



## 24 **Abstract**

25 Local adaptation to broad-scale environmental heterogeneity can increase species' distributions  
26 and diversification, but which environmental components commonly drive local adaptation—  
27 particularly the importance of biotic interactions—is unclear. Biotic interactions should drive  
28 local adaptation when they impose consistent divergent selection; if this is common we expect  
29 experiments to detect more frequent and stronger local adaptation when biotic interactions are  
30 left intact. We tested this hypothesis using a meta-analysis of common-garden experiments from  
31 138 studies (149 taxa). Across studies, local adaptation was common and biotic interactions  
32 affected fitness. Nevertheless, local adaptation was neither more common nor stronger when  
33 biotic interactions were left intact, either between experimental treatments within studies (control  
34 vs. biotic interactions experimentally manipulated) or between studies that used natural vs.  
35 biotically-altered transplant environments. However, tropical studies, which comprised only 7%  
36 of our data, found strong local adaptation in intact environments but not when negative biotic  
37 interactions were ameliorated, suggesting that interactions frequently drive local adaptation in  
38 the tropics. Our results suggest that biotic interactions often fail to drive local adaptation even  
39 though they affect fitness, perhaps because the temperate-zone biotic environment is less  
40 predictable at the spatiotemporal scales required for local adaptation.

## 41 **Introduction**

42

43 Adaptation to local site conditions is fundamental to species' evolutionary and biogeographic  
44 dynamics. Local adaptation among populations, where local individuals outperform foreign  
45 individuals at their home site, can significantly improve mean population fitness (Griffith and  
46 Watson 2005), lead to population differentiation that contributes to ecological speciation  
47 (Reznick and Ghalambor 2001), and drive range expansions by enabling colonization of  
48 previously uninhabitable locations (Holt 1996; Levin 2000; Hargreaves and Eckert 2019). The  
49 practical importance of local adaptation among populations is also well recognized. Foresters  
50 seek genotypes best-suited to planting sites (Liepe et al. 2016), locally-adapted populations are  
51 prioritized in restoration and conservation (McKay et al. 2005; Bonin et al. 2007), and biologists  
52 increasingly recognize local adaptation's role in the spread of invasive species (Colautti and  
53 Barrett 2013; Oduor et al. 2016).

54

55 While the importance of local adaptation is well recognized, it is less clear which environmental  
56 factors most commonly drive it, particularly the importance of interactions among species.  
57 Seminal tests of local adaptation have traditionally focused on abiotic factors (e.g. climate  
58 (Bateman 1967), soil (Antonovics 1975), photoperiod (Griffith and Watson 2005)). Yet all  
59 environments include other species, and species composition often shifts predictably along  
60 abiotic gradients (Maron et al. 2014). A handful of case studies show that biotic interactions can  
61 promote local adaptation among populations (e.g. Rice and Knapp 2008), but it is unknown how  
62 common this is across studies. This uncertainty impedes our understanding of the dominant

63 drivers of diversification, and our ability to predict when local adaptation will facilitate success  
64 in environments with novel biotic conditions (Aitken and Whitlock 2013; Alexander et al. 2015).

65

66 To drive local adaptation among populations, biotic interactions must affect fitness differently  
67 among populations, and this divergent selection must be consistent across generations (Levins  
68 1968). Studies of species distributions suggest biotic interactions often meet the first criterion;  
69 interactions commonly limit fitness at geographic scales (Wisz et al. 2013; Hargreaves et al.  
70 2014) and can have different fitness consequences among sites. For example, negative  
71 interactions like competition and herbivory can limit one end of a species' range with little  
72 impact at the other (Barton 1993; Scheidel and Bruelheide 2001), and are more often involved in  
73 limiting the low-elevation and latitude ends of species distributions (Hargreaves et al. 2014).  
74 How often such spatial variation in fitness leads to consistent divergent selection is less clear,  
75 given that biotic interactions can be highly dynamic as species move, vary in population size,  
76 and evolve (Schemske 2009). If biotic interactions vary unpredictably relative to the speed of  
77 adaptation or scale of gene flow, they are unlikely to drive local adaptation even if they strongly  
78 affect fitness.

79

80 Given the rich experimental literature on local adaptation, why is the importance of biotic  
81 interactions in driving it still unresolved? First, meta-analyses have focused on the frequency of  
82 local adaptation more than its drivers (Leimu and Fischer 2008; Hereford 2009)—this is a gap  
83 our current study aims to fill. Additionally, we suspected that common features of reciprocal  
84 transplant experiments—the gold standard for testing local adaptation (Kawecki and Ebert  
85 2004)—may obscure the effect of biotic interactions. While empirical evidence suggests that

86 interactions most strongly affect early life stages (e.g. competition; Goldberg et al. 2001), many  
87 studies transplant older juveniles or adults. Further, a meta-analysis of transplant studies across  
88 species range edges found that 42% alter the transplant site conditions (e.g. by mowing all plots)  
89 in ways that disproportionately affect biotic interactions (Hargreaves et al. 2014). If the same is  
90 true of local adaptation experiments, they may miss the full effect of biotic interactions and could  
91 erroneously detect ‘maladaptation’, where foreign populations outperform the local population.  
92 For example, when anti-herbivore defense involves a tradeoff with growth (Züst and Agrawal  
93 2017), plants from high-herbivory sites may be locally adapted to natural conditions, but be  
94 outperformed by poorly-defended but fast-growing foreign plants if herbivory is artificially  
95 reduced.

96  
97 Here we test how biotic interactions impact local adaptation among populations by synthesizing  
98 experiments that transplanted individuals from local and foreign populations into a common field  
99 site (i.e. common garden and reciprocal transplant studies) and reported at least one component  
100 of lifetime fitness (emergence, survival, reproduction;  $n = 138$  studies, Fig. 1). From these we  
101 constructed two datasets (Table 1). Dataset 1 (controlled manipulations within studies) is the  
102 subset of studies that experimentally manipulated the environment with a control treatment,  
103 enabling direct tests of treatment effects. Dataset 2 (uncontrolled manipulations across studies)  
104 includes the most natural transplant conditions from all studies, including many that altered the  
105 environment of all plots without a control treatment. Although uncontrolled manipulations often  
106 obscure the effect of biotic interactions within studies, they enable among-study comparisons of  
107 local adaptation in natural vs. biotically-altered environments with a larger and more diverse

108 dataset. As few studies altered only the abiotic environment, we focus on how altering biotic  
109 interactions affects local adaptation; Appendix 1 gives results from all manipulations.

110

111 We use these datasets to investigate the overall importance of biotic interactions on local  
112 adaptation and fitness (*Questions 1-4*), and assess whether it is more important for some life  
113 stages or ecosystems (*Questions 5-6*). We ask: Does the frequency (*Question 1*) or strength  
114 (*Question 2*) of local adaptation differ when biotic interactions are left intact vs. altered (both  
115 datasets)? If local adaptation to the biotic environment is common, we should detect more  
116 frequent and stronger local adaptation when biotic interactions are left intact. We use the subset  
117 of studies that experimentally manipulated biotic interactions (dataset 1) to ask: Do biotic  
118 interactions affect fitness (*Question 3*), since this is a prerequisite for inducing local adaptation?;  
119 and How often does altering biotic interactions generate ‘false maladaptation’, where local  
120 adaptation is detected under control conditions but foreign advantage detected when biotic  
121 interactions were ameliorated (*Question 4*)?

122

123 Finally, we test theory predicting that biotic interactions are especially likely to induce local  
124 adaptation in some case. If biotic interactions are most important at early life stages, we expect  
125 altering the biotic environment to have the greatest effect on detecting local adaptation at  
126 emergence compared to survival or reproduction. Using both data sets we ask: Do the effects of  
127 biotic interactions on local adaptation differ among life stages (*Question 5*)? Biologists have long  
128 speculated that biotic interactions may be more evolutionarily important in the tropics  
129 (Dobzhansky 1950; Schemske 2009). We test: ‘Is there a stronger signal of local adaptation to

130 biotic interactions in the tropics?’ (*Question 6*) using dataset 2 as no tropical studies manipulated  
131 the biotic environment.

## 132 **Methods**

### 133 *Literature search*

134 We began with a comprehensive database of transplant experiments compiled to test the effects  
135 of climate anomalies on local adaptation (Bontrager et al. *in prep*). This database was based on a  
136 Web of Science search (19 March 2017) for transplant experiments in terrestrial and shallow-  
137 water environments that measured at least one component of lifetime fitness (emergence,  
138 survival, reproduction). Due to the emphasis on adaptation to large-scale climate gradients,  
139 studies that moved populations <1 km distance or <200 m elevation were discarded. The final  
140 Bontrager et al. database included 149 studies of 166 taxa (further details are in the SI).

141  
142 For the current study, we adjusted the Bontrager et al. database in two ways. First, we re-  
143 evaluated 73 studies that had been excluded for encompassing too small a geographic scale (<1  
144 km distance or <200 m elevation), and included any that tested local adaptation to different sites  
145 ( $n = 3$  studies added; as we were specifically interested in local adaptation among sites, tests of  
146 microhabitats within sites were still excluded).

147  
148 Second, we defined local adaptation as a local source population outperforming foreign sources  
149 at its home site (Kawecki and Ebert 2004), so excluded data from sites that lacked either a local  
150 or foreign source population. For each transplant site, we categorized each source as ‘local’ if it  
151 was from that site or an ecologically similar (defined by the authors) site within 100 km and 100

152 m elevation, or else as ‘foreign’. We explore the effect of this definition of local in Appendix 1.  
153 Median (mean) distance between source origin and transplant sites was 0 km (5.0 km) for local  
154 sources and 234 km (588 km) for foreign sources. These refinements yielded a dataset of 138  
155 studies on 149 taxa (usually species but occasionally subspecies or ploidy levels), of which 22  
156 also conducted controlled manipulations of the biotic or abiotic environment (Fig. 1, Table 1).

157

### 158 *Data collection*

159 Data were sourced from tables, figures using WebPlotDigitizer (Rohatgi 2018), or from authors.  
160 For each study, we collected mean fitness for each combination of taxon, source population,  
161 transplant site, life stage at which the source was transplanted (seeds/eggs, seedlings/juveniles, or  
162 adults), temporal replicate (e.g. if transplants were replicated in multiple years), fitness  
163 component (germination/emergence, survival, reproduction, or composites of these), and  
164 experimental treatment (treatment is only relevant for the 22 studies that experimentally  
165 manipulated the environment); hereafter, each taxon  $\times$  source population  $\times$  transplant site  $\times$  life  
166 stage  $\times$  temporal replicate  $\times$  fitness component  $\times$  treatment combination is referred to as a ‘data  
167 point’. When multiple variables could be used for a single fitness component (e.g. both flower  
168 counts and total seed weight reported as ‘reproductive output’), we used the one that most  
169 closely represented fitness. If germination or survival was reported multiple times for the same  
170 temporal replicate (e.g. first and second season survival for a perennial plant), only the final  
171 estimates were recorded as a proportion of the initial number of individuals. If multiple estimates  
172 of reproductive output were reported for a single temporal replicate (e.g. first and second season  
173 fruit production), we summed these to calculate cumulative reproduction. For studies that did not  
174 report composite fitness but did report at least two of emergence rate, survival rate, and

175 reproductive output, we calculated composite fitness as their product.

176

177 To assess the effect of biotic interactions on the expression of local adaptation, we recorded  
178 whether and how the biotic or abiotic environment was altered for each data point (possible  
179 alterations listed in footnotes of Table 1). Alterations intended to mimic the natural environment  
180 (e.g. irrigation for stream-dwelling species planted outside of riparian habitat; Angert and  
181 Schemske 2005) were not counted. We also categorized whether each data point was part of an  
182 experimental treatment testing the effect of biotic or abiotic factors (i.e. experimentally applied  
183 manipulations or their concurrent control treatments). Note that even the control treatment of an  
184 experimental manipulation can be subject to an uncontrolled alteration of the environment. For  
185 example, a study might grow all transplants in a herbivore enclosure, then apply an irrigation  
186 treatment to half (an uncontrolled biotic manipulation with a controlled abiotic manipulation;  
187 Center et al. 2016). Based on whether studies included controlled experimental manipulations,  
188 we created two datasets as described below.

189 *Dataset 1) studies with controlled experimental manipulations of biotic or abiotic environment*

190 Dataset 1 includes only transplant experiments that experimentally manipulated (i.e. with an  
191 appropriate control treatment) the biotic or abiotic environment. Controlled manipulations were  
192 done on 16 herbaceous perennials, 6 woody perennials, 7 annual plants, and one mollusc. We  
193 categorized the most natural treatment as the control, and categorized manipulative treatments  
194 based on a) whether they directly affected biotic interactions, the abiotic environment, or both,  
195 and b) whether authors expected treatments to increase or decrease transplant performance  
196 (Table 1). However, due to low sample size of treatments expected to affect the abiotic  
197 environment or decrease performance, we focus on control treatments and biotic treatments that

198 increase performance ( $n = 15$  studies including 22 taxa: 14 herbaceous perennials, 7 annuals, one  
199 mollusk). Online appendix Fig. A1 shows results from all categories.

#### 200 Data manipulation: Dataset 1

201 We calculated two metrics of local adaptation that directly compare performance of local vs.  
202 foreign source populations in each experimental treatment at each site. For each site we averaged  
203 across data points to get  $\text{mean}(\text{fitness}_{\text{local}})$  and  $\text{mean}(\text{fitness}_{\text{foreign}})$  for each taxon  $\times$  treatment  $\times$   
204 life stage  $\times$  temporal replicate  $\times$  fitness component (Blanquart et al. 2013). To assess the  
205 probability of local adaptation (*Question 1*), we calculated a binary variable ('yes' if  
206  $\text{mean}(\text{fitness}_{\text{local}}) > \text{mean}(\text{fitness}_{\text{foreign}})$ , otherwise 'no') to qualitatively assess direction of  
207 differences given that statistical significance was not always reported. To assess the strength of  
208 local adaptation (*Question 2*), we calculated a quantitative effect size as:  
209  $\ln(\text{mean}(\text{fitness}_{\text{local}})/\text{mean}(\text{fitness}_{\text{foreign}}))$ . Positive effect sizes indicate local adaptation, while  
210 negative values indicate foreign advantage. When  $\text{mean}(\text{fitness}_{\text{foreign}}) = 0$ , this ratio yields  
211 +infinity. We handled this by replacing 0 foreign fitness with 1% of the mean local fitness at the  
212 site (7 data points). We reasoned that these are instances of strong adaptation, but due to finite  
213 sample sizes zeros are more likely than very small values. Similarly,  $\text{mean}(\text{fitness}_{\text{local}}) = 0$  yields  
214 a ratio of -infinity. We reasoned that these are cases of strong maladaptation and replaced local  
215 fitness of 0 with 1% of mean foreign source fitness (7 data points). Five cases where fitness = 0  
216 for all sources were excluded from both binary and log-ratio metrics.

217

218 We also calculated a 'standardized fitness' metric to compare performance among local vs.  
219 foreign sources (strength of local adaptation without having to adjust zero values; *Question 2*)  
220 and control vs. biotically-altered environments (fitness effect of biotic interactions; *Question 3*).

221 For each taxon  $\times$  life stage  $\times$  temporal replicate  $\times$  fitness component combination, we divided the  
222 fitness of each data point by the maximum fitness achieved by any source in any treatment at that  
223 site. This removes the effect of variation in site quality, and transforms a dataset of very different  
224 scales to values between 0 and 1. Note that standardized fitness has a bigger sample size than the  
225 log ratio measure of local adaptation strength, as each source at a site contributes data, rather  
226 than being combined into a single local-foreign comparison.

227 *Dataset 2) most natural treatment from all studies*

228 Dataset 2 includes the most natural treatment from all studies, including the control treatment  
229 from studies in dataset 1 (138 studies of 149 taxa: 80 herbaceous perennials, 37 woody  
230 perennials, 20 annual plants, 5 arthropods, 4 molluscs, 2 fish, 1 fungus). However, even the most  
231 natural conditions of each study were often subject to procedures that altered the biotic and/or  
232 abiotic environment. We categorized each data point based on whether it was subject to  
233 alterations that directly affected biotic interactions, the abiotic environment, both, or neither.  
234 Unlike experimental manipulations, all uncontrolled alterations were expected to improve  
235 transplant performance and success (Table 1). Due to the low sample size of alterations that  
236 affect the abiotic environment alone, and the difficulty of disentangling the roles of biotic and  
237 abiotic factors when they are altered simultaneously, we focus on transplants where conditions  
238 were entirely natural vs. those where only biotic interactions were directly altered ( $n = 117$   
239 studies of 122 taxa: 60 herbaceous perennials, 32 woody perennials, 18 annuals, 5 arthropods, 4  
240 molluscs, 2 fish, 1 fungus). Results from all categories are shown in Fig. A1.

241 Data manipulation: Dataset 2

242 As with dataset 1, we calculated three response variables (binary local adaptation, effect size of  
243 local adaptation, and standardized fitness), the difference being that data from any experimental  
244 manipulations of the environment were excluded from calculations. Thus, there is one binary-  
245 local-adaptation and one effect-size value for every taxon × site × life stage × temporal replicate  
246 × fitness component, and one standardized-fitness value for every taxon × site × source × life  
247 stage × temporal replicate × fitness component. Standardized fitness was calculated by dividing  
248 the fitness of each data point by the maximum fitness of any source in the most natural treatment  
249 at each site, so will differ from Dataset 1 if the maximum fitness was achieved when the  
250 environment was manipulated. Eighteen cases where fitness = 0 for all sources were excluded  
251 from both binary and log-ratio metrics.

252 *Analyses*

253 Analyses used R version 3.3.3 (R Core Team 2017). Datasets 1 and 2 were analyzed using  
254 separate mixed effects models (*lmer* and *glmer*, ‘lme4’ package). As data points from the same  
255 study or taxon are not independent and fitness components could vary in their ability to detect  
256 local adaptation, models included random intercepts for study, taxon, and fitness component  
257 (Bolker et al. 2009). Re-running models using only the fitness component that most closely  
258 approximated lifetime fitness did not alter conclusions (Table A1), thus studies that measured  
259 multiple fitness components do not over-influence our results. For *Questions 1, 2, 3 & 5* we  
260 tested the importance of fixed effects (including interactions) by comparing models with and  
261 without the effect of interest using likelihood ratio tests and a  $\chi^2$  distribution (*anova*, base R).  
262 Differences among factor levels within significant fixed effects or between fixed effects and zero

263 were assessed using *lsmeans* from the 'lsmeans' package (Lenth 2016). Figures present means  
264 and partial residuals after partialling out variance attributable to random factors ('visreg' package;  
265 Breheny and Burchett 2017), while 95% confidence intervals (CI) were extracted via *lsmeans*.

266 Question 1) Is local adaptation more common when biotic interactions are left intact?

267 Using the binary local adaptation metric and binomial generalized linear mixed models  
268 (GLMMs; log link function), we tested whether the probability of detecting local adaptation  
269 differs with biotic alteration (i.e. control vs. biotically-ameliorated treatments in dataset 1,  
270 natural vs. biotically-ameliorated transplant conditions in dataset 2). Biotic amelioration affects  
271 local adaptation if the effect of treatment/alteration is significant. An overall signal of local  
272 adaptation exists if the mean frequency of local adaptation is  $>0$  (lower 95% confidence limit  
273  $>0$ ), which is a 50% probability on the logit scale.

274 Question 2) Is local adaptation stronger when biotic interactions are left intact?

275 We compared the strength of local adaptation among natural vs. biotically-ameliorated  
276 environments using the effect size of local adaptation (direct local-foreign comparison) and  
277 standardized fitness (larger dataset) metrics. Effect sizes were analyzed using a Gaussian error  
278 distribution. As log ratios already incorporate the difference between local and foreign source  
279 populations, the only fixed effect in these models was whether biotic interactions had been  
280 ameliorated (treatment/alteration in dataset 1/dataset 2, respectively). Biotic amelioration affects  
281 local adaptation if the effect of amelioration is significant. An overall signal of local adaptation  
282 exists if the mean effect size of a treatment exceeds a null expectation of 0 (i.e. no difference in  
283 performance between local and foreign sources) as above. Standardized fitness is bounded  
284 between 0 and 1, so we used a binomial GLMM and logit link function with treatment

285 (control/natural vs. biotically-ameliorated) and source (local vs. foreign) as interacting fixed  
286 effects. Biotic amelioration affects the strength of local adaptation if the effect of being local  
287 depends on the biotic environment (i.e. significant source  $\times$  treatment interaction). When this  
288 was the case, we tested the effect of being local within each environment using the Tukey  
289 correction to maintain  $\alpha = 0.05$ ; overall local adaptation was detected if local sources had greater  
290 mean fitness than foreign sources.

291 Question 3) Do biotic interactions affect fitness?

292 For biotic interactions to generate local adaptation, they must affect fitness. We tested whether  
293 this was the case by comparing standardized fitness in control vs. biotically-ameliorated  
294 treatments in dataset 1 (we did not use dataset 2 as the effect of biotic amelioration is  
295 confounded with study). This was equivalent to the reduced model from *Question 2*, i.e.  
296 treatment and source (local vs. foreign) were non-interacting fixed effects.

297 Question 4) Does altering biotic interactions lead to false detections of ‘maladaptation’?

298 First, we asked how often ameliorating biotic interactions changed the qualitative conclusion  
299 about local adaptation. We assessed this question using 74 taxon  $\times$  site  $\times$  life stage  $\times$  temporal  
300 replicate  $\times$  fitness component combinations from dataset 1 with both a control and a biotically-  
301 ameliorated treatment. For each of the 74 comparisons, we determined whether both treatments  
302 yielded the same qualitative conclusion about  $\text{mean}(\text{fitness}_{\text{local}})$  vs.  $\text{mean}(\text{fitness}_{\text{foreign}})$  (i.e. both  
303 find local  $>$  foreign or both find local  $<$  foreign or both find local = foreign) or different  
304 conclusions (Table 2). We assessed qualitative differences as authors did not always test these  
305 contrasts statistically; we tally these results but do not perform a statistical test because we do not  
306 have a null hypothesis to compare to.

307 Second, we asked whether ameliorating biotic interactions led to false detections of  
308 ‘maladaptation’ more often than expected by chance (i.e. if local adaptation to biotic interactions  
309 was common and reduced performance in environments where biotic interaction were  
310 ameliorated). We define false maladaptation as cases where local adaptation (local > foreign)  
311 was detected under the most natural (control) conditions, but foreign advantage (foreign > local)  
312 detected when biotic interactions were experimentally ameliorated (Table 2G). We tallied such  
313 cases from the 74 comparisons described above. To assess whether biotic amelioration leads to  
314 false detections of maladaptation more often than expected by chance, we also tallied cases of  
315 the opposite pattern (foreign advantage in the control and local adaptation in the biotic  
316 amelioration treatment; Table 2C). Of 21 cases where local adaptation was detected in one  
317 treatment and foreign advantage in the other (Table 2 C+G), most involved unique taxa × site  
318 combinations; for two taxa × site combinations that contributed comparisons for both survival  
319 and composite fitness, we retained only composite fitness as it is closest to lifetime fitness (final  
320  $n = 19$  comparisons from 11 studies). We compared the detections of false maladaptation vs. the  
321 opposite pattern to a null expectation of 50:50 using a one-tail binomial test (*binom.test*, base R).

322 Question 5) Do biotic interactions affect local adaptation most strongly at early life stages?

323 If biotic interactions are most important at early life history stages, we expect the greatest  
324 difference in local adaptation between natural vs. biotically ameliorated environments to be  
325 detected in measurements of emergence vs. survival or reproduction. Using both datasets, we  
326 tested whether the effect of biotic amelioration on the frequency and effect size of local  
327 adaptation differed among fitness components (i.e. a treatment/alteration × fitness component  
328 interaction). We excluded composite measures as these confound multiple life stages.

329 Question 6) Is there stronger local adaptation to biotic interactions in the tropics?

330 Whereas biologists have long speculated that biotic interactions may be more evolutionarily  
331 important in the tropics, most experiments come from the temperate zone (Fig. 1). Thus our  
332 analyses may underestimate the global importance of biotic interactions for local adaptation. We  
333 test this by rerunning models from *Questions 1* and *2* with an additional random factor  
334 ‘latitudinal zone’, where data from sites between 23.5° N and 23.5° S are classified as ‘tropical’  
335 and those closer to poles classified as ‘temperate’. We use dataset 2 as only tropical studies in  
336 dataset 1 (Fig. 1) experimentally manipulated the abiotic environment (Fetched et al. 2000;  
337 Center et al. 2016), which also means we are unable to redo *Question 3*.

338 **Results**

339 Of the 138 studies in our data, less than half (41%, i.e. 57 studies) had at least some transplants  
340 in unaltered natural environments (Table 1). 61% universally altered the biotic environment for  
341 at least one life stage (numbers sum to >100% as some studies alter the environment of some life  
342 stages but not others). By far the most frequently altered components of the environment were  
343 biotic: competition (60 studies via herbicide, weeding, clipping, or planting in tilled gardens or  
344 pots), and herbivory/predation (43 studies via fences, cages, and poisons). Only 22 studies paired  
345 transplants with experimental manipulations of factors that might cause local adaptation, of  
346 which only 10 included a control treatment in an unaltered environment (Thompson et al. 1991;  
347 Kindell et al. 1996; Knight and Miller 2004; Sambatti and Rice 2006; Abdala-Roberts and  
348 Marquis 2007; Ariza and Tielbörger 2011; Hufford and Mazer 2012; Stanton-Geddes et al. 2012;  
349 Tomiolo et al. 2015; Hughes et al. 2017).

350 *Question 1) Is local adaptation detected more often when biotic interactions are left intact?*

351 No—ameliorating negative biotic interactions (i.e. reducing competition, herbivory, or  
352 predation) did not affect the probability of detecting local adaptation (Fig. 2). Local adaptation  
353 was equally probable in control and biotically-ameliorated treatments within experimental  
354 studies (Fig. 2A), and between studies using natural vs. biotically-ameliorated environments  
355 (Fig. 2B). This was consistent whether analyses included all fitness components (Table 3) or just  
356 the component closest to lifetime fitness for each comparison (Table A1).

357 *Question 2) Is local adaptation stronger when biotic interactions are left intact?*

358 No—the strength of local adaptation was generally not affected by biotic amelioration, but in  
359 one analysis local adaptation was stronger when interactions were ameliorated (i.e. opposite of  
360 predictions; Table 3). Ameliorating biotic interactions did not alter the effect size of local  
361 adaptation (Fig. 3A&B) or the fitness advantage of local sources compared to their fitness  
362 advantage in control treatments from the same study (Fig. 3C). However, studies that universally  
363 ameliorated biotic interactions detected a greater standardized fitness advantage of local sources  
364 than studies that used natural environments (Fig. 3D).

365

366 We did not detect an overall signal of local adaptation measured as effect size ( $\ln(\text{mean local}$   
367  $\text{fitness}/\text{mean foreign fitness})$ ; Fig. 3A&B), but did detect overall local adaptation measured as the  
368 fitness advantage of all local sources vs. all foreign sources (Fig. 3C&D). This discrepancy is  
369 likely due to the much larger  $n$  for standardized fitness vs. effect size (Fig. 3).

370 *Question 3) Do biotic interactions affect fitness?*

371 Yes—transplant fitness was almost twice as high when negative biotic interactions were  
372 experimentally ameliorated (i.e. reduced herbivores, competitors, or predators) compared to  
373 when they were left intact (mean  $\pm$  SE across studies and sources: control =  $0.49 \pm 0.14$ ,  
374 biotically ameliorated =  $0.87 \pm 0.07$ ; Fig. 3C, Table 3).

375 *Question 4) Does ameliorating biotic interactions lead to false detections of ‘maladaptation’?*

376 Among studies that experimentally ameliorated interactions (dataset 1), manipulating the biotic  
377 environment changed the qualitative signal of local adaptation in 22 (30%) of 74 comparisons  
378 (each comparison is local vs. foreign fitness per taxon  $\times$  site  $\times$  life stage  $\times$  temporal replicate). Of  
379 19 taxon  $\times$  site comparisons where the signal changed from local adaptation in one treatment to  
380 foreign advantage in the other, ameliorating interactions led to false detections of maladaptation  
381 (local adaptation in the control treatment but foreign advantage in biotic amelioration treatment)  
382 twice as often as the reverse pattern (13 vs. 6 comparisons), but the difference was not quite  
383 significant ( $P = 0.08$  in binomial test compared to null expectation of 50:50).

384 *Question 5) Do biotic interactions have a greater effect on local adaptation at early life stages?*

385 No—biotic interactions did not affect local adaptation more strongly at emergence vs. later life  
386 stages (Table 4). In the only analysis in which local adaptation varied among fitness components  
387 (binary local adaptation; Table 4), biotic amelioration did not affect the frequency of local  
388 adaptation in emergence or survival, but increased the detection of local adaptation for  
389 reproduction (i.e. the latest life stage), opposite of our predictions.

390 *Question 6) Is local adaptation to biotic interactions stronger in the tropics?*

391 While we have relatively few tropical studies with which to test the question, the best available  
392 data suggest the answer is ‘yes’. Latitude interacted with biotic amelioration to affect the  
393 probability of local adaptation (alteration  $\times$  latitudinal zone:  $\chi^2_{df=1} = 4.8$ ,  $P = 0.029$ ). Whereas  
394 temperate studies did not detect local adaptation more often in natural environments (as in Fig.  
395 2A), tropical studies did; all four tropical study  $\times$  taxon  $\times$  replicate data points in natural  
396 environments detected local adaptation compared to 0.46 of 19 tropical data points in biotically-  
397 ameliorated environments, though the lsmeans contrast was not significant ( $P > 0.5$ ). The effect  
398 size of local adaptation showed the same pattern, but the interaction was not significant ( $\chi^2_{df=1} =$   
399  $0.74$ ,  $P = 0.39$ ). The strongest result was in standardized fitness, for which the relationship  
400 between biotic amelioration and being local vs. foreign varied significantly between latitudinal  
401 zones (alteration  $\times$  local/foreign  $\times$  latitudinal zone:  $\chi^2_{df=1} = 5.3$ ,  $P = 0.021$ ). In temperate  
402 environments, local sources outperformed foreign sources equally in natural and biotically-  
403 ameliorated environments, suggesting local adaptation is driven primarily by abiotic factors. In  
404 contrast, across tropical studies local sources only outperformed foreign sources in natural  
405 environments (least squared means z ratio local vs foreign = 2.4,  $P = 0.018$ ), and not if negative  
406 interactions were ameliorated (z ratio = 0.8,  $P = 0.41$ ), suggesting biotic interactions frequently  
407 drive local adaptation in the tropics.

## 408 **Discussion**

409 Across studies (which were heavily biased toward temperate latitudes), we found little evidence  
410 that biotic interactions are broadly important in driving local adaptation among populations.  
411 Local adaptation was not more common or stronger in control treatments than treatments that  
412 experimentally ameliorated negative interactions (competition, herbivory, predation), nor in

413 studies that used intact transplant environments vs. studies that ameliorated negative biotic  
414 interactions for all transplants (Figs. 2 & 3). Importantly, the apparent lack of overall local  
415 adaptation to biotic interactions was not because interactions did not affect fitness, as  
416 experimental alleviation of negative interactions significantly improved fitness across studies  
417 (Fig. 3C). Nor does it seem due to constraints on local adaptation in general, as local source  
418 populations had significantly higher fitness than foreign source populations overall (Fig. 3C&D).  
419 Below we discuss potential explanations for inconsistent local adaptation to biotic interactions,  
420 despite their effect on fitness, and how these could be tested in future work.

421  
422 First, biotic interactions might often be unpredictable at the spatial or temporal scale required for  
423 local adaptation. The abundance and identity of interacting species can vary greatly within a  
424 population of a focal species, as species are often patchily distributed (Wagner et al. 2000) and  
425 enter and exit via colonization, dormancy, and local extinction (White et al. 2006). Further, many  
426 pairwise species interactions are mediated by other species (Mayfield and Stouffer 2017) and the  
427 abiotic environment (Adler et al. 2006; Germain et al. 2018). This spatiotemporal variability  
428 reduces the interaction consistency between any two species (Magurran and Henderson 2010).  
429 Therefore, one explanation for our results is that the biotic environment is less predictable among  
430 populations than the abiotic environment, and so more likely to select for increased phenotypic  
431 plasticity than local adaptation at this scale. To our knowledge this has rarely been directly  
432 tested, and would be an exciting area of future research.

433  
434 Second, if adaptation to biotic interactions rarely involved trade-offs, it could commonly result in  
435 adaptation but rarely in local adaptation. Adaptation without tradeoffs would result in universally

436 superior populations (Hereford 2009), e.g. when plants compete for light, bigger might always be  
437 better. Superior populations would outperform other populations whether in their home site or  
438 not, so a reciprocal transplant would not detect an overall home site advantage. However, our  
439 results hint that adapting to biotic interactions is not always trade-off free. Experimentally  
440 reducing negative interactions altered the conclusion about local adaptation in almost a third of  
441 cases, and these changes were biased two-to-one toward ‘false maladaptation’, where local  
442 genotypes were at a disadvantage when biotic interactions were ameliorated (*Question 4*). This  
443 suggests a testable possibility that some interactions select for universally superior genotypes,  
444 whereas others select for context dependent adaptations (e.g. anti-herbivore defenses) and so  
445 should more often spur local adaptation.

446

447 Third, most of our data came from the temperate zones (Fig. 1), whereas large-scale experiments  
448 suggest biotic interactions are strongest in the tropics (Roslin et al. 2017; Hargreaves et al. 2019).  
449 If stronger interactions produce stronger selection (Benkman 2013), data from mostly temperate  
450 ecosystems may underestimate the global importance of adaptation to biotic interactions. In  
451 contrast to the lack of evidence for local adaptation to biotic interactions overall, our admittedly  
452 limited tropical data show a strikingly different pattern: local adaptation across studies in natural  
453 environments, but no local adaptation when negative biotic interactions are ameliorated. While  
454 more tropical data are clearly needed, our results using the best available data support the long-  
455 standing prediction that interactions are more evolutionarily important in tropical ecosystems.

456

457 Our results have important implications for how local adaptation is tested in the field. One  
458 interpretation is that biotic interactions mostly add ‘noise’ to tests of local adaptation. Overall—

459 though driven by temperate ecosystems—studies that ameliorated negative interactions detected  
460 stronger local adaptation (Fig. 3D), perhaps because protecting transplants increased sample  
461 sizes or reduced variability in fitness. If the research goal is to test for local adaptation to the  
462 abiotic environment, reducing negative interactions may increase experimental power to do so.  
463 However, if the goal is to detect which components of the environment drive local adaptation, to  
464 assess the fitness consequences of local adaptation for natural populations, or to test local  
465 adaptation in environments where interactions are strong (e.g. at low latitudes and elevations;  
466 Roslin et al. 2017; Hargreaves et al. 2019), biotic interactions should be left intact as they affect  
467 fitness (Fig. 3C&D), can alter the expression of local adaptation (*Question 4*), and may drive  
468 local adaptation in the tropics. Protecting some transplants from negative interactions with a  
469 control treatment in natural conditions is a win-win design (e.g. Stanton-Geddes et al. 2012),  
470 increasing power to detect local adaptation to both the abiotic and biotic environment.

471  
472 An important caveat to our conclusions is that we could only robustly test the effect of  
473 ameliorating competition and consumption. No studies ameliorated other negative interactions  
474 (e.g. parasitism, disease), and too few altered mutualistic interactions to test their effects (Table  
475 1) even though mutualisms have been widely implicated in ecological speciation (Whittall and  
476 Hodges 2007; van der Niet and Johnson 2009), for which local adaptation is presumably often a  
477 precursor (Anderson and Johnson 2009). Thus it remains an open question whether local  
478 adaptation to other types of interactions is common at geographic scales.

## 479 **Conclusions**

480 Together, the best available experimental tests of local adaptation among populations show that  
481 negative biotic interactions often reduce fitness, that local adaptation among populations is

482 common, but that biotic interactions only increase the overall strength and probability of local  
483 adaptation in the tropics. These conclusions support the proposed importance of interactions in  
484 tropical ecology and evolution, and raise interesting possibilities that would have profound  
485 implications for our understanding of eco-evolutionary dynamics in temperate ecosystems: that  
486 the biotic environment is less predictable in time and/or space than the abiotic environment, and  
487 that adaptation to biotic interactions often involves fewer tradeoffs than adaptation to the abiotic  
488 environment, creating universal winners and losers rather than home-site advantage. While many  
489 studies explore environmental variability or adaptive tradeoffs, we are not aware of any that  
490 explicitly compare the relative contributions of the biotic vs. abiotic environment in these  
491 contexts. Transplants that experimentally manipulate the environment with appropriate controls  
492 remain surprisingly rare, and have much to teach us about the drivers of adaptation. Finally, the  
493 extent of local adaptation varied greatly in both intact and ameliorated conditions, and  
494 preliminary evidence suggests at least some of this variation maybe be explained by predictable  
495 differences among ecosystems—this remains an exciting area for future research.

496

## 497 **Acknowledgements**

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500 Canada (Discovery grants to ALH and ALA), Fonds de Recherche du Québec (Nouveau  
501 Chercheur grant to ALH), the Killam Trust and UBC Biodiversity Research Centre (fellowships  
502 to RMG), UBC (fellowship to MB), and McGill Biology Department (scholarship to JP).

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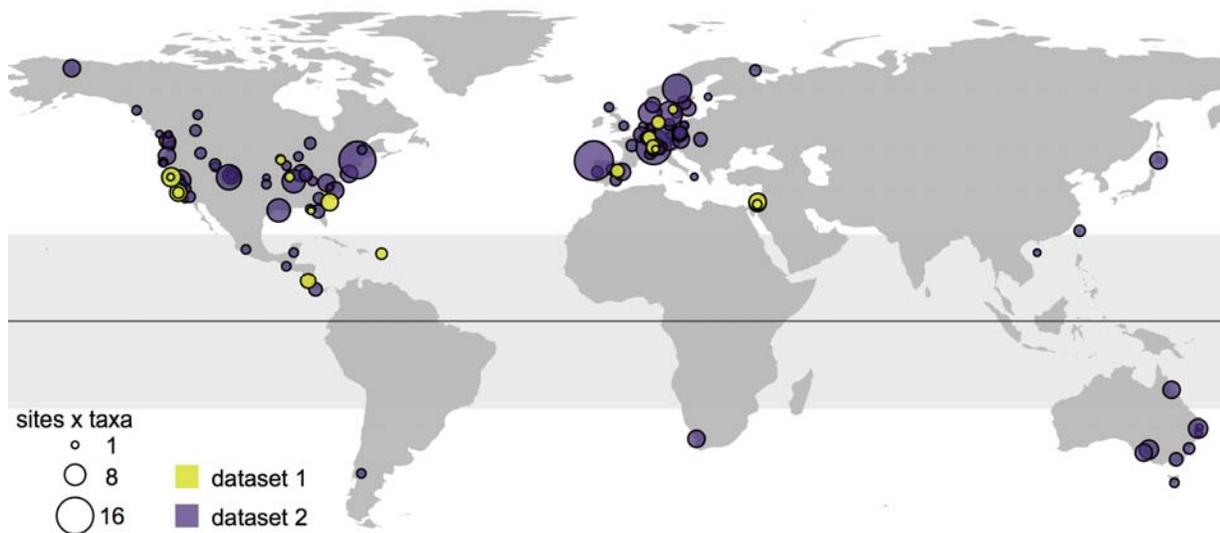
504 **Author contributions**

505 ALA and MB conceived the idea of using the Bontrager et al database of transplant studies  
506 (designed and curated by MB) to study biotic interactions. ALH designed the current study with  
507 input from all authors. JP collected the additional data for dataset 1. ALH analysed the data with  
508 support from RMG and MB. ALH wrote the manuscript with contributions from all authors.

509 **Figures**

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513

514 **Fig. 1. Geographic distribution of transplant experiments comparing local and foreign**

515 **sources at a common site.** 138 studies transplanted a local and foreign source to a common field

516 site (purple + yellow points), of which 22 studies also experimentally manipulated the biotic or

517 abiotic environment of transplants with an appropriate control (yellow). Map shows 1 point per

518 study; when studies included multiple sites we used their average latitude and longitude. Point

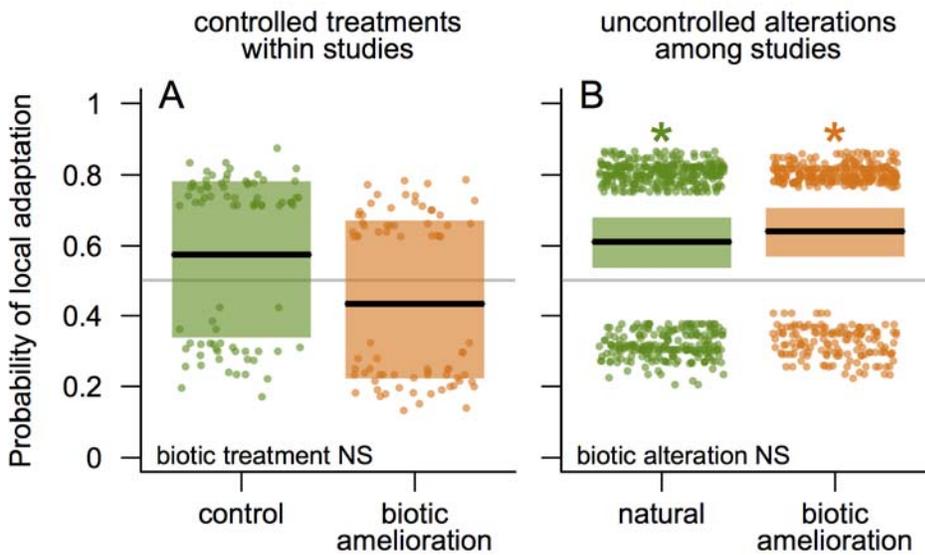
519 size reflects the total number of sites × number of taxa per study. Shaded rectangle indicates the

520 tropics (-23.5 to 23.5° latitude).

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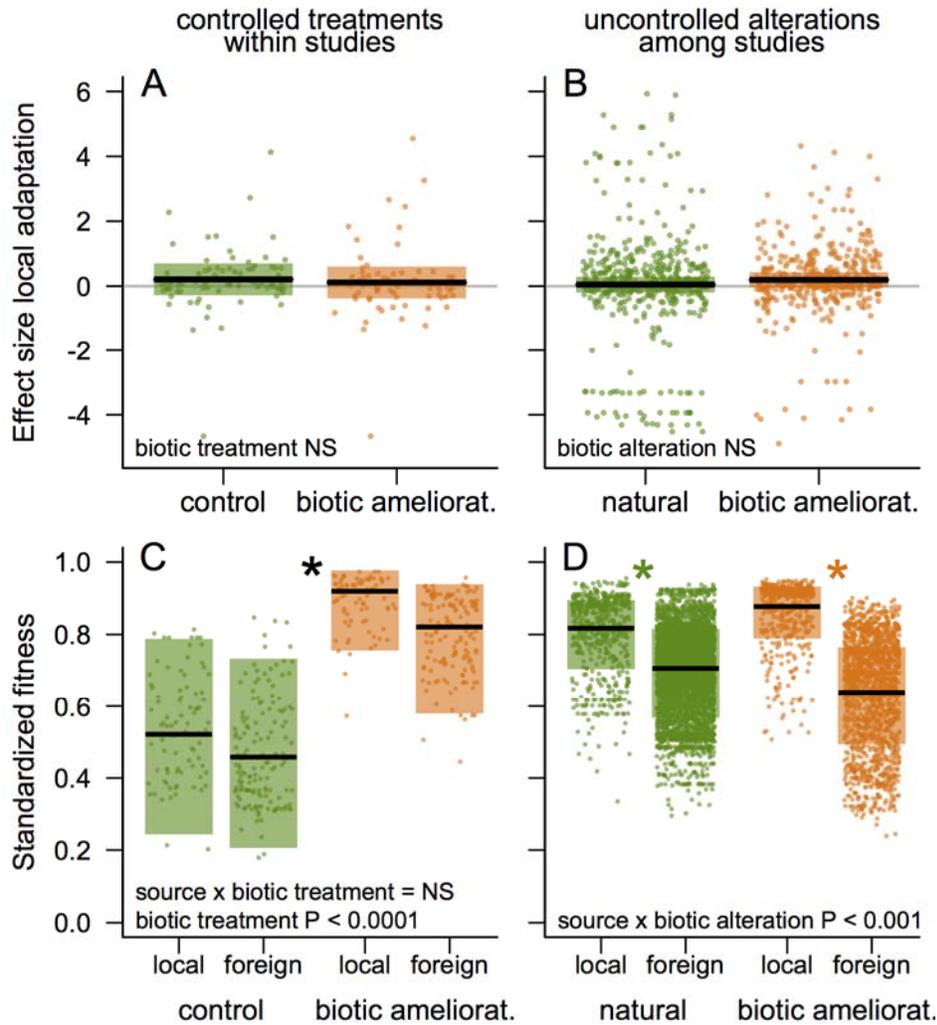
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**Fig 2. Local adaptation was not detected more often when biotic interactions were left intact.** Local adaptation was scored as ‘yes’ if mean fitness of local sources > mean fitness of foreign sources for a taxon × site × life stage × temporal replicate × fitness component. Central lines, points, and rectangles are means, partial residuals, and 95% CI extracted from models and back-transformed from the logit scale; scatter on y axis is residual variation after accounting for random effects of study, taxon, and fitness component. Green = control or natural transplant environments, and orange = biotically-ameliorated environments. (A) Studies that experimentally ameliorated biotic interactions with a control treatment ( $n = 155$  data points from 15 studies; dataset 1). (B) Most natural conditions from all studies ( $n = 924$  data points from 117 studies; dataset 2). \* indicates local adaptation was detected more often than expected by chance across studies (i.e. probability >0.5 for those conditions). Full statistical results in Table 3.



537  
538

539 **Fig 3. Local adaptation was not stronger when biotic interactions were left intact.** The  
540 strength of local adaptation was assessed directly as an effect size ( $\ln(\text{mean local fitness}/\text{mean}$   
541  $\text{foreign fitness})$ ) for each taxon  $\times$  site  $\times$  life stage  $\times$  temporal replicate  $\times$  fitness component (A &  
542 B; significant local adaptation if CI do not overlap 0); and indirectly but with a larger  $n$  using the  
543 standardized fitness of each taxon  $\times$  site  $\times$  source population  $\times$  life stage  $\times$  temporal replicate  $\times$   
544 fitness component (C & D; significant adaptation if local > foreign performance for C  
545 indicates whether manipulating biotic interactions affected the strength of local adaptation  
546 (*Question 2*, all panels) and/or fitness (*Question 3*, panel C 'biotic treatment'). \* indicates overall  
547 local adaptation (i.e. 95% CI do not overlap 0 for A & B, local > foreign performance for C  
548 (across treatments, black) & D (given separately by treatment due to interaction)). (A & C)  
549 Within studies that experimentally manipulated biotic interactions (dataset 1), local adaptation

550 was not stronger in the control treatment, even though biotic interactions affected fitness (*C*). (*B*  
551 & *D*) Across all studies (dataset 2), biotic amelioration did not affect the effect size of local  
552 adaptation (*B*), but increased the difference in standardized fitness of local vs. foreign sources  
553 (*D*). *n* data points (studies): *A* = 155 (15); *B* = 924 (117); *C* = 456 (15); *D* = 6586 (117); colours  
554 as in Fig. 2.

555 **Tables**

556

557 **Table 1: Summary of biotic and abiotic alterations.** For each of 138 studies that transplanted  
 558 149 taxa, we noted whether authors manipulated components of the biotic or abiotic  
 559 environment. Data were grouped into two datasets: 1) all treatments from studies that conducted  
 560 controlled manipulations of the environment (22 studies, 31 taxa), or 2) the most natural  
 561 conditions from all 138 studies, some of which manipulated the environment without a control  
 562 treatment. Controlled experiments included manipulations expected to increase or decrease  
 563 transplant fitness, whereas uncontrolled alterations were always expected to increase fitness.  
 564 Study sample sizes for Dataset 2 sum to >138 as some studies applied different alterations to  
 565 different life stages.

566

Environment manipulated:	Biotic		Abiotic		Both	None <sup>6</sup>
	Increase fitness <sup>1</sup>	Decrease fitness <sup>2</sup>	Increase fitness <sup>3</sup>	Decrease fitness <sup>4</sup>	Increase fitness <sup>5</sup>	—
Dataset 1) Treatments from studies with controlled manipulations (23 studies)						
Studies	15	1	4	2	0	22
Taxa	22	1	6	2	0	30
Dataset 2) Most natural conditions from all studies (139 studies)						
Studies	63	0	2	0	22	57
Taxa	73	0	2	0	33	60

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1. Manipulations: fencing, caging, insecticide, molluscicide, weeding, mowing, tilling soil, planting in pots using local soil (i.e. microorganisms still present)
2. Manipulations: reducing ant mutualists
3. Manipulations: irrigation in dry environments, shading seeds to reduce photoinhibition of germination, warming in cold environments, wind-barriers, fertilizing
4. Manipulations: warming in hot environments, exposing seeds to full sunlight (increasing potential photoinhibition)
5. Manipulations: planting in gardening soil, planting in old agricultural fields (that presumably had enriched soil and reduced canopy height), combinations of individual biotic and abiotic alterations (e.g. weeding + irrigation)
6. Note: even if transplants from dataset 1 are in the control treatment (i.e. environment not experimentally manipulated; treatment = None), they may still be subject to uncontrolled manipulations, so are not necessarily in the 'Environment manipulated = None' category in Dataset 2.

581 **Table 2. Comparisons in Question 4.** Using dataset 1, we compared the relative fitness of local  
 582 vs. foreign sources between control treatments and paired treatments that ameliorated the biotic  
 583 environment. We asked how often ameliorating biotic interactions changed the conclusion about  
 584 local adaptation by tallying cases where treatments reached the same conclusion (grey cells) vs.  
 585 different conclusions (white cells). We tested whether ameliorating interactions led to false  
 586 detections of ‘maladaptation’ (G) more often than the reverse (C).

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

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**Table 3: Analyses for Questions 1 to 3: biotic interactions vs. local adaptation (LA) and fitness.** We tested whether local sources outperformed foreign sources more frequently (binary LA) or more strongly (effect size LA, standardized fitness) in control treatments vs. treatments that experimentally ameliorated biotic interactions (‘treatment’; dataset 1), or between studies that transplanted into natural, unaltered environments vs. those that ameliorated biotic interactions without a control treatment (‘alteration’; dataset 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 vs. foreign sources; biotic interactions affect local adaptation if treatment/alteration is significant. For standardized fitness, biotic interactions affect local adaptation if the effect of being local differs between natural vs. biotically-ameliorated environments. Overall local adaptation is detected if confidence intervals do not overlap 0 (binary and effect size local adaptation), or if local > foreign standard fitness (tested against no-interaction model if interaction NS). Significant effects in bold. ‘Figure’ indicates where data are shown. All models include random intercepts for taxon, study, and fitness component.

<i>Question</i>			Do biotic interactions affect LA (Q1&2) or fitness (Q3)? (likelihood $\chi^2_{df=1}, P$ )	Overall local adaptation? <sup>1</sup>	Figure
Dataset	Response	Fixed effects			
<i>Question 1) Is LA more probable when biotic interactions are left intact or ameliorated?</i>					
1	binary LA	treatment	no: treatment NS (2.5, $P = 0.11$ )	no	2A
2	binary LA	alteration	no: alteration NS (0.3, $P = 0.56$ )	<b>yes</b>	2B
<i>Question 2) Is LA stronger when biotic interactions are left intact or ameliorated?</i>					
1	effect size LA	treatment	no: treatment NS (0.3, $P = 0.59$ )	no	3A
1	standardized fitness	treatment $\times$ local/foreign	no: interaction NS (1.8, $P = 0.18$ )	<b>yes: local/foreign significant</b> ( $\chi^2_{df=2} 6.8, P = 0.033$ ) local > foreign	3C

2	effect size LA	alteration	no: alteration NS (1.0, $P = 0.32$ )	no	3B
2	standardized fitness	alteration $\times$ local/foreign	<b>yes: interaction signif</b> (13.9, $P = 0.0002$ )	<b>natural: yes</b> (local > foreign: $P < 0.0001$ ) <b>bio.amel: yes</b> (local >> foreign: $P < 0.0001$ )	3D

*Question 3) Do biotic interactions affect fitness?*

1	standardized fitness	treatment + local/foreign <sup>2</sup>	<b>yes: treatment signif</b> (70.4, $P < 0.0001$ ) bio.amel > control	<b>yes: local/foreign significant</b> ( $\chi^2_{df=1} 5.1, P = 0.024$ ) local > foreign	3C
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1. The null frequency for categorical local adaptation is 0 as means are calculated on the transformed scale from binomial models, where 0 represents a frequency of 50% (i.e. no significant adaptation or maladaptation)
2. Model in Question 3 is the reduced form of the second model from Question 2 (standardized fitness, dataset 1) with the NS interaction removed

**Table 4. Biotic interactions did not affect local adaptation more strongly at early life stages (Question 5).** ‘Treatment’/‘alteration’ compare fitness under ameliorated biotic interactions (‘bio.manip’) to fitness in more natural conditions in either a concurrent control treatment (‘control’, dataset 1) or from other studies (‘natural’, dataset 2), respectively. ‘Fitness component’ is emergence, survival, or reproduction. A significant treatment/alteration × fitness component interaction means the effect of biotic interactions on the frequency (binary LA) or strength (effect size LA) of local adaptation differs among fitness components. If the interaction was not significant, it was removed and the effects of treatment/alteration and fitness component were assessed to test whether local adaptation varied with biotic amelioration or among life stages, respectively. Data differ from *Questions 1 & 2* as composite fitness metrics are excluded. Responses and significance testing are as in Table 3. Models include random effects for taxon and study.

Dataset	Response	Initial fixed effects	Significance of fixed effects			Overall signal of local adaptation?
			Interaction $\chi^2_{df=1}$	Treatment / Alteration <sup>1</sup> $\chi^2_{df=1}$	Fitness component <sup>2</sup> $\chi^2_{df=2}$	
<i>Dataset 1) Studies with controlled manipulations of biotic interactions</i>						
binary LA	treatment × fitness comp	4.5 $P = 0.11$	<b>4.9</b> $P = \mathbf{0.027}$ (LA more common in control)	1.7 $P = 0.43$		no
effect size LA	treatment × fitness comp	1.1 $P = 0.57$	3.5 $P = 0.062$	2.5 $P = 0.25$		no
<i>Dataset 2) Most natural conditions from all studies</i>						
binary LA	alteration × fitness comp	<b>6.9</b> $P = \mathbf{0.031}$	Emerg: NS Surv: NS <b>Repro:</b> LA stronger in bio.amel than natural	natural: NS <b>bio.amel:</b> LA stronger for repro than emerg		<b>natural:</b> LA in survival <b>bio.amel:</b> LA in survival & repro
effect size LA	alteration × fitness comp	2.0 $P = 0.37$	2.8 $P = 0.43$	2.2 $P = 0.71$		no

1. Comparing model with treatment + fitness component to a model without treatment.
2. Comparing model with treatment + fitness component to a model without fitness component.

## Supplementary Material

### 1. Details of the Bontrager et al database

Our study leveraged a comprehensive database of transplant experiments compiled to test the effects of climate anomalies on local adaptation (Bontrager et al. *in prep*). This database was based on a Web of Science search (19 March 2017) for transplant experiments in terrestrial and shallow-water environments that measured at least one component of lifetime fitness (germination/emergence, survival, reproduction). The search string was: *("reciprocal transplant\*" OR "egg transfer experiment") OR ("local adaptation" AND "transplant\*") OR "provenance trial" OR "local maladapt\*" OR (("common garden\*") AND ("fitness" OR "surviv\*" OR "reproduc\*" OR "mortality" OR "intrinsic growth rate" OR "population growth rate") AND (adapt\*)) OR (("common garden\*" OR "reciprocal\* transplant\*" OR "transplant experiment" OR "assisted migration") AND (temperature OR climat\* OR latitud\* OR elevation\* OR altitud\*)) AND ("fitness" OR "surviv\*" OR "reproduc\*" OR "mortality" OR "intrinsic growth rate" OR "population growth rate" OR "establish\*" OR "success\*" OR "perform\*")) NOT invas\* NOT marine NOT microb\*).*

This search returned 2111 studies. Some of these were discarded, if they met any of the following conditions: were not transplant experiments; compared performance among species or reproductively-isolated subspecies rather than within species; transplanted only hybrids or inbred lines; or tested performance in a lab, a greenhouse, or outside the species' natural range. Due to the emphasis on local adaptation at biogeographic scales rather than to microhabitats within sites, studies that moved populations <1 km distance or <200 m elevation were also discarded. Additional appropriate studies from the references of previous reviews of transplant experiments (Leimu and Fischer 2008; Hereford 2009; Hargreaves et al. 2014; Gibson et al. 2016; Lee-Yaw et al. 2016; Oduor et al. 2016) or that were encountered while gathering data were added, yielding a total of 221 studies for data extraction. Some of these were excluded during data extraction if the required data were unavailable (e.g. results averaged across sources, performance measured using growth or other traits not directly related to fitness), or were reported in multiple studies. The final Bontrager et al. database included 149 studies of 166 taxa.

### 2. How local is local? Effect of the distance between source population origin and transplant site

To maintain a robust sample size of studies we use a generous definition of 'local', excluding a 'local' source only if it came from >100 km or 100 m elevation away from the transplant site; 16% of 'local' sources originated >2 km away from the transplant site and may not be functionally 'local' if biotic interactions differ at finer spatial scales. We tested whether studies that use more local sources are more likely to detect local adaptation in general, and to biotic interactions specifically, by rerunning our analyses for *Questions 1-2* with an additional random effect (this excluded one study from which we could not extract exact locations). For analyses of probability and effect size of local adaptation we added a random effect for the distance between the mean 'local' source populations' sites of origin and the transplant site. We also explored the effect of how far sources originated from the transplant site on the strength of local adaptation using standardized fitness. Because each source population contributes a standard fitness data point, it did not make sense to account for only the distance between local source origins and

transplant sites. Rather, we reran models with a random effect for distance between each source and transplant site.

**Results:** Accounting for the distance between local source population site and the transplant site did not change the qualitative results for the probability or effect size of local adaptation (i.e. none of the contrasts in Table 2, Fig. 1, and Fig. 2A-C went from significant to nonsignificant or vice versa). Thus, our estimates of local adaptation do not seem biased by inclusion of studies using local sources originating farther from the transplant sites. Interestingly, while accounting for the distance between source origin and transplant site did not affect the conclusions about local adaptation vs. biotic interactions (Table 2, column 4), it did decrease the overall signal of local adaptation for dataset 1; the overall effect of being native became insignificant ( $\chi^2_{df=1} = 5.1$ ,  $P = 0.077$ , compared to  $P = 0.033$  in Table 2 column 5). This confirms that performance at a given site is partially dependent on how far away sources comes from that site, i.e. geographic distance partially predicts ‘local’ adaptation.

### *3. Analyses using one fitness metric per taxon*

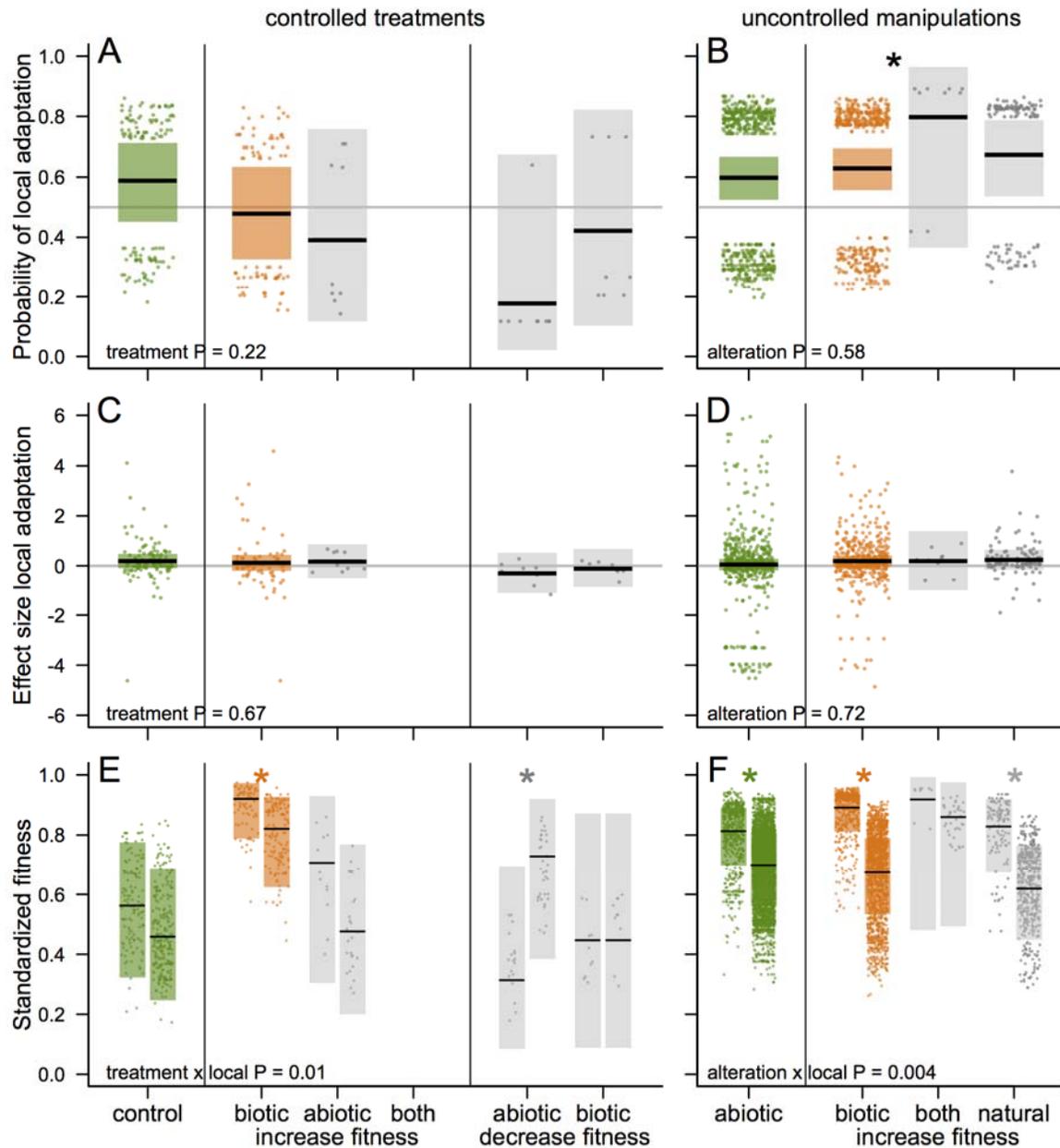
Analyses of the original Bontrager *et al.* dataset showed that large studies that report multiple fitness metrics can over-influence meta-analysis results despite the inclusion of random intercepts for both taxon and study (Bontrager et al unpublished data). To see whether this was the case in our analyses, we reran all analyses using only the fitness metric closest to lifetime fitness for each study x taxon. We ranked the fitness metrics based on how well they reflected lifetime fitness, as follows: composite fitness including reproduction (germination x survival x reproduction or survival x reproduction) > reproduction > germination x survival > survival > germination. Switching ambiguous rankings (reproduction < germination x survival, survival < germination) did not affect results (not shown).

**Table A1: Analyses using only the fitness component closest to lifetime fitness per study yield the same results as models including multiple components (Table 3).** Results from models including multiple fitness components per taxon  $\times$  study  $\times$  site  $\times$  life-stage transplanted are shown in Table 3; comparable models using only the component closest to lifetime fitness are shown below.

<i>Question</i>			Do biotic interactions affect LA (Q1&2) or fitness (Q3)? (likelihood $\chi^2_{df=1}, P$ )	Overall signal of local adaptation?
Dataset	Response	Fixed effects		
<i>1) Is LA more common when biotic interactions are left intact or ameliorated?</i>				
1	binary LA	treatment	no: treatment NS (1.3, $P = 0.26$ )	no
2	binary LA	alteration	no: alteration NS (0.6, $P = 0.45$ )	<b>yes</b>
<i>2) Is LA stronger when biotic interactions are left intact or ameliorated?</i>				
1	effect size LA	treatment	no: treatment NS (0.11, $P = 0.74$ )	no
1	standardized fitness	treatment $\times$ local/foreign	no: interaction NS (1.0, $P = 0.31$ )	<b>yes</b> ; see Question 3 <sup>2</sup>
2. All	effect size LA	alteration	no: alteration NS (1.9, $P = 0.17$ )	no
2. All	standardized fitness	alteration $\times$ local/foreign	no: interaction NS (4.3, $P = 0.038$ )	<b>natural: yes</b> (local > foreign: $P < 0.0001$ ) <b>bio.manip: yes</b> (local >> foreign: $P < 0.0001$ )
<i>3) Do biotic interactions affect fitness?</i>				
1	standardized fitness	treatment + local/foreign <sup>2</sup>	<b>yes: treatment signif</b> 72.9, $P < 0.0001$ ) biotic+ > control	<b>yes: local/foreign signif</b> ( $\chi^2_{df=1} 7.4, P = 0.006$ ) local > foreign

1. The null frequency for categorical local adaptation is 0 as lsmeans are calculated on the transformed scale from binomial models, where 0 represents a frequency of 50% (i.e. no significant adaptation or maladaptation)

2. Model in Question 3 is the reduced standardized fitness model from Question 2 with the NS interaction removed



**Fig. A1. Local adaptation vs. the biotic or abiotic environment.** This figure corresponds to Fig. 2 (A&B) & Fig. 3 (C-F), except that all combinations of the environmental component altered (none, biotic, abiotic, or both), and anticipated effect on transplant fitness (none, increase, or decrease) are retained (sample sizes in Table 1). As in Figs. 2 & 3: the most natural conditions (control, natural) are green while biotically-ameliorated conditions are orange; and for E&F within each treatment the pair of bars shows local (left) and foreign (right) fitness. For A-D the reference lines at 0.5 and 0, respectively, indicate an equal probability (A&B) or strength (C&D)

of local adaptation vs. foreign advantage ('maladaptation'). Central lines, points, and shaded rectangles are means, partial residuals, and 95% confidence intervals extracted from each model. Text in the bottom left of each panel indicates whether altering the environment affected the frequency (*A&B*) or strength (*C-F*) of local adaptation. Stars (\*) indicate whether there was significant fitness difference between local and foreign sources across studies, either across treatments/alterations if treatment/alteration was not significant (black, *B*), or within each treatment/alteration (*E&F*). In most cases we detected no difference or significant local adaptation, but when the abiotic environment was experimentally worsened, foreign source populations performed better than local populations (*E*).

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