explicitly compared biotic and abiotic drivers (Briscoe Runquist et al. 2020). Nor does it seem to be due to constraints on local adaptation in general, as local source populations had significantly higher fitness than foreign source populations overall (fig. 3C, 3D). Below we discuss potential explanations for inconsistent local adaptation to biotic interactions, despite their effect on fitness, and how these could be tested in future work.

First, biotic interactions might often be unpredictable at the spatial or temporal scale required for local adaptation. The abundance and identity of interacting species can vary greatly within a focal species' population, as species are often patchily distributed in space (Wagner et al. 2000) and time (White et al. 2006), and many pairwise interactions are mediated by other species (Mayfield and Stouffer 2017) and the abiotic environment (Adler et al. 2006; Germain et al. 2018), reducing the interaction consistency between any two species (Magurran and Henderson 2010). Therefore, one explanation for our results is

that biotic interactions (or at least the generalized negative interactions most often ameliorated in transplant experiments) is less predictable among populations than the abiotic environment. Thus, biotic interactions may generally select for increased phenotypic plasticity more than local adaptation, with the testable exception of more specialized interactions.

Second, if adaptation to biotic interactions rarely involves trade-offs, it could commonly result in adaptation but rarely in local adaptation. Adaptation without trade-offs would result in universally superior populations (Herford 2009); for example, when plants compete for light, bigger might always be better. Superior populations would outperform other populations whether in their home site or not, so a reciprocal transplant would not detect an overall home site advantage. However, our results hint that adapting to biotic interactions is not trade-off free. Experimentally reducing negative interactions altered the conclusion about local adaptation in almost a third of cases, and these changes were biased two-to-one toward false maladaptation, where local genotypes were at a disadvantage when biotic interactions were ameliorated (question 4). This suggests a testable hypothesis that some interactions select for universally superior genotypes, whereas others select for context-dependent adaptations (e.g., antiherbivore defenses) and so should more often spur local adaptation (O'Brien et al. 2018).

Third, most transplant experiments came from temperate areas (fig. 1), whereas large-scale experiments suggest that biotic interactions are strongest in the tropics (Roslin et al. 2017; Hargreaves et al. 2019). If stronger interactions produce stronger selection (Benkman 2013), temperate-biased data may underestimate the global importance of adaptation to biotic interactions. Indeed, in contrast to the lack of evidence for local adaptation to biotic interactions overall, the limited tropical data available suggest that local adaptation to biotic interactions may be more common in the tropics (fig. 4). While this does not explain the surprising lack of local adaptation to interactions in the temperate zone despite strong effects on fitness (fig. 3C), it highlights the need for tropical tests of local adaptation and suggests that there could be large-scale mechanisms that govern the prevalence of local adaptation to the biotic environment.

Our results have important implications for how local adaptation is tested in the field. One interpretation is that biotic interactions mostly add “noise” to tests of local adaptation. Overall—although driven by temperate ecosystems—studies that ameliorated negative interactions detected stronger local adaptation (fig. 3D), perhaps because protecting transplants increased sample sizes or reduced variability in fitness. If the research goal is to test for local adaptation to the abiotic environment, reducing negative

interactions may increase experimental power to do so. However, if the goal is to detect which components of the environment cause local adaptation, to assess the fitness consequences of local adaptation for natural populations, or to test local adaptation in environments where interactions are strong (e.g., at low latitudes and elevations; Roslin et al. 2017; Hargreaves et al. 2019), biotic interactions should be left intact as they affect fitness (fig. 3C, 3D) and can alter the expression of local adaptation (as found in question 4 and in a parallel meta-analysis by Briscoe Runquist et al. [2020]).

Two important caveats to our conclusions stem from the fact that most of our data come from plants and that we could robustly test only the effect of ameliorating competition and consumption. Plants are overrepresented among local adaptation studies as they are experimentally tractable and should experience strong selection for local adaptation since they cannot leave unfavorable sites after germination. The bias toward plants was even stronger in our data than in previous meta-analyses (Hereford 2009), as we excluded studies that measured only growth. It remains to be seen whether the patterns we have detected here are similar for other taxonomic groups. Second, no studies ameliorated other negative interactions (e.g., parasitism, disease), too few altered mutualistic interactions to test their effects (table 1), and it is unclear how specialized the manipulated interactions were. Mutualisms, particularly pollination, and specialized antagonisms have been implicated in ecological speciation (van der Niet and Johnson 2009; Coley and Kursar 2014), for which local adaptation is presumably often a precursor (Van der Niet et al. 2014). Thus, the relative importance of local adaptation to other types of biotic interactions remains an open question that, if answered, may help link microevolutionary processes to evolution on longer timescales.

Conclusions and Recommendations for Future Work

It has been more than 70 years since Clausen et al.'s (1940) pioneering work on local adaptation to climate, 15 years since Kawecki and Ebert (2004) clarified how to test local adaptation experimentally, and a decade since Hereford's (2009) seminal review kicked-started interest in quantifying overarching patterns in local adaptation. Yet we still have a limited understanding of the selective agents that commonly drive local adaptation. Our synthesis of local adaptation experiments suggest that negative biotic interactions often reduce fitness and that local adaptation is common but that biotic interactions do not commonly promote local adaptation, except perhaps in the tropics. These conclusions offer tantalizing support for the proposed importance of interactions in tropical ecology and evolution and raise interesting possibilities that would have profound

implications for our understanding of eco-evolutionary dynamics in temperate ecosystems: that the biotic environment is less predictable in time or space than the abiotic environment and that adaptation to biotic interactions often involves fewer trade-offs than adaptation to the abiotic environment, creating universal winners and losers rather than home-site advantage.

We end by summarizing promising experimental approaches that stand to make the biggest contributions to future research on local adaptation to biotic interactions.

Approach 1: Experimental manipulations of the transplant environment with a control treatment. We believe many researchers would be surprised at how rare these remain (fig. 1), despite earlier calls for more of them (Parachnowitsch and Lajeunesse 2012). Without more and better tests, our understanding of local adaptation's drivers remains tentative (Briscoe Runquist et al. 2020). Experiments in natural environments could add a manipulation to test mechanisms thought to underlie local adaptation (e.g., Hargreaves and Eckert 2019), while those that reduce negative interactions to maintain sample sizes could retain some transplants in a natural environment as a control (e.g., Stanton-Geddes et al. 2012). Such direct tests will teach us the most about the selective agents of local adaptation.

Approach 2: Comparisons of spatiotemporal variability in biotic versus abiotic selective agents. Perhaps the strongest explanation for the lack of overall local adaptation to biotic interactions despite their effect on fitness is greater variability in the biotic environment. While many studies explore environmentally variability, we are unaware of any that explicitly compare the relative contribution of biotic and abiotic agents. Multiyear selection analyses would be particularly beneficial, although challenging to execute (Shaw and Etterson 2012).

Approach 3: Tropical transplant experiments. Some of the strongest examples of species-level adaptation to biotic interactions come from the tropics (Fine et al. 2004), but intraspecific experiments of population differentiation remain rare, particularly those that measure direct components of fitness in unaltered environments. Ultimately, the most biological insight will be gained from moving beyond temperate-tropical comparisons to addressing the mechanisms that might drive latitudinal patterns (e.g., biodiversity, climatic stability) and testing whether these contribute to the high variability in local adaptation to biotic environments found within as well as between latitudinal zones.

Approach 4: Creative approaches to testing local adaptation to the biotic environment. While manipulating abiotic factors is often relatively straightforward, manipulating interacting species can be logistically challenging, potentially explaining why most manipulations are limited to relatively simple competition/consumer reduction. Exciting potential approaches include cross-infection experiments

of multiple host and specialist herbivore (or symbiont) populations (e.g., Garrido et al. 2012) and manipulating the structures, signals, or chemicals involved in animal pollination (e.g., Suinyuy et al. 2015), guarding mutualisms (e.g., Abdala-Roberts and Marquis 2007), or antipathogen defenses (e.g., Tewksbury et al. 2008). Combining these with reciprocal transplants would be a powerful step forward in testing local adaptation to the full suite of biotic interactions.

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Temperate herbivory was one of the most commonly tested interactions. Here, a seed-eating caterpillar reduces the fitness of temperate plant *Rhinanthus minor*. Photo credit: Anna L. Hargreaves.