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Context dependence of local adaptation to abiotic and biotic environments: a quantitative and qualitative synthesis

Supplementary Materials

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Supplemental analyses of positive local-foreign contrasts indicative of local adaptation

METHODS

We subsetted our dataset of local-foreign (L-F) contrasts to include only SMD (standard mean difference) values that were potentially indicative of local adaptation (i.e. SMD > 0). In parallel to the analyses conducted on the full dataset, we used linear mixed-effect models to test for the effects of taxonomy (plant or animal, we excluded the one study that contained contrasts for bacteria), and local environment (abiotic, biotic, or both) on the magnitude of the SMD of L-F contrasts. In addition, for contrasts from plant studies, we tested for an effect of life history (annual, perennial) and local environment (abiotic, biotic, or both) on the magnitude of SMD. We tested for differences among means using bootstrap analysis, stratified by studies.

As in the analyses of the full dataset, there were a subset of experiments that had no 'home' biotic treatment (e.g. biotic factors were tested using exclusion or removal). For these experiments, we paired the local-foreign SMDs in the presence and absence of the biotic factor and then took the difference (*hereafter 'biotic influence contrasts'*). For the new analysis, we retained pairs where either one or both SMDs were positive (e.g. local genotypes outperformed foreign genotypes in both the presence and/or absence of a biotic interactor). Parallelling the main analyses, we tested for the effect of taxonomy (plant, animal, bacteria) on positive biotic influence contrasts. In a second analysis limited to plants, we tested whether SMD differed according to life history (annual, perennial).

We also tested for an association between mean SMD for L-F contrasts and latitude. Similar to analyses on the full dataset, latitude was the location of the common gardens, and for lab experiments latitude was the location of the source populations. We calculated the Pearsons's correlation coefficient for abiotic and biotic contrasts separately and we excluded contrasts that had the local environment of 'both'. Because latitude and experiment are highly co-linear, we did not include experiment in the analysis and calculated correlation coefficients using all SMDs as independent data points; we assessed the significance of observed correlations using a t-tests. We then tested for the difference between correlation coefficients using a Fisher z-transformation and a one-tailed test.

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RESULTS & DISCUSSION

The results of our new analyses were qualitatively similar to those of the full dataset. The restricted dataset of positive L-F contrasts contained 186 contrasts (47.8% of the total dataset) from all 24 papers, and from 29 of 31 unique experiments reported by these papers. The mean SMD of all positive contrasts was 1.29 ± 0.08 ($\bar{x} \pm$ SE).

Local adaptation - Variation in positive SMDs was best explained by a model that included taxonomy (plant or animal), local environment (abiotic, biotic, or both), their interaction, and the random effect of experiment (AICc = 607.5; $R^2 = 0.52$; Table S1). The mean SMD of plants and animals did not differ significantly ($P > 0.05$), nor did the overall mean SMD of abiotic, biotic, or both local environments ($P > 0.05$). However, there were significant differences among particular combinations of plants/animals and their local environments (abiotic, biotic, both): all plant-local environment combinations (i.e. plant-abiotic SMD, plant-biotic SMD, and plant-both SMD), were greater than animals in their local abiotic environment (i.e. plant-abiotic; $P < 0.05$; Figure S1).

In plants, variation in positive L-F SMDs was best explained by a model with only the random effect of experiment (AICc = 479.2, $R^2 = 0.15$). This model was not a significantly better fit than a model including an effect of life history (ΔAICc = 1.5, $R^2 = 0.16$); however, there was no significant difference between perennial and annual plants ($P > 0.1$; Figure S2).

Biotic Influence Contrasts - When we restricted analysis of biotic influence contrasts to include cases where at least one of the contrasts indicated local adaptation (i.e. SMD > 0), we retained 115 cases (62.3%) of the total dataset. In this analysis, local adaptation was significantly stronger in the presence compared to the absence of the biotic interactor ($\bar{x} \pm$ SE: $\bar{x}_{pres} = 0.94 \pm 0.18$; $\bar{x}_{abs} = 0.50 \pm 0.17$; $P = 0.05$). These results are qualitatively similar to those based on the full dataset.

A model including taxonomy and the random effect of experiment was the best fit to the data (AICc = 473.8, $R^2 = 0.49$; Table S3). The biotic influence contrasts were significantly positive for plants ($\bar{x} \pm$ SE: 0.68 ± 0.27; bootstrap $P = 0.001$; Figure S3) and significantly negative for animals ($\bar{x} \pm$ SE: -0.96 ± 0.08; bootstrap $P < 0.001$; Figure S3), indicating that plants and animals respond differently to the presence versus absence of biotic interactors when locally adapted.

For plants, the best-fit model included only the random effect of experiment (AICc = 295.9, R^2 = 0.66; Table S4). However, the mean values of biotic influence contrasts were not significantly different between annuals and perennials (Figure S3).

***Latitudinal gradient* –** The restricted dataset of positive L-F contrasts contained 133 contrasts (from 23 experiments). Similar to the analysis on the full dataset, we found that SMDs of L-F contrasts were significantly greater at high than low latitudes (Pearsons's r = 0.24, bootstrap P = 0.001; Figure S4). For local adaptation to biotic factors, the correlation was negative but not significantly different from zero (Pearsons's r = -0.15, $P_{df = 6}$ = 0.71; Figure 7A). Whereas, for local adaptation to abiotic factors, the correlation was positive and significant (r = 0.28, $P_{df = 73}$ = 0.01). The difference between biotic and abiotic correlation coefficients was not greater than expected by chance (Fisher z-transformation score = 0.98; one-tailed P = 0.16).

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Figure S1. Local-foreign contrast values ($\overline{x}$ ± SE) in relation to if the local environment was the abiotic environment, biotic environment, or both abiotic and biotic environment for animals and plants. Greater positive values of SMD indicate greater estimates of local adaptation. Numbers adjacent to each point-range indicate the number of contrasts and, in parentheses, the number of independent experiments. Letters adjacent to point-range values indicate post hoc comparisons of mean differences ($P < 0.05$).

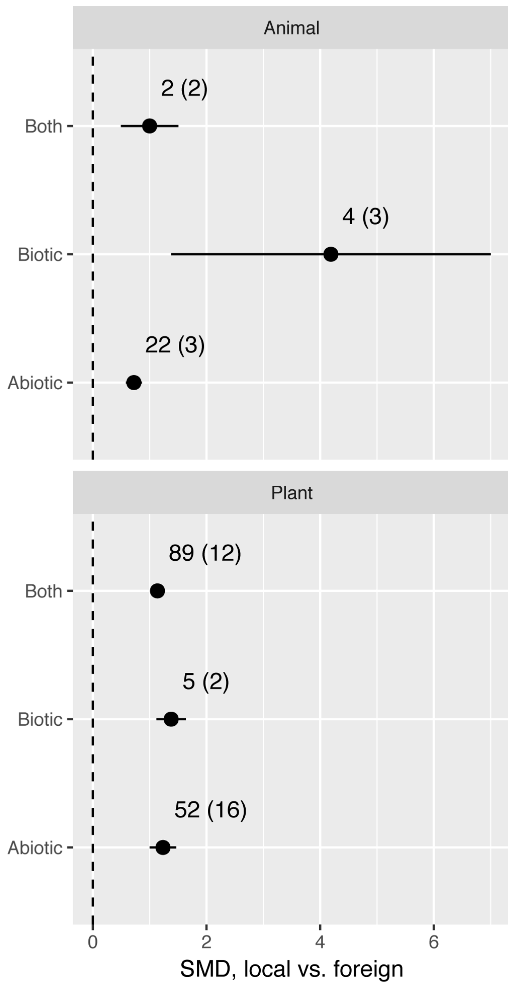

Figure S2. Local-foreign contrast values for plants split by life history. Greater positive values of SMD indicate greater estimates of local adaptation. Numbers adjacent to each point-range indicate the number of contrasts and, in parentheses, the number of independent experiments. Pairwise comparison of means was not greater than expected by chance (bootstrap p > 0.05).

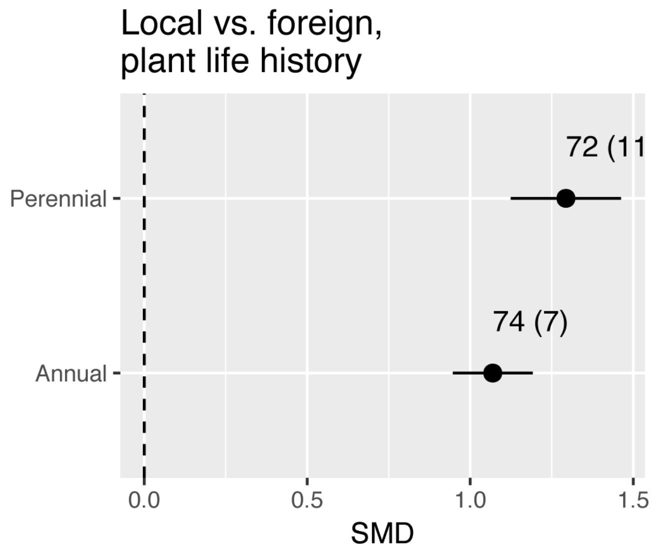

Figure S3. Biotic influence contrasts ($\bar{x} \pm$ SE) in (A) plants or animals, and (B) perennials or annuals. Positive values of the contrast indicate that the local-foreign contrast was greater in the present than the absence of biotic interactors and negative values indicate that the local-foreign contrast was greater in the absence than the presence of biotic interactors. Numbers adjacent to each point-range indicate the number of contrasts and, in parentheses, the number of independent experiments. Letters adjacent to point-range values indicate post hoc comparisons of mean differences ($P < 0.05$).

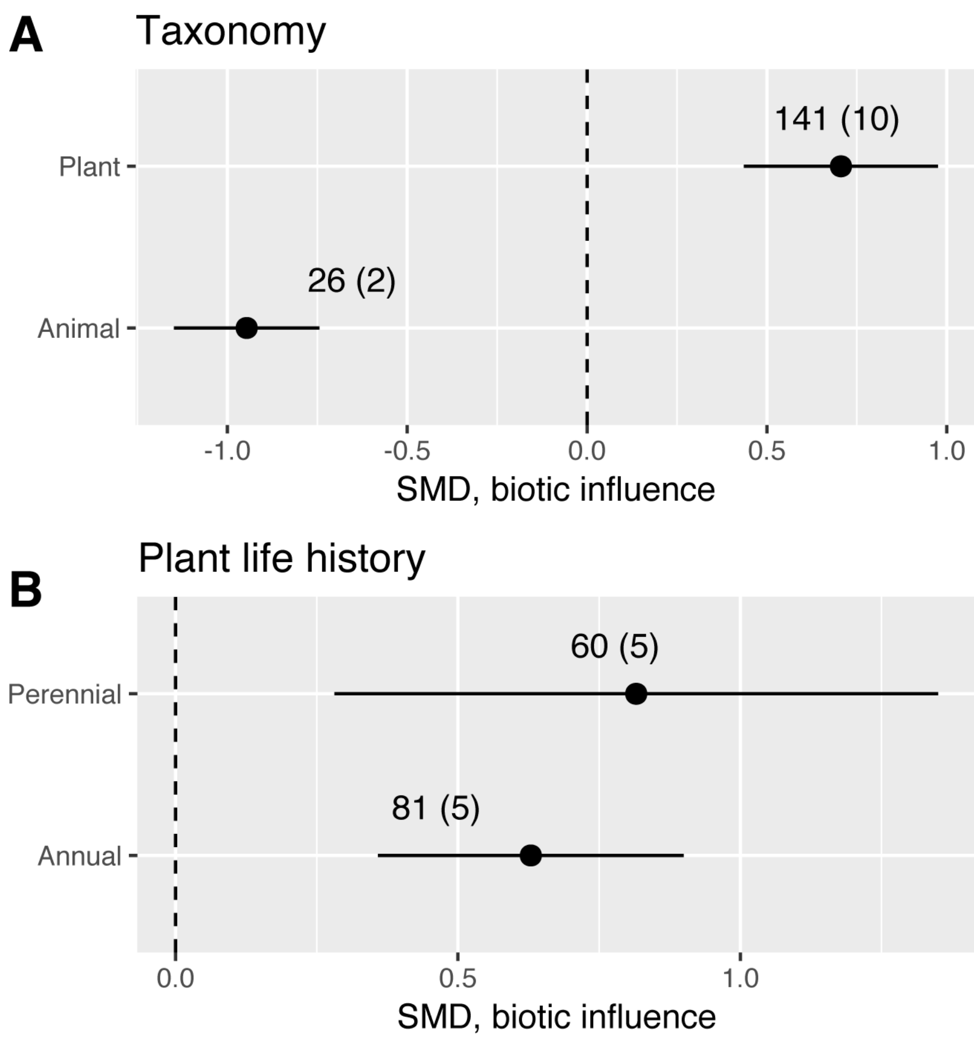

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Figure S4. Scatterplots of SMD versus source population latitude for positive local-foreign contrasts.

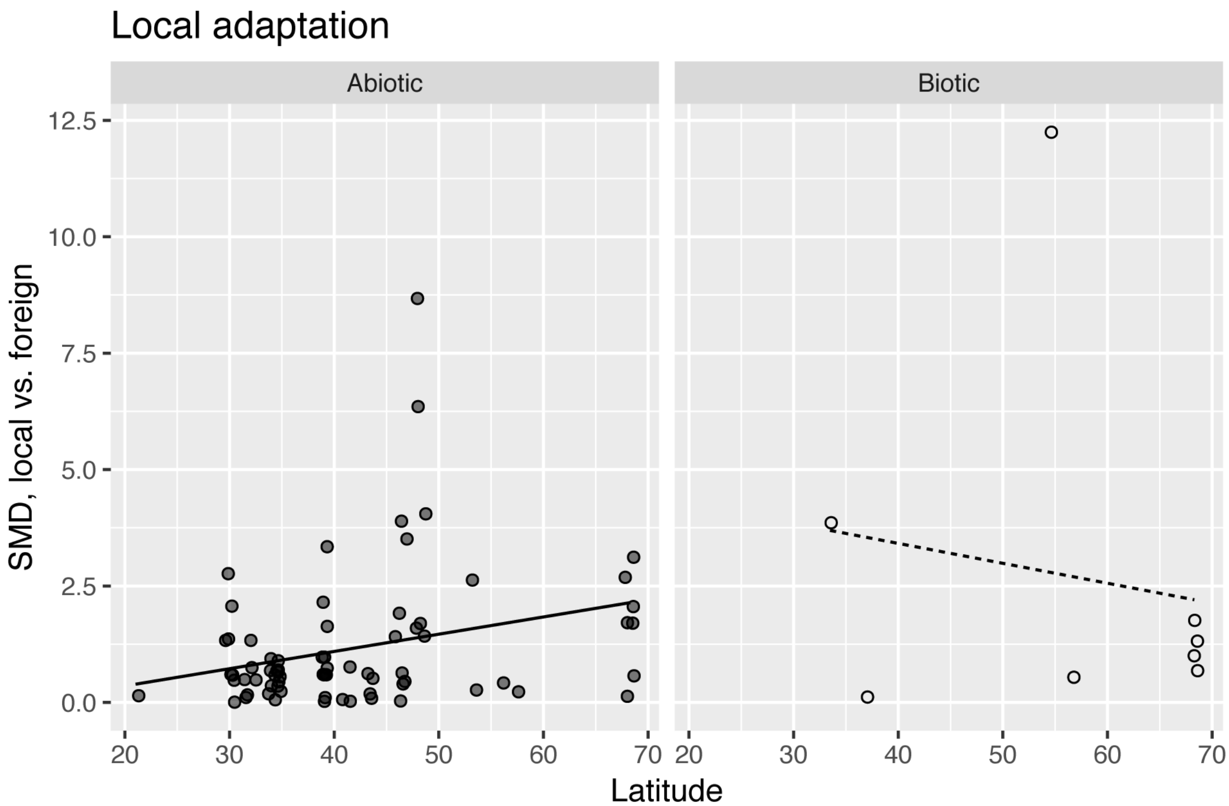

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Table S1. Restricted analysis of locally adapted (SMD >0) local-foreign contrasts across taxonomy. Model fit estimates for linear mixed models examining the effect of taxonomy (plant, animal; data from a single study of bacteria were excluded from this analysis), environment type (abiotic, biotic, or both), and experiment identity (random) on the local-foreign SDM. The column 'df' indicates the number of estimated parameters in the model.

Explanatory Factors	df	AICc	ΔAICc	R^2
(experiment)	3	613.2	5.7	0.67
taxonomy + (experiment)	4	609.9	2.4	0.69
environment + (experiment)	5	614.9	7.4	0.60
taxonomy + environment + (experiment)	6	612.8	5.3	0.66
taxonomy * environment + (experiment)	8	607.5	0.0	0.53

Table S2. Restricted analysis of locally adapted (SMD >0) local-foreign contrasts for plant life-history. Model fits estimates for linear mixed models examining the effect of plant life-history (annual, perennial), environment type (abiotic, biotic, or both), and experimental identity (random) on the local-foreign SMD. The column 'df' indicates the number of estimated parameters in the model.

Explanatory Factors	df	AICc	ΔAICc	R^2
(experiment)	3	479.2	0.0	0.15
life history + (experiment)	4	480.8	1.6	0.16
environment + (experiment)	5	483.1	3.9	0.16
life history + environment + (experiment)	6	485.0	5.8	0.17
life history * environment + (experiment)	7	485.4	6.1	0.19

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Table S3. Restricted analysis of locally adapted (one SMD >0) biotic influence contrasts across taxonomy. Model fit estimates for linear mixed models estimating the effect of taxonomy (animal or plant) and experiment identity (random) on biotic influence SMD. The column 'df' indicates the number of estimated parameters in the model.

Explanatory Factors	df	AICc	ΔAICc	R^2
(experiment)	3	474.9	1.1	0.47
taxonomy + (experiment)	4	473.8	0.0	0.49

Table S4. Restricted analysis of locally adapted (one SMD >0) biotic influence contrasts for plant life history. Model fit estimates for linear mixed models examining the effect of plant life history (annual, perennial) and experiment identity (random) on the biotic influence SMD. The column 'df' indicates the number of estimated parameters in the model.

Explanatory Factors	df	AICc	ΔAICc	R^2
(experiment)	3	295.9	0.0	0.64
life history + (experiment)	4	295.9	0.01	0.66

Table S5. A comparison of three review approaches, modified from Grant and Booth (2009), Bettanny-Saltikov (2010).

Review	**Process of selecting articles**	**Question**	**Analysis**
Literature review	Not clear, explicit or described	Not focused on a single question; may describe an overview	Chronological, thematic or conceptual
Meta-analysis	Clear and explicit; comprehensive search conducted in a systematic way	Focused on a single question	Numerical analysis of measures of effect
Meta-synthesis	Clear and explicit; comprehensive search conducted in a systematic way	Focused on a single question	Thematic analysis

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Table S6. Summary of major themes used in the qualitative meta-synthesis across each of phases or readings.

Phase 1 themes (quotes)	Phase 2 themes (quotes)	Phase 3 themes (summary)
- Abiotic factor - Biotic factor - Focal species - Biotic interaction type - Was local adaptation found? - Using environmental extremes or selection of conditions *a priori* - Latitude, elevation and geographic distance - Lab, field or greenhouse experiments - Temporal issues - Coevolution - Strict (home-away and local-foreign) vs broad definition of local adaptation - Plasticity - Maternal effects - Fitness traits measured - Global change - Gene flow - Importance of studying local adaptation	Theoretical basis ● Geographic mosaic theory of coevolution ● Coevolution ● Stress gradient hypothesis ● Classic local adaptation Biotic interactions ● Parasitism, predation, and pathogenicity ● Plant-plant competition ● Plant-microbe mutualisms ● Animal-animal competition Site selection and experimental levels ● Explanation for experimental levels and sites chosen Taxonomic bias ● Study system ● Motivation for study system Global change ● Global change (including invasion and conversation)	• Theoretical basis • Biotic interactions • Site selection and experimental levels • Taxonomic bias • Global change

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Table S7. Breakdown of major themes found in the qualitative analysis by paper.

Major theme	**Topic**	**References**
Site selection and experimental levels	Selection of abiotic gradients or phenotypic differentiation in response to abiotic conditions	Alexander et al. 2015 Ariza 2011 Barton 1993 Bray et al. 2018 Bryner 2011 Compagnoni and Adler 2014 Coulatti and Barrett 2013 Crémieux et al. 2008 Egea-Seranno 2014 Gortner et al. 2016 Grassein 2014 Hughes et al. 2017 Lehndal and Ågren 2015 Liancourt 2013 O'Brien et al. 2018 Rice and Knapp 2008 Schwarzer and Joshi 2017 Smith and Ruize 2004 Tomiolo et al. 2015 Volis et al. 2002 Wendling et al. 2015 Yang et al. 2016
	Ease of manipulating abiotic variables in field sites, greenhouses or environmental chambers	Tomiolo et al. 2015 Barton 1993 Bray et al. 2018 Bohrer et al. 2003 Crémieux et al. 2008 Germain et al. 2016 Germain et al. 2018 Gortner et al. 2016 Heath et al. 2010 Laine 2008 Menke et al. 2007 Molina-Montenegro et al. 2012 Pahl et al. 2013 Parain et al. 2016 Pickles et al. 2015 Rice and Knapp 2008 Schwarzer and Joshi 2017 Sikes et al. 2013 Thrall et al. 2008 Tomiolo et al. 2015 Wendling et al. 2015
	Strongly contrasting and well-studied abiotic variables	Alexander et al. 2015 (extreme temperatures using elevation) Barton 1993 (extreme temperatures) Branco 2009 (serpentine) Bray et al. 2018 (salinity) Buser 2012 (pollution)

		Castro et al. 2013 (salinity) Crémieux et al. 2008 (temperature) Doubkova 2012 (serpentine) Egea-Seranno 2014 (acid) Eranen 2009 (pollution) Espeland and Rice 2007 (serpentine) Germain et al. 2016 (soil moisture) Germain et al. 2018 (soil moisture) Gomez-Mestre 2002 (salinity) Jurjavcic et al. 2002 (serpentine) Landis et al. 2012 (extreme temperatures) Mitchell 2005 (extreme temperatures) Rice and Knapp 2008 (temperature and precipitation) Sambatti and Rice 2006 (serpentine) Schwarzer and Joshi 2017 (extreme temperatures and water table) Taheri and Bever 2010 (pollution) Thrall et al. 2008 (salinity) Tomiolo et al. 2015 (precipitation) Vinebrooke 1996 (pollution) Wendling et al. 2015 (extreme water temperatures)
Biotic interactions	Shifts from parasitism to mutualisms in plant-microbe interactions	Antunes et al. 2010 Heath et al. 2010 Pickles et al. 2015 Sherrard and Maherali 2011 Sullivan and Faeth 2008 Taheri and Bever 2010 Thrall et al. 2008
	Presence-absence and local-foreign - microbes	Bankier 2017 Bohrer et al. 2003 Branco et al. 2009 Johnson et al. 2010 Kardol et al. 2014 Laukau et al. 2013 Pankova et al. 2014 Parain et al. 2016 Pickles et al. 2015 Sherrard and Mehrali 2011 Taheri and Bever 2010
	Presence-absence - plant competition	Ariza and Tielborger 2011 Castro et al. 2013 Compagnoni and Adler 2014 Grassein et al. 2014 Jurjavcic et al. 2002 Kindell et al. 1996 Knight and Miller 2004 Liancourt et al. 2013 Liancourt and Tielborger 2009 Muhamed et al. 2013 Pahl et al. 2013

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		Rice and Knapp 2008 Stanton-Geddes et al. 2012 Thompson et al. 1991 Tomiolo et al. 2015 Welk et al. 2002
	Presence-absence - predation + herbivory	Abdala-Roberts and Marquiz 2007 Fine et al. 2004 Hufford and Mazer 2012 Hughes et al. 2017 Lehndal and Ågren 2015 Vinebrooke 1996 Welk et al. 2014
	Multi-level plant competition or manipulation of identity of competitor	Alexander et al. 2015 Bischoff et al. 2006 Crémieux et al. 2008 Fey and Cottingham 2011 Germain et al. 2016 Germain et al. 2018 Gomez-Mestre and Tejedo 2002 Koutecka and Leps 2013 Menke et al. 2007 Molina-Montenegro et al. 2013 O'Brien et al. 2018 Schwarzer and Joshi 2017 Shoen et al. 1986 Volis et al. 2002
	Host-parasite coevolution	Bryner and Rigling 2011 Gortner et al. 2016 Heath et al. 2013 Laine 2008 Padfield et al. 2019 Sullivan and Faeth 2008 Wendling et al. 2015
	Local adaptation at multiple time points in a lab or greenhouse	Lopez Pascue et al. 2011 terHorst et al. 2014
Taxonomic biases	Plants - Annuals or short-lived perennials	Crémieux et al. 2008 Espeland and Rice 2007 Germain et al. 2016 Germain et al. 2018 Jurjavcic et al. 2002 Molina-Montenegro et al. 2013 Stanton-Geddes et al. 2012 Tomiolo et al. 2015
	Plants - long-lived	Barton 1993 Bohrer et al. 2003 Eranen et al. 2009 Fine 2004 Pickles et al. 2015 Rice and Knapp 2008

		Thompson et al. 1991
	Microbes	Bankier 2017 Gortner et al. 2016 Padfield et al. 2019 Parain et al. 2016
	Animals	Cunningham et al. 2009 Hughes et al. 2017 O'Brien et al. 2018 Wendling et al. 2015
Theory	Parasites + pathogens	Bankier 2017 Bryner and Rigling 2011 Echaubard et al. 2014 Gortner et al. 2016 Wendling et al. 2015 King et al. 2011 Laine 2008 Landis et al. 2012 Lopez Pascua et al. 2011 McCoy et al. 2002 Mitchell et al. 2005 Padfield et al. 2019 Rodl and Ward 2002 Scharf et al. 2010 Schoebel et al. 2010
	Predation across gradients	Bray et al. 2018 deBlock et al. 2013 Egea-Seranno et al. 2013 Fine 2004 Lehndal and Ågren 2015 Molina-Montegro et al. 2013 Parain et al. 2016 Pellisier et al. 2014 Poisot et al. 2011 Rolan-Alvarez et al. 1997 Skelly 1995 Smith and Ruiz 2004 Vinebrook 1996
	Stress-gradient hypothesis - direct	Ariza and Tilerborger 2011 Castro et al. 2013 Compagnoni and Adler 2014 Ehlers et al. 2012 Eranen et al. 2009 Espeland and Rice 2007 Jurjavic et al. 2002 Grassein et al. 2014 Lianourt and Tielborger 2009 Liancourt et al. 2013 Molina-Montenegro et al. 2013 Muhammed et al. 2013 Tomiolo et al. 2015

		Vinebrooke 1996 Volis et al. 2002 Welk et al. 2014
	Plant-plant interactions - density	Barton 1993 Bischoff et al. 2006 Donohue et al. 2000 Donohue et al. 2001 Kindell et al. 1996 Knight and Miller 2004 Koutecka and Leps 2013 Liancourt and Tielborger 2009 Rice and Knapp 2008 Sambatti and Rice 2006 Stanton-Geddes et al. 2012 Thompson et al. 1991
	Plant-plant interactions - neighbor identity	Alexander et al. 2015 Ehlers and Thompson 2004 Germain et al. 2016 Germain et al. 2018 Schwarzer and Joshi 2017 Shoen et al. 1986
Global Change	Abiotic changes in environment (temperature, salinity, etc.)	Antunes et al. 2011 (general climate) Ayes et al. 2009 (general climate) Bray et al. 2018 (salinity) Bischoff et al. 2006 (temperature) Bryner and Rigling 2011 (temperature) Compagnoni and Adler 2014 (temperature) Cunningham et al. 2009 (pollution, land-use) deblock et al. 2013 (temperature) Echaubard et al. 2014 (temperature) Egea-Serrano et al. 2014 (general climate, pollution) Eranen and Kozlov 2009 (general climate) Fey et al. 2011 (general climate) Gortner et al. 2016 (temperature) Grassein et al. 2014 (temperature) Heath et al. 2010 (general climate) Kardol et al. 2014 Liancourt et al. 2013 (temperature and precipitation) Muhamed et al. 2013 O'Brien et al. 2018 (temperature) Padfield et al. 2019 Parain et al. 2016 (temperature) Pickles et al. 2015 (precipitation) Schwarzer and Joshi 2017 (temperature) Stanton-Geddes et al. 2012 (temperature) Tomiolo et al. 2015 (precipitation) Wendling et al. 2015
	Biotic changes in environment	Alexander et al. 2015

		Antunes et al. 2011 Echaubard et al. 2014 Egea-Serrano et al. 2014 Eranen and Kozlov 2009 Liancourt et al. 2013 O'Brien et al. 2018 Pickles et al. 2015 Tomiolo et al. 2015 Yang et al. 2016
	Invasions	Ayes et al. 2009 Coulatti and Barrett 2013 Compagnoni and Adler 2014 Crémieux et al. 2008 Cunningham et al. 2009 Egea-Serrano et al. 2014 Espeland and Rice 2007 Fey et al. 2011 Germain et al. 2016 Germain et al. 2018 Menke et al. 2007 Rice and Knapp 2008
	Restoration and conservation	Bohrher et al. 2003 Braco et al. 2009 Hughes et al. 2017 Johnson et al. 2010 Pickles et al. 2015 Rice and Knapp 2008
	Disease outbreaks	Buser et al. 2012 Echaubard et al. 2014 Hughes et al. 2017 Wendling et al. 2015

Table S8. Local-foreign contrasts across taxonomy. Model fit estimates for linear mixed models examining the effect of taxonomy (plant, animal; data from a single study of bacteria were excluded from this analysis), environment type (abiotic, biotic, or both), and experiment identity (random) on the local-foreign SMD. The column 'df' indicates the number of estimated parameters in the model.

Explanatory factors	df	AICc	ΔAICc	R^2
(experiment)	3	1407.6	16.1	0.06
taxonomy + (experiment)	4	1407.0	15.5	0.32
environment + (experiment)	5	1410.4	19.0	0.05
taxonomy + environment + (experiment)	6	1410.6	19.1	0.33
taxonomy × environment + (experiment)	8	1391.4	0.0	0.24

Table S9. Local-foreign contrasts for plant life history. Model fit estimates for linear mixed models examining the effect of plant life history (annual, perennial), environment type (abiotic, biotic, or both), and experiment identity (random) on the local-foreign SMD. The column 'df' indicates the number of estimated parameters in the model.

Explanatory factors	df	AICc	ΔAICc	R^2
(experiment)	3	1141.5	0.0	0.02
life history + (experiment)	4	1144.7	3.1	0.03
environment + (experiment)	5	1144.7	3.2	0.05
life history + environment + (experiment)	6	1147.6	6.0	0.06
life history × environment + (experiment)	7	1148.7	7.2	0.08

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Table S10. Biotic influence contrasts across taxonomy. Model fit estimates for linear mixed models examining the effect of taxonomy (animal or plant) and experiment identity (random) on the biotic influence SMD. The column 'df' indicates the number of estimated parameters in the model.

Explanatory factors	**df**	**AICc**	**ΔAICc**	**R^2**
(experiment)	3	702.5	0.9	0.33
taxonomy + (experiment)	4	701.6	0.0	0.35

Table S11. Biotic influence contrasts and plant life history. Model fit estimates for linear mixed models examining the effect of plant life history (annual, perennial) and experiment identity (random) on the biotic influence SMD. The column 'df' indicates the number of estimated parameters in the model.

Explanatory factors	**df**	**AICc**	**ΔAICc**	**R^2**
(experiment)	3	614.1	0.0	0.30
life history + (experiment)	4	614.9	0.8	0.32

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Table S12. Fitness effects across taxonomy. Model fit estimates for linear mixed models examining the effect of taxonomy (plant, invertebrate, vertebrate), treatment type (abiotic, biotic), and experiment identity (random) on the SMD in biotic or abiotic environments. The column 'df' indicates the number of estimated parameters in the model.

Explanatory factors	df	AICc	ΔAICc	R^2
(experiment)	3	7038.3	38.2	0.43
treatment type + (experiment)	4	7046.4	46.4	0.43
taxonomy + (experiment)	5	7041.0	41.0	0.47
taxonomy + treatment type + (experiment)	6	7049.1	49.1	0.47
taxonomy x treatment type + (experiment)	8	7000.0	0.0	0.48

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Table S13. Fitness effects for plant life history. Model fit estimates for linear mixed models examining the effect of plant life history (annual, perennial), treatment type (abiotic, biotic or both), and experiment identity (random) on the SMD in biotic or abiotic environments. The column 'df' indicates the number of estimated parameters in the model.

Explanatory factors	**df**	**AICc**	**ΔAICc**	R^2
(experiment)	3	6277.9	15.7	0.18
treatment type + (experiment)	4	6285.2	23.1	0.18
life history + (experiment)	4	6282.6	20.5	0.18
life history + treatment type + (experiment)	5	6290.1	27.9	0.18
life history x treatment type + (experiment)	6	6262.1	0.0	0.19

Figure S5. Scatterplots of SMD versus population latitude for with all data points included for (A) local-foreign contrasts and for (B) genotype-environment contrasts with biotic (open circles) and abiotic (black circles) treatments. Points have been jittered on the x-axis for greater clarity.