

Appendices from Hargreaves et al (2020) Local adaptation to biotic interactions

Appendix A: Supplemental analyses

1. Analyses including manipulations of abiotic factors and those designed to decrease fitness

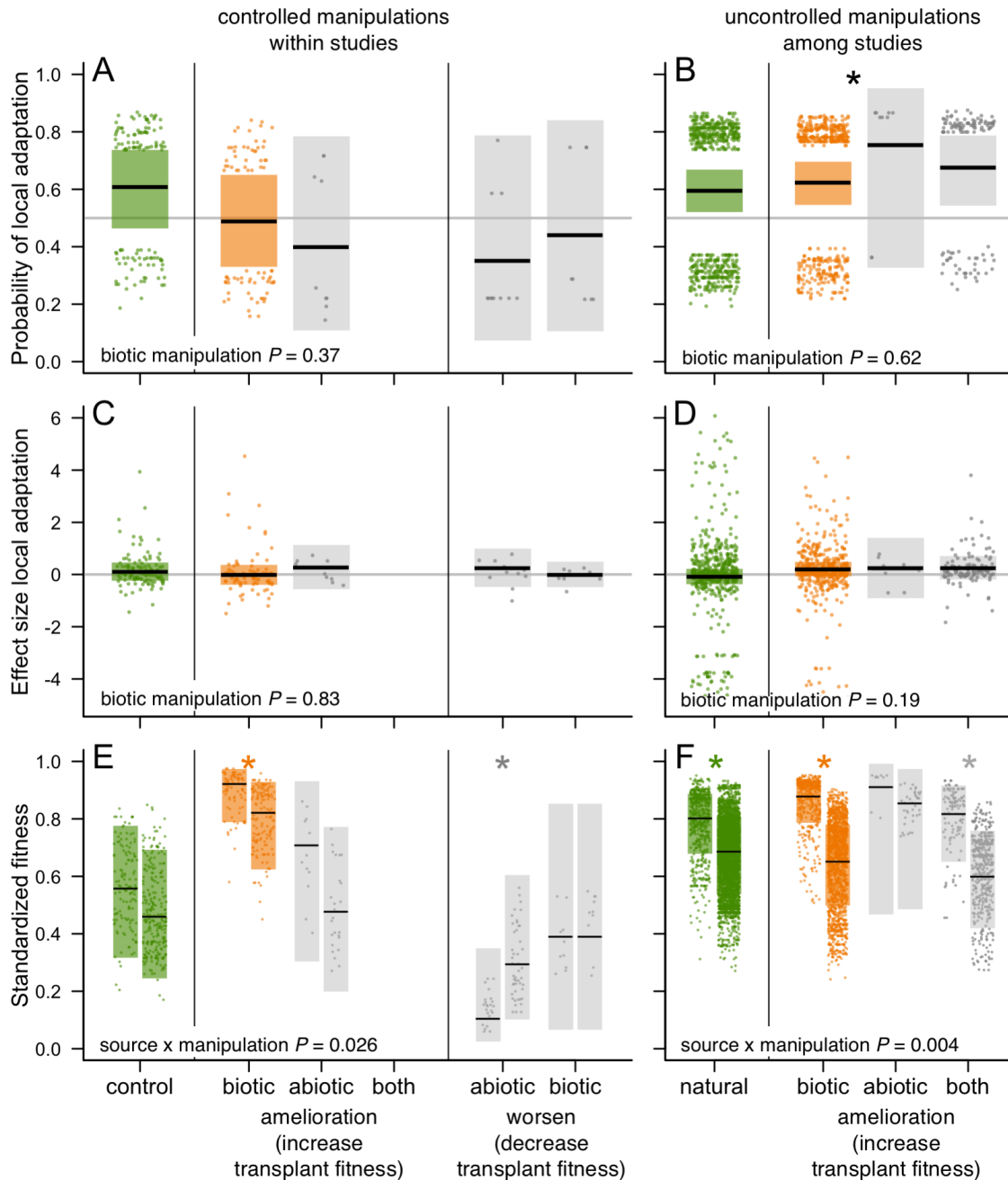


Fig. S1. Local adaptation vs. the biotic or abiotic environment. *A* & *B* correspond to Fig. 2 and *C* - *F* correspond to Fig. 3, except that all combinations of the environmental component altered (none, biotic, abiotic, both), and anticipated effect on transplant fitness (none, increase, decrease) are retained; sample sizes in Table 1. As in Fig. 2-4 the most natural conditions (control, natural)

are green, while biotically-ameliorated conditions are orange. *A-D*: 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'). *E&F*: within each environment the pair of bars shows local (left) and foreign (right) fitness. Central lines, points, and shaded rectangles are means, partial residuals, and 95% confidence intervals extracted from models. Bottom text indicates whether altering the environment affected the frequency (*A&B*) or strength (*C-F*) of local adaptation. * denotes significant differences between local and foreign sources across studies, either across treatments/alterations if treatment/alteration was not significant (black, *B*), otherwise by treatment/alteration (*E&F*). Note that the significant source difference in *E* when the abiotic environment was experimentally worsened is 'maladaptation'; other *'s indicate local adaptation.

2. Effect of the distance between local source population origin and transplant site

While we used the author's definition of 'local' whenever possible, trusting their on-the-ground intuition, in a few cases 'local' sources came from distances away that stretched a reasonable definition of local, e.g. >1000 km. We therefore applied a cutoff, re-categorizing 'local' sources as 'foreign' if they originated ≥ 100 km or ≥ 100 m elevation from the transplant site. After applying this cutoff, the median distance between local source origin and transplant site was 0 km and 0 masl (Fig. S1).

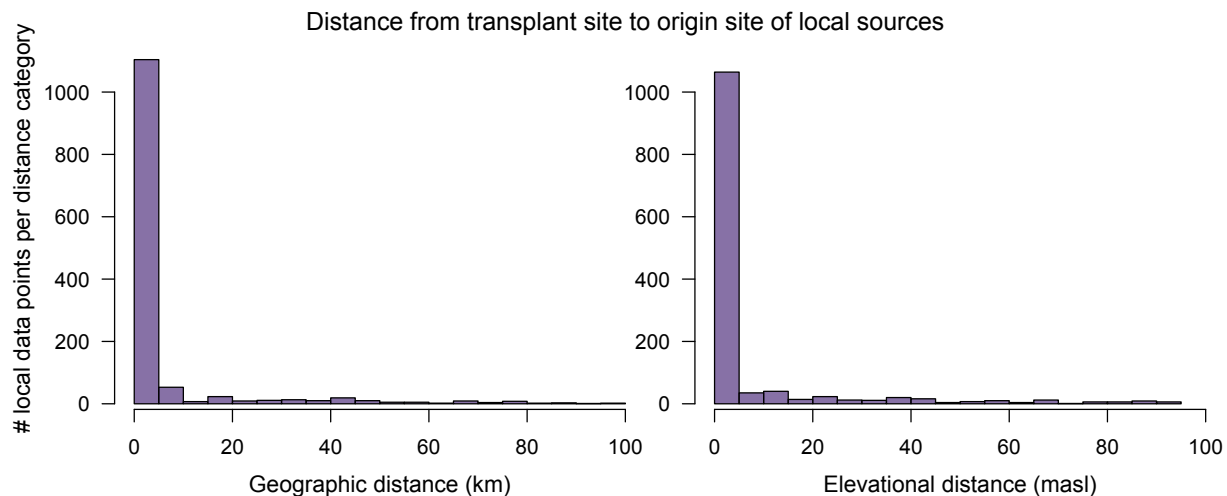


Fig. S2. Distance from site origin to transplant site for each local source in the full data (Dataset 2, all 149 studies), after applying the distance threshold used in the main paper (local sources must be from <100 km and <100 masl of the transplant site).

Since any cutoff is arbitrary, we tested the effect of this cutoff in two ways. First, we reran analyses for *Questions 1-3* using a stricter cutoff of <50 km and <100 masl. This had little effect on sample sizes for Dataset 1 (lost 2 data points but retained all 15 studies), but reduced n for Dataset 2 by 3 studies, 3 taxa (lost 2 genera and 1 family) and 24 data points. Second, we reran *Questions 1-3* models for the probability and effect size of local adaptation including a random covariate for the mean distance between local source populations' origin and the transplant site. The random covariate was nested within environments (control/natural vs. biotically ameliorated), and excluded one study from which we could not extract exact locations. We did not use this approach for standardized fitness as each source population, both local and foreign, contributes a data point, and foreign sources are always from farther away than local sources.

Results: With one exception, neither reducing the distance cutoff for 'local' sources nor accounting for their localness as a covariate changed conclusions (Table S1). The exception is that with a stricter definition of local, the stronger effect size of local adaptation under biotic amelioration was no longer significant (Table S1 Question 2), likely for two reasons. 1) Reduced sample size (reduced by <3%, but the eliminated effect sizes had larger than average n 's so were weighted more strongly in analyses). 2) Reduced difference among environments. Eliminating the 'least-local' data points reduced the strength of local adaptation in biotically ameliorated sites (though it remained positive, i.e. local > foreign: effect size from $l_{\text{means}} \pm \text{SE}$ changed from 0.21 ± 0.14 to 0.18 ± 0.15) and increased local adaptation strength in natural environments (though it remained negative, i.e. foreign > local: -0.08 ± 0.15 to -0.05 ± 0.17).

Table S1. Effect of localness of local sources. Results from main analyses in Table 3 (local source cutoff of <100 km & <100 masl), compared to analyses using a stricter definition of local (local source cutoff <50 km & <100 masl) or including a random covariate for the distance between local source origin site and the transplant site (nested within manipulation). Analyses of standardized fitness were not redone with the random covariate for distance (see above). Grey fill indicates results from reanalysis differed from main analyses.

Question		Do biotic interactions affect LA (Q1&2) or fitness (Q3)? (likelihood $\chi^2_{df=1}$, P) Overall local adaptation?		
		Main analyses (Table 3)	Stricter definition of local	Random covariate for local distance
<i>Question 1) Is LA more probable when biotic interactions are left intact or ameliorated?</i>				
1 – binary	treatment	no: treatment NS (2.5, $P = 0.12$) no	no: treatment NS (1.5, $P = 0.22$) no	no: treatment NS (1.2, $P = 0.28$) no
2 – binary	alteration	no: alteration NS (0.5, $P = 0.47$) yes	no: alteration NS (0.4, $P = 0.52$) yes	no: alteration NS (0.5, $P = 0.46$) yes
<i>Question 2) Is LA stronger when biotic interactions are left intact or ameliorated?</i>				
1 – effect size	treatment	no: treatment NS (0.8, $P = 0.38$) no	no: treatment NS (0.8, $P = 0.38$) no	no: treatment NS (<0.01, $P > 0.9$) ¹ no
1 – std fitness	treatment × local/foreign	no: interaction NS (1.8, $P = 0.18$) yes: local > foreign (5.1, $P = 0.025$)	no: interaction NS (1.4, $P = 0.23$) yes: local > foreign (5.5, $P = 0.019$)	–
2 – effect size	alteration	yes: bio.amel > nat (4.1, $P = 0.043$) no	no (2.6, $P = 0.10$) no	yes: bio.amel > nat (3.9, $P = 0.048$) no
2 – std fitness	alteration × local/foreign	yes: interact. signif (13.7, $P = 0.0002$) yes (both envs, but stronger in bio.amel)	yes: interact. signif (10.7, $P = 0.001$) yes (both envs but stronger in bio.amel)	–
<i>Question 3) Do biotic interactions affect performance?</i>				
1 – std fitness	treatment + local/foreign	yes: bio.amel > ct (70.5, $P < 0.0001$) yes: local > foreign (5.1, $P = 0.025$)	yes: bio.amel > ct (61.9, $P < 0.0001$) yes: local > foreign (5.5, $P = 0.019$)	–

1. models did not converge properly so exact test statistics and significance may not be reliable

3. Analyses using one fitness metric per taxon

We assessed whether large studies that measure many fitness components unduly influence results by re-running analyses using only the fitness metric closest to lifetime fitness for each study \times taxon. We ranked the fitness metrics based on how well they reflected lifetime fitness, as follows: composite fitness including reproduction (emergence \times survival \times reproduction or survival \times reproduction) $>$ reproduction $>$ emergence \times survival $>$ survival $>$ emergence. Results (Table S2) are almost identical to those using multiple fitness components (Table 3). Switching ambiguous rankings (reproduction $<$ germination \times survival, survival $<$ germination) did not affect results (not shown).

Table S2: 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 × study × site × life-stage transplanted are shown in Table 3; comparable models using only the component closest to lifetime fitness are shown below.

Question			Do biotic interactions affect LA (Q1&2) or fitness (Q3)? (likelihood χ^2 , 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, $P = 0.44$)	yes
<i>2) Is LA stronger when biotic interactions are left intact or ameliorated?</i>				
1	effect size LA	treatment	no: treatment NS (0.43, $P = 0.51$)	no
1	standardized fitness	treatment × local/foreign	no: interaction NS (1.3, $P = 0.86$)	yes ; see Question 3 ¹
2	effect size LA	alteration	yes: alteration signif (4.1, $P = 0.043$) bio.amel > control	no
2	standardized fitness	alteration × local/foreign	yes: interaction signif (4.4, $P = 0.036$)	natural: yes (local > foreign: $P < 0.0001$) bio.manip: yes (local >> foreign: $P < 0.0001$)
<i>3) Do biotic interactions affect fitness?</i>				
1	standardized fitness	treatment + local/foreign ¹	yes: treatment signif (70.0, $P < 0.0001$) biotic+ > control	yes: local/foreign signif ($\chi^2_{df=1} 7.8$, $P = 0.005$) local > foreign

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

4. Sensitivity to phylogenetic correction

Our main analyses account for phylogenetic relatedness by including a nested taxonomic random effect. We also tested whether our results would differ if we conducted a formal phylogenetic correction. The motivation for this was two-fold: to test whether our results hold after accounting for phylogenetic distance, and to test for a phylogenetic signal to local adaptation. Whereas phylogenetically-corrected comparative analyses commonly consider traits or a trait responses, our response variables reflect the propensity of a species to locally adapt; the possibility that local adaptation has phylogenetic structure has not, to our knowledge, been tested.

We first needed a phylogenetic tree. Because >90% of species our study were plants, and long branches can strongly bias phylogenetic analyses (Uyeda et al. 2018) we subset our dataset to include only plants. We then used an extensive publicly available megaphylogeny (Qian and Jin 2016) which included 74% of our 149 plant species. For the remaining 38 plant species, we searched the published literature for family- or genus-level phylogenetic trees to manually add to the megaphylogeny text file. Our final tree is fully resolved, excluding *Myosotis nemorosa*; we could not find a published phylogeny that included this species, but it was also not in the subset of data we analyzed for phylogenetic structure (described below). We visualized the final tree using ‘phytools’ (Revell 2012) in R; Fig. S3.

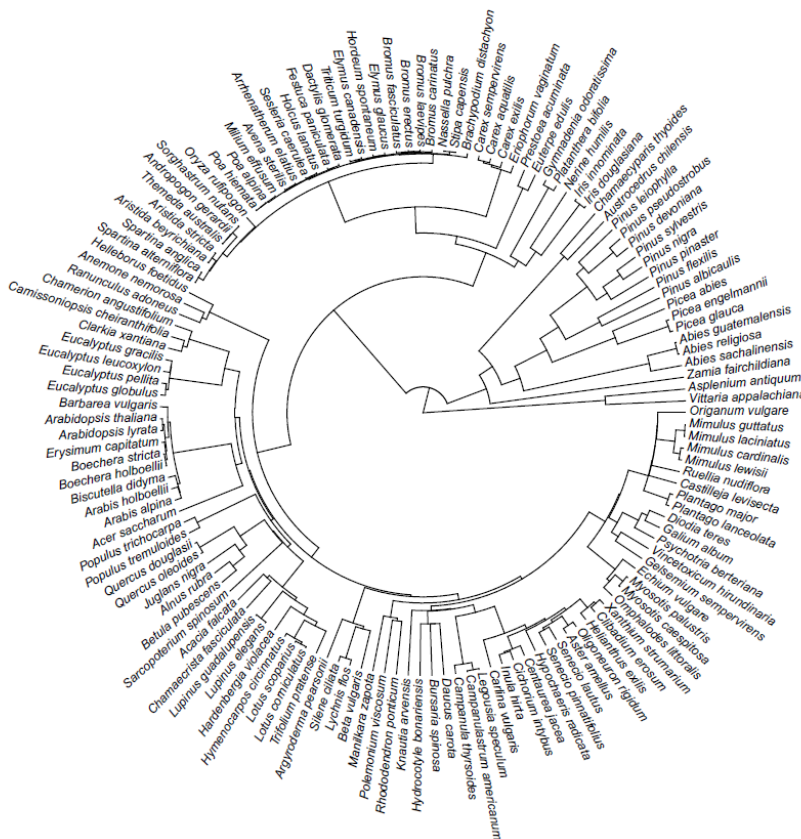


Fig. S3. Phylogenetic relationships among angiosperm species in our meta-analysis. The tree was created by pruning an existing megaphylogeny (Qian and Jin 2016).

Our challenge was to find a statistical package that could incorporate phylogenetic structure into our already complex generalized mixed model. The ‘Hmsc’ package by Tikhonov (Tikhonov et al. 2019) was most appropriate, allowing phylogenetic relationships to be included as a hierarchical random effect in what would otherwise be a standard mixed effects model. Using this approach, we repeated a core analysis from our paper (*Question 2 ‘Is local adaptation stronger when biotic interactions are left intact?’*, using Dataset 2; Fig. 3D)), comparing a model accounting for phylogeny to an equivalent model (that also included only plants) that did not. Hmsc does not yet allow logit regression so we used probit regression, nor does it allow data points to be weighted by sample size so we omitted weights (weighting by sample size had negligible effects on main analyses). As Hmsc uses Bayesian model fitting with Gibbs MCMC sampling, we ran each model for 1000 iterations, discarding the first 500 as a burn in, for each of two chains. We visually inspected trace plots to confirm that the two chains converged and were well mixed.

Results: These analyses confirmed that formally accounting for phylogeny does not alter the conclusions of our main analyses. Both models explained the same amount of total variation in the data set (29.6% without phylogeny, 28.5% with phylogeny; Fig. S4). The variance attributable to phylogenetic relationships in the phylogenetic model was captured in the ‘taxon’, ‘study’, and ‘fitness components’ random effects in the non-phylogenetic models (Fig. S4).

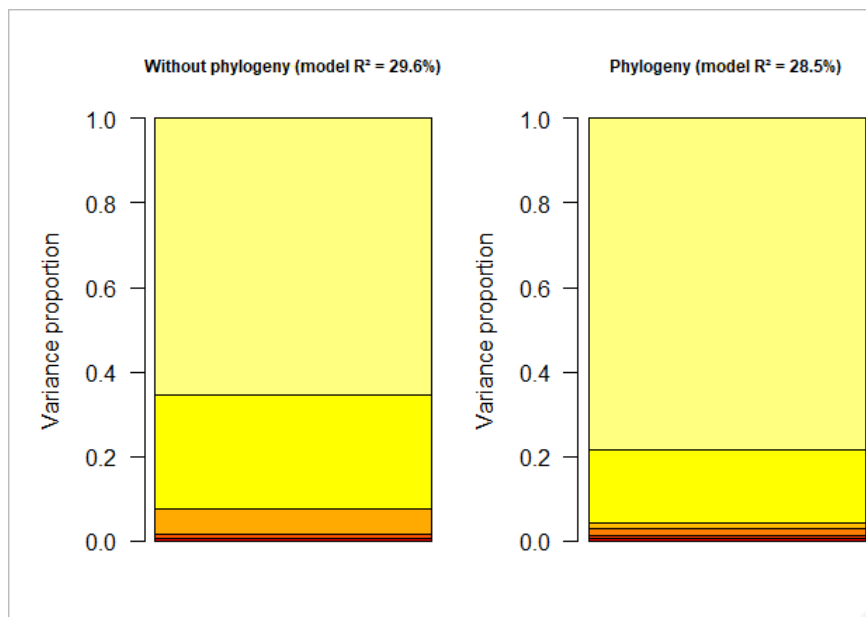


Fig. S4. Comparing variance partitioned among models without and with phylogenetic relatedness as a random factor. Both models explain a comparable total amount of variation, but this total variation is partitioned differently among random effects; adding phylogeny primarily acts to absorb variation originally attributable to ‘taxon’, ‘study’, and ‘fitness component’. Color key: Light yellow = study, yellow = fitness type, light orange = taxon, dark orange = phylogeny, red bars = fixed effects.

Appendix B: Literature search details

Our study leveraged a 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 the following:

- 1) 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)
- 2) 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*).
- 3) Additional studies encountered while gathering data (up to 2017)
- 4) Additional searches targeted at studies from the tropics, to counter the bias toward temperate zones in studies obtained in 1-3. This effort included emails to colleagues who work in the tropics, a public request for studies on twitter, a Google Scholar search with the above string translated to Spanish, and a repeat of the above search term with
 - a. the transplant term expanded to include 'translocation'
 - b. the geographic term (temperature OR climat* OR latitud* OR elevation* OR altitud*) replaced with one targeted at the tropics: (tropic* OR equator* OR rainforest* OR Mexico* OR (Central America*) OR (South America*) OR Africa*)
 - c. the search timeframe extended to June 2019.

These searches returned >2000 studies. Based on titles and abstracts, studies 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; 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 individuals within sites/populations (as defined by the authors) were also discarded. This yielded ~250 studies for data extraction. Some of these were excluded during data extraction if the required data were unavailable (e.g. results were averaged across sources or sites, performance was only measured using growth), or were reported in multiple studies.

References

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