

Utah State University

From the Selected Works of Kari E. Veblen

2018

Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition

Kari E. Veblen



Available at: https://works.bepress.com/kari_veblen/88/

LETTERS

Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition

Peter B. Adler,^{1*} Danielle Smull,¹
Karen H. Beard,¹ Ryan T. Choi,¹
Tucker Furniss,¹ Andrew
Kulmatiski,¹ Joan M. Meiners,²
Andrew T. Tredennick¹ and
Kari E. Veblen¹

¹Department of Wildland Resources
and the Ecology Center, Utah State
University, Logan, UT 84322, USA²
School of Natural Resources and
Environment, University of Florida,
Gainesville, FL 32611, USA

*Correspondence: E-mail:
peter.adler@usu.edu

Abstract

Theory predicts that intraspecific competition should be stronger than interspecific competition for any pair of stably coexisting species, yet previous literature reviews found little support for this pattern. We screened over 5400 publications and identified 39 studies that quantified phenomenological intraspecific and interspecific interactions in terrestrial plant communities. Of the 67% of species pairs in which both intra- and interspecific effects were negative (competitive), intraspecific competition was, on average, four to five-fold stronger than interspecific competition. Of the remaining pairs, 93% featured intraspecific competition and interspecific facilitation, a situation that stabilises coexistence. The difference between intra- and interspecific effects tended to be larger in observational than experimental data sets, in field than greenhouse studies, and in studies that quantified population growth over the full life cycle rather than single fitness components. Our results imply that processes promoting stable coexistence at local scales are common and consequential across terrestrial plant communities.

Keywords

Biodiversity, competition coefficient, forests, grasslands, Lotka–Volterra, meta-analysis.

Ecology Letters (2018) 21: 1319–1329

INTRODUCTION

After almost a century of research (Lotka 1925; Volterra 1926; Gause 1932), questions about species coexistence continue to fascinate researchers (e.g. Levine *et al.* 2017). Understanding coexistence is not only an enduring intellectual puzzle, but can help address management problems including the conservation of rare species (DeCesare *et al.* 2010), the control of biological invasions (MacDougall *et al.* 2009), and the forecasting of climate change impacts (Chu *et al.* 2016). A core tenet of coexistence theory, based on models of pairwise interactions among competitors, is that intraspecific density dependence must be stronger than interspecific density dependence (Chesson 2000b). In fact, the overall niche difference between a pair of species can be defined as a ratio of interspecific:intraspecific competition coefficients (Chesson 2013). When interspecific competition is weaker than intraspecific competition, each species in a community limits its own population growth more than it limits the population growth of its competitors. The result is negative frequency dependence: the rarer a species becomes in a community, the more its population growth rate increases, buffering it against competitive exclusion. Many different kinds of coexistence mechanisms, such as differential responses to spatial and temporal environmental variation (Chesson 1994, 2000a), resource partitioning (Tilman 1982), and species-specific natural enemies (Janzen 1970; Connell 1971), all lead to niche differences and negative frequency dependence (Adler *et al.* 2007). Wherever these mechanisms play a role in maintaining the diversity of natural communities, we should observe that intraspecific competition is stronger than interspecific competition (we use

“competition” to refer broadly to all negative plant–plant interactions, regardless of their underlying mechanism).

Plant ecologists have published thousands of papers on competition, so if the difference in the strength of intra- and interspecific competition is as pervasive as classical coexistence theory suggests, empirical evidence should be easy to find. Surprisingly, reviews published in the 1990s did not find evidence for the predicted pattern. Goldberg & Barton (1992) found a dozen experimental studies that compared intra- and interspecific competition in some way. Collectively, the papers showed no evidence that intraspecific competition was stronger than interspecific competition. Gurevitch *et al.*'s (1992) meta-analysis came to a similar conclusion. To our knowledge, the question has not been reviewed since, leaving us with a clear theoretical prediction that empirical studies have failed to convincingly support (Siepielski & McPeck 2010; Velend 2016).

One explanation for the lack of empirical evidence is that coexistence is not stabilised at the fine spatial and short temporal scales captured by most field studies, but that local biodiversity is maintained by processes operating over broader spatial and temporal scales (Chesson 1994, 2000a; Hart *et al.* 2017). Another possibility is that stabilising coexistence mechanisms are not actually maintaining diversity in many natural communities. Perhaps coexistence is unstable, and high species richness reflects close to neutral dynamics in which extinctions are balanced by speciation events (Bell 2000; Hubbell 2001). However, many studies have failed to support the assumptions and predictions of neutral theory (e.g., Clark & MacLachlan 2003; McGill 2003; Adler 2004), and the rare studies that have quantified the strength of coexistence found

strong evidence for stability (Levine & HilleRisLambers 2009; Chu & Adler 2015; but see Kraft *et al.* 2015). Perhaps coexistence in complex multispecies communities is stabilised not by pairwise interactions but by interaction chains and higher order interactions. Little empirical evidence is available to evaluate this hypothesis (Levine *et al.* 2017).

A much different explanation points to problems in the empirical studies rather than the theoretical predictions. Goldberg & Barton (1992) and Gurevitch *et al.* (1992) found few papers that compared intra- and interspecific competition. If the difference in these forms of competition is small, then it would be hard to detect with limited sample size. Adding more recent papers that have accumulated in the two decades since their reviews could help reveal the pattern. Compounding the problem of limited sample size, many competition experiments do not measure the quantities needed to directly test the theoretical prediction. For example, replacement series and additive designs detect competition but do not quantify the per capita competitive effects needed to compare the strength of intra- and interspecific density dependence (Inouye 2001).

We conducted a quantitative review of the terrestrial plant competition literature to answer two research questions: (1) Is there evidence from phenomenological studies of plant–plant interactions that intraspecific competition is stronger than interspecific competition and if so, how large is the difference? (2) What factors affect variation in the relative strength of intra- and interspecific competition? For example, observational studies might suffer from statistical artifacts leading to overestimates of the strength of intraspecific competition (Freckleton *et al.* 2006), while short-term experimental studies might underestimate intraspecific limitation by minimising plant–soil feedback. Study setting could also be important: greenhouse experiments may offer fewer opportunities for niche differentiation than field studies by reducing environmental heterogeneity and simplifying food webs. Similarly, studies focused on only one fitness component or one life stage may limit potential for niche differences to express themselves compared to studies of per capita population growth rate across the full life cycle. Finally, differences between intra- and interspecific competition may vary among vegetation types: competition may be stronger in light-limited forest communities than in grasslands where species compete for multiple belowground resources (Harpole *et al.* 2016). Evidence for such differences would provide insights into the mechanisms maintaining diversity in natural communities and inform the design of future coexistence research.

METHODS

Literature search

We conducted the following ISI Web of Science search of the peer-reviewed literature on 2 October 2014: ((“plant” OR “plants”) AND “coexistence”) OR ((“plant” OR “plants”) AND ((“intra*” AND “inter*” AND “*specific”) OR (“con*” AND “hetero*” AND “*specific”)) AND (“competit*” OR “effect”)) OR ((“plant” OR “plants”) AND “replacement” AND (“series” OR “experiment”)). We excluded all document types that were not articles and, because we had decided to

focus on terrestrial plant communities, we excluded the research area “Marine related (marine freshwater biology, oceanography, fisheries).” The search produced 5433 records.

We screened these publications to identify those that estimated both interspecific and intraspecific competition coefficients in terrestrial plant communities. All of the studies that met these criteria used a regression approach to estimate the per unit effect of competitors on the performance of the focal species. Studies did differ in their measure of performance (growth, survival, fecundity, or per capita population growth), in the method used to describe abundance of competitors (e.g. biomass, density, cover), and in the source of variation in competitor abundances (natural variation in observed studies, manipulated variation in experimental studies). We include information about these varying factors in Table 1. To extract data from each of these studies, we first carefully read the methods to make sure that the authors had estimated, and reported, both intra- and interspecific per capita effects. We were forced to discard some studies in which authors reported p-values for estimated competitive effects, but not the coefficients. We also had to discard studies if we could not understand the methods or the model used to estimate competition coefficients well enough to be confident about using those estimates in a comparative analysis. The studies that we ultimately used are listed in Table 1.

For the studies that clearly measured and reported per capita intra- and interspecific effects, we extracted data as follows. Each row in the data table (available in the zip archive of data and computer code on the Dryad Digital Repository: <https://doi.org/10.5061/dryad.q5mg97b>) corresponds to one estimate of the per capita effect of one species on one target species, or of one group of species, such as all heterospecifics, on one target species. In addition to the value of the estimated competition coefficients and any associated uncertainty, we also entered information about the study’s experimental design, laboratory vs. field setting, fitness component and life stage studied, and vegetation type.

How to compare interspecific and intraspecific competition?

Our literature search produced a data set composed of pairs of intraspecific and interspecific competition coefficients. For some species pairs, we have all four of the relevant coefficients, but for other species pairs we have only one intra- and one interspecific coefficient. To guide our analysis of this heterogeneous data set, we turn to theory.

Lotka–Volterra competition models motivated much of the empirical work on competition that Goldberg & Barton (1992) and Gurevitch *et al.* (1992) reviewed. Even today, sophisticated data-driven models (Levine & HilleRisLambers 2009; Chu & Adler 2015) typically follow the phenomenological approach of Lotka–Volterra models rather than mechanistic consumer–resource models (e.g. Dybzinski & Tilman 2007). The studies characterise the net outcome of plant–plant interactions, without attempting to distinguish between exploitation, interference and apparent competition or between direct and indirect effects. Here, we review the Lotka–Volterra approach, with a focus on how to measure and compare intra- and interspecific competition.

The classic two-species Lotka–Volterra competition model, although often expressed with a carrying capacity term, can also be written with an explicit intraspecific competition coefficient:

Table 1 Characteristics of the 39 studies included in the analysis. “Performance” is the measure of individual or population performance, “Neighbours” is the method used to quantify competitive pressure, and “Design” distinguishes observational studies (“Obs.”) from experimental manipulations (“Exp.”) of competitive pressure. Values under “Data set” give the number of observations for each of the four data sets we analysed: ρ is niche overlap, “Effects” is the ratio of inter- to intraspecific effect, “Response” is the ratio of inter- to intraspecific response, and “Pooled” refers to studies that estimated overall average responses to conspecifics and all heterospecifics

Source	Vegetation	Performance	Neighbours	Design	Data set			
					ρ	Effects	Response	Pooled
Adler <i>et al.</i> (2006)	Grassland	Survival	Cover	Obs.	3	6	6	0
Adler <i>et al.</i> (2010)	Steppe	Survival, Growth, Fecundity	Cover	Obs.	6	36	36	0
Baribault & Kobe (2011)	Forest	Growth	Basal diameter	Obs.	0	1	4	0
Ngo Bieng <i>et al.</i> (2013)	Forest	Growth	Basal area	Obs.	0	1	1	0
Boivin <i>et al.</i> (2010)	Forest	Growth	Basal diameter	Obs.	5	12	20	0
Call & Nilsen (2005)	Forest	Growth	Density	Exp.	0	2	2	0
Collet <i>et al.</i> (2014)	Forest	Growth	Density	Exp.	3	7	7	0
Comita & Hubbell (2009)	Forest	Survival	*Density; Basal area	Obs.	0	0	0	2
Coomes <i>et al.</i> (2002)	Dune	Pop. growth	Density	Obs.	1	6	6	0
Farrer <i>et al.</i> (2010)	Grassland	Growth	Density	Obs.	3	16	23	0
Forrester <i>et al.</i> (2011)	Forest	Growth	Basal area	Exp.	0	0	6	0
Forrester <i>et al.</i> (2013)	Forest	Growth	Basal area	Obs.	0	1	1	0
Francis & Pyke (1996)	Steppe	Growth	Density	Exp.	1	2	2	0
Freckleton <i>et al.</i> (2000)	Agriculture	Pop. growth	Density	Exp.	9	18	18	0
Gazol & Julio Camarero (2012)	Steppe	Growth	Cover	Obs.	0	0	6	0
Geijzenendorffer <i>et al.</i> (2011)	Grassland	Pop. growth	Biomass	Exp.	26	90	90	0
Godoy & Levine (2014)	Grassland	Pop. growth	Density	Exp.	0	0	9	0
Hartnett <i>et al.</i> (1993)	Grassland	Growth	Density	Exp.	3	8	8	0
Kim <i>et al.</i> (2013)	Agriculture	Pop. growth	Density	Exp.	3	6	6	0
Kubota & Hara (1996)	Forest	Growth	Biomass	Obs.	0	2	2	0
Lebrija-Trejos <i>et al.</i> (2013)	Forest	Survival	Density	Obs.	0	0	0	2
Lin <i>et al.</i> (2012)	Forest	Survival	*Density; Basal area	Obs.	0	0	0	5
Martorell & Freckleton (2014)	Grassland	Pop. growth	Density	Obs.	10	58	46	0
Medina-Roldán <i>et al.</i> (2012)	Grassland	Growth	Density	Exp.	2	4	4	0
Moloney & Chiariello (1998)	Grassland	Fecundity	Density	Exp.	6	12	12	0
Nanami <i>et al.</i> (2011)	Forest	Growth	Basal area	Obs.	0	0	9	0
Osunkoya <i>et al.</i> (2005)	Forest	Growth	Density	Exp.	2	4	4	0
Rees <i>et al.</i> 1996	Grassland	Pop. growth	Density	Obs.	12	24	24	0
Sheley & Larson (1994)	Grassland	Growth	Density	Exp.	1	2	2	0
Sheley & Larson (1995)	Steppe	Growth	Density	Exp.	1	2	2	0
Sheley & James (2014)	Steppe	Growth	Density	Exp.	0	8	8	0
Suter <i>et al.</i> (2007)	Grassland	Growth	Biomass	Exp.	9	20	20	0
Turkington & Jolliffe (1996)	Agriculture	Growth	Density	Exp.	0	4	4	0
Turnbull <i>et al.</i> (2004)	Grassland	Pop. growth	Density	Obs.	21	42	42	0
Uriarte <i>et al.</i> (2004)	Forest	Growth	Basal area	Obs.	0	0	60	0
Uriarte <i>et al.</i> (2005)	Forest	Survival	Basal area	Obs.	0	0	49	0
Vasquez <i>et al.</i> (2008)	Steppe	Growth	Density	Exp.	0	3	3	0
Webb <i>et al.</i> (2006)	Forest	Survival	Density	Obs.	0	0	0	2
Zarnetske <i>et al.</i> (2013)	Dune	Pop. growth	Biomass	Obs.	9	180	180	0
TOTALS					136	577	722	11

*These studies estimated the effects of seedling density and adult basal area on seedling survival.

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1 - \alpha_{12} N_2) \quad (1)$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \alpha_{21} N_1 - \alpha_{22} N_2)$$

where N_i is the density of species i and r is the intrinsic growth rate. The α 's translate increases in conspecific and heterospecific density into decreases in population growth. For example, α_{12} represents the per capita reduction in growth of species 1 caused by each additional individual of

species 2, and α_{11} is the intraspecific density dependence of species 1. Carrying capacity for species 1 in monoculture is $1/\alpha_{11}$.

When we know all four α 's for a pair of species, we can calculate the magnitude of difference in interspecific and intraspecific competition as

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} \quad (2)$$

where ρ is a measure of niche overlap (Chesson 2013). In this two species model, when both $\frac{\alpha_{21}}{\alpha_{11}}$ and $\frac{\alpha_{12}}{\alpha_{22}}$ are <1 , coexistence

will be stable. More generally, and especially in more complex phenomenological models with additional terms affecting intrinsic growth rates and fitness differences, $\rho < 1$ does not ensure an outcome of stable coexistence, but lower values of ρ still represent stronger stabilising effects. Coexistence criteria are also more complex in multispecies communities, but if intraspecific competition is much stronger than interspecific competition for all species pairs then community stability becomes more likely. Thus, for our purpose, ρ represents the “gold standard” comparison of inter- and intraspecific effects.

If we are missing any one of the coefficients (many studies do not estimate all four), or if any one coefficient takes the opposite sign (facilitation), we cannot calculate ρ . But we might still have the data to compare one of the interspecific effects with one of the intraspecific effects. The question is, does it matter which of the coefficients we pair together? When we began this project, we expected that it would matter—that certain comparisons would be more meaningful than others. This assumption makes sense if our goal is to determine whether a given pair of species can coexist, which can be determined by applying the invasibility criteria. If species 1 can invade a monoculture of species 2, it can persist indefinitely, and vice versa. The population growth rate of species 1 as it invades a monoculture of species 2 at its equilibrium, $1/\alpha_{22}$, is

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{\alpha_{12}}{\alpha_{22}} \right). \quad (3)$$

If species 2 has a weaker per capita effect on species 1 than it has on itself, then species 1 can invade. The relevant comparison is the *effect* of a species on itself compared to its *effect* on another species.

The alternative pairing would compare α_{11} with α_{12} , the *response* of species 1 to intra- and interspecific competition. However, this comparison does not provide any inference about the ability of either species to persist. Perhaps species 1 is a large plant that exerts strong per capita effects and only reaches low densities, while species 2 is small and exerts weak per capita effects but builds up to high densities. We might imagine the following competition coefficients:

$$\alpha_{11} = 0.1, \alpha_{21} = 0.08, \alpha_{22} = 0.01, \alpha_{12} = 0.02.$$

The comparison of α_{11} and α_{12} would indicate that species 1 is little affected by species 2 (relative to its impact on itself). But the more appropriate comparison of α_{22} and α_{12} would indicate, correctly, that species 1 cannot invade species 2. The opposite mistake—finding misleading evidence for competitive exclusion—is also possible. Consider a scenario where species 1 is small and reaches high densities, and species 2 is large, reflected by the following competition coefficients:

$$\alpha_{11} = 0.01, \alpha_{21} = 0.09, \alpha_{22} = 0.1, \alpha_{12} = 0.09.$$

The comparison of α_{11} and α_{12} would indicate that species 2 has a tremendous impact on species 1 relative to species 1's impact on itself. But in fact, species 1 can invade species 2 because $\alpha_{22} > \alpha_{12}$.

While the distinction between competitive effects and responses is critical for making inferences about coexistence for a particular pair of species, that distinction is irrelevant for our goal of estimating the average difference between inter- and intraspecific competition coefficients for a sample containing many species pairs. We learned this by simulating Lotka–Volterra competition coefficients for many pairs of species, calculating ρ , and then comparing the ability of one pair of competitive effects or competitive responses to estimate ρ . We drew all intraspecific competition coefficients from a uniform distribution between 0.0001 and 0.01 and all interspecific competition coefficients from a uniform distribution between 0.00005 and 0.005. Our simulation (CompRegress_simulation.r, included in the files archived at the Dryad Digital Repository) showed that: (1) the mean value of $\log \rho$, $\log \frac{\alpha_{12}}{\alpha_{22}}$ (the competitive effect ratio), and $\log \frac{\alpha_{12}}{\alpha_{11}}$ (the competitive response ratio) converge as sample size increases, (2) the variance around that mean is larger for the competitive effect and response ratios than for ρ , and (3) for a given sample of species pairs, the competitive effect and response ratios may give biased estimates of ρ (Fig. S1), but the direction of the bias varies from one sample to another, reflecting the influence of outliers.

Based on these results, we calculated and analysed all three metrics. For every species pair for which we had four competition coefficients and no facilitation, we calculated ρ . In order to represent a larger sample of values collected from the literature, we also calculated the competitive effect and competitive response ratios. These three data sets are largely, but not completely, overlapping (Table 1), and thus provide some complementary information. Note that we calculated ρ and the ratios of interspecific–intraspecific coefficients for each species pair within each study; we never calculated a ratio of coefficients that were estimated using different methods in different studies. These unitless measures of the relative strength of inter- and intraspecific competition are what we compared across studies.

Analysis

Before analysing ρ and the ratios of competitive effects and responses, we counted the number of observations representing different ecosystems, study designs (observational vs. experimental, field vs. greenhouse) and different types of responses (e.g. growth vs. survival). We then divided the competitive effect and response data sets into four qualitatively different outcomes: (1) both inter- and intraspecific effects are positive (facilitation); (2) the interspecific effect is positive but the intraspecific effect is negative; (3) the interspecific effect is negative but the intraspecific effect is positive; and (4) both effects are negative (competition).

For the fourth and most common outcome, in which all effects are negative, we estimated the relative difference in the strength of inter- and intraspecific competition. In cases where all four coefficients were available for a pair of species, the response ratio is $\log(\rho)$. The log transformation normalises the skewed distribution of ρ , which cannot take negative values, but can take large positive values. If $\log \rho$ is less than 0, then interspecific competition is weaker than intraspecific competition. We estimated the mean of $\log \rho$ using a linear, mixed effect model. The simplest model estimates $\log \rho$ with

study included as a random effect to recognise that observations from the same study are not independent. For example, ten observations that all come from one study will have much less influence on the estimate of the overall mean than ten observations coming from ten independent studies. We also explored more complex models in which the mean of $\log p$ could be affected by fixed effects including experimental design (experimentally manipulated vs. naturally observed variation in neighbour densities), setting (greenhouse or field), the fitness component measured (e.g. per capita population growth rate or individual survival, growth, or fecundity), the life stage studied (early or mature), and the vegetation type. We fit the models using the lme4 package (Bates *et al.* 2015) in R 3.4.1 (R Development Core Team 2017), and evaluated the statistical significance of these additional factors, relative to the simplest model, using likelihood ratio tests.

We took a similar approach with the competitive effects and competitive responses data sets. Here the goal is to estimate the mean of the log ratio of interspecific:intraspecific competition. Once again, the log ratio is < 0 when interspecific competition is weaker than intraspecific competition. The simplest model estimates the mean log ratio with both study and species within study included as random effects. In our comparison of competitive effects, we based species random effects on the species exerting the competition coefficients. For the competitive responses comparison, we based species random effects on the target species—the recipient of the competitive effects. As in our analysis of p , we then used likelihood ratio tests to compare the simplest model to more complex models accounting for additional sources of variation among the data sets.

These models are not formal meta-analyses because they do not account for variation among studies in the uncertainty of

the estimated competition coefficients. We were unable to account for uncertainty because information on the variability of the estimates was often not reported, and even when it was reported the type of information available was inconsistent among studies. Therefore, we weight all observations equally, even though some estimates are undoubtedly more precise than others.

We also had 11 observations from four studies which estimated responses to conspecific and heterospecific competition pooled across many species (Table 1). We did not calculate ratios of interspecific–intraspecific responses or conduct a statistical analysis of this small data set, but we did summarise the values for the sake of completeness.

RESULTS

For our comparison of competitive effect ratios, we had a total of 577 observations from 29 studies (Table 1). For the comparison of competitive response ratios, we had 722 observations from 35 studies (Table 1). Most observations came from studies in natural grasslands where per capita population growth was measured over the full life cycle (Figs 1, S2 and S3). Facilitation was much rarer than competition, and where facilitation was observed it usually involved interspecific (26% of observations), not intraspecific (2% of observations), interactions (Table 2). Of the nine cases in the competitive effects data set for which the intraspecific effect was facilitative and the interspecific effect competitive, a recipe for competitive exclusion based on priority effects, all were conducted in the greenhouse. In the competitive responses data set, there were 13 such cases, 9 of which were conducted in the greenhouse. The intra- and interspecific terms were both competitive in 67% of the effects comparisons (384/577 species pairs), and in

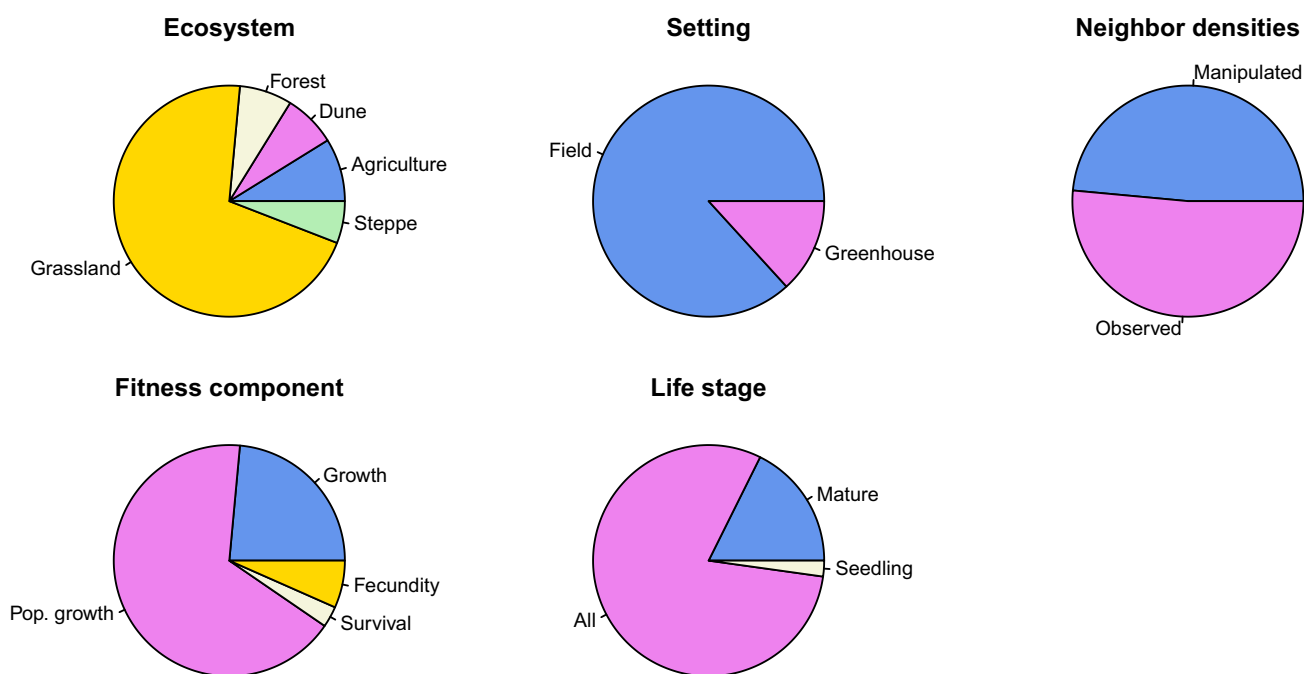


Figure 1 Characteristics of the studies contributing the 136 observations of niche overlap, p . Figs S2 and S3 show the same information for the competitive effects and responses data sets.

73% of the response comparisons (527/722 species pairs; Table 2).

For the 136 observations of niche overlap, ρ , our simplest mixed effects model estimated a mean on the log scale of -1.57 with a 95% confidence interval from -2.24 to -0.86 (Table 3, Fig. 2a). Transforming back to the arithmetic scale, the mean value of ρ is 0.21 (95% CI: 0.11, 0.42), indicating low niche overlap and strong stabilising effects on coexistence. Seventy-seven percent of the ρ values were < 1 . Our analyses of the competitive effects and responses data sets returned similar results: the mean ratios of interspecific–intraspecific competition, back-transformed from the log scale, were 0.25 for the effects data set and 0.27 for the responses data set (Table 3, Fig. 2b and c).

Our second research question asked if accounting for differences among studies could explain additional variation in niche overlap, ρ , and the ratios of competitive effects and responses. The strongest statistical differences emerged for study design: observational studies showed larger differences between inter- and intraspecific competition than studies which manipulated the densities of competitors (Fig. 3a). We found marginally significant support for models that accounted for variation in study setting, with values of ρ and the log ratios lower in field than greenhouse experiments (Fig. 3b). We also found marginal evidence for lower values of ρ and the log ratios in studies based on population growth than studies based on single fitness components (Fig. 3c). Similarly, values of niche overlap were marginally lower for studies integrating across all stages than for single stage studies (Fig. 3d). We found no evidence that accounting for variation among vegetation type improved the models (Fig. 3e).

Four studies pooled estimates of inter- and intraspecific effects across species (Table 1). Of the 11 observations from these four studies, the pooled intraspecific effect was positive (facilitative) in only one case, while the pooled interspecific effect was positive in six cases. A boxplot of the raw values (Fig. S4) shows that the intraspecific effects appear to be stronger and more negative.

DISCUSSION

Is there evidence that intraspecific competition is stronger than interspecific competition and, if so, how large is the difference?

Our analysis provides very strong evidence that intraspecific competition is stronger than interspecific competition for most pairs of co-occurring species, and that the difference is often large, resolving the mismatch between theory and observation

Table 2 The direction of inter- and intraspecific interactions for the competitive effects and responses data sets. Values are the number of pairwise species comparisons within each category for the (effects | responses) data set.

	Interspecific competition	Interspecific facilitation
Intraspecific competition	384 527	180 181
Intraspecific facilitation	9 13	4 1

Table 3 Summary of the mixed effects models to estimate log ρ , and the log ratios of competitive Effects and Responses. “Source” are random effects associated with individual studies. “Var” is variance.

	log ρ	Effects	Responses
Intercept	-1.57	-1.40	-1.31
[95% C.I.]	$[-2.24; -0.86]^*$	$[-2.00; -0.75]^*$	$[-1.79; -0.79]^*$
Num. obs.	136	384	527
Num. groups:	21	27	33
Source			
Var: Source	1.37	1.07	1.05
Var: Residual	4.06	6.10	5.47
Num. groups:	–	86	200
Species:Source			
Var: Species:Source	–	1.24	0.44

*0 outside the confidence interval.

reflected in the reviews of the 1990s (Goldberg & Barton 1992; Gurevitch *et al.* 1992). Several lines of evidence support this conclusion. First, in the 67% of cases in which both inter- and intraspecific effects were negative, intraspecific competition was on average four to five-fold stronger than interspecific competition. Second, in roughly 30% of our comparisons of competitive effects and responses, the intraspecific effect was negative and the interspecific effect positive, a situation which should promote coexistence. Finally, cases in which both inter- and intraspecific effects were facilitative ($\sim 1\%$), or in which the intraspecific effect was facilitative but the interspecific effect was competitive ($\sim 1\%$), were rare. The latter case, which should destabilise coexistence, was encountered primarily in greenhouse studies. In summary, most empirical studies show evidence for ecologically significant differences in inter- and intraspecific competition. These differences alone do not guarantee coexistence, because average fitness differences must also be considered (Chesson 2000b), but they do fulfill a necessary condition for stable coexistence.

Our finding that intraspecific competition is much stronger than interspecific competition is largely, but not entirely, consistent with results of recent prominent papers that were not included in our search. We know of one recent study that could be incorporated in our quantitative analysis of niche overlap, ρ . Godoy *et al.* (2014) estimated ρ for 97 pairs of California annual species based on seed production responses to experimentally imposed variation in neighbour densities (these are the same data used in Kraft *et al.* 2015). The mean of these values, calculated on the log scale and back transformed, is 0.85, considerably greater than our overall mean ρ of 0.21, as well as the mean from experimental studies of 0.37. However, including this study in our original analysis would only increase our overall estimate of ρ to 0.24, and would further strengthen the contrast between observational and experimental studies. Three studies supported the pattern we described for responses to conspecifics and heterospecifics pooled across species (Fig. S4). LaManna *et al.* (2017) studied sapling recruitment in 24 forests worldwide and found that conspecific density dependence was always negative and often strong (mean across sites: -1.65 ; standard deviation: 1.29), while heterospecific density dependence was weak and sometimes positive (mean: -0.008 , standard deviation: 0.014).

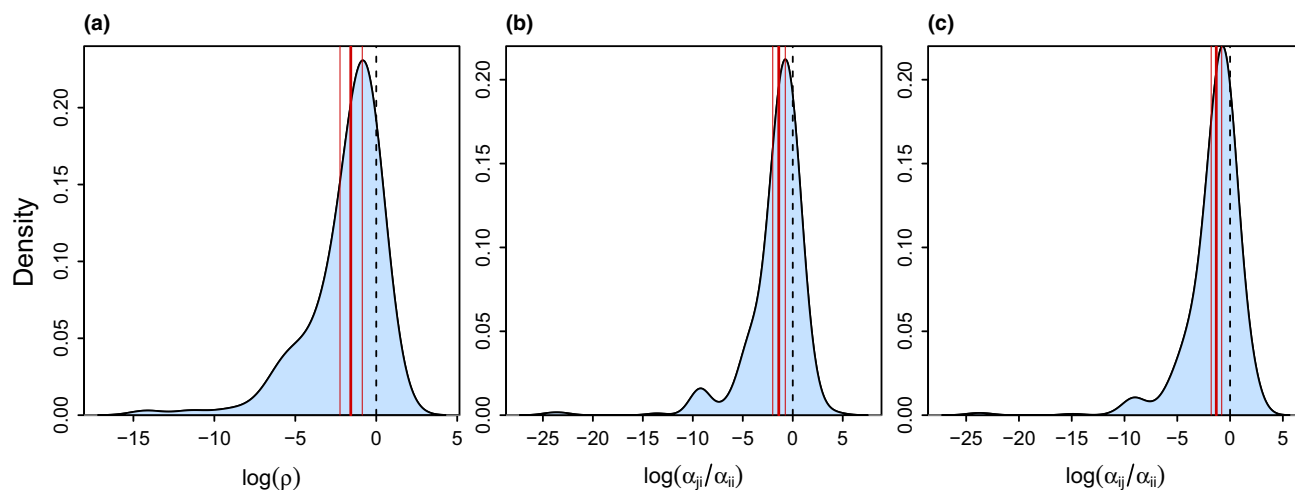


Figure 2 Distribution of $\log \rho$ (a) and the log ratio of competitive effects (b) and responses (c). The thick red lines show the means estimated by mixed effects models (Table 3), and the thin red lines bound the 95% confidence intervals around these estimates. The vertical dashed line indicates the value at which inter- and intraspecific effects are equal. Values to the left of the dashed line occur when interspecific effects are weaker than intraspecific effects.

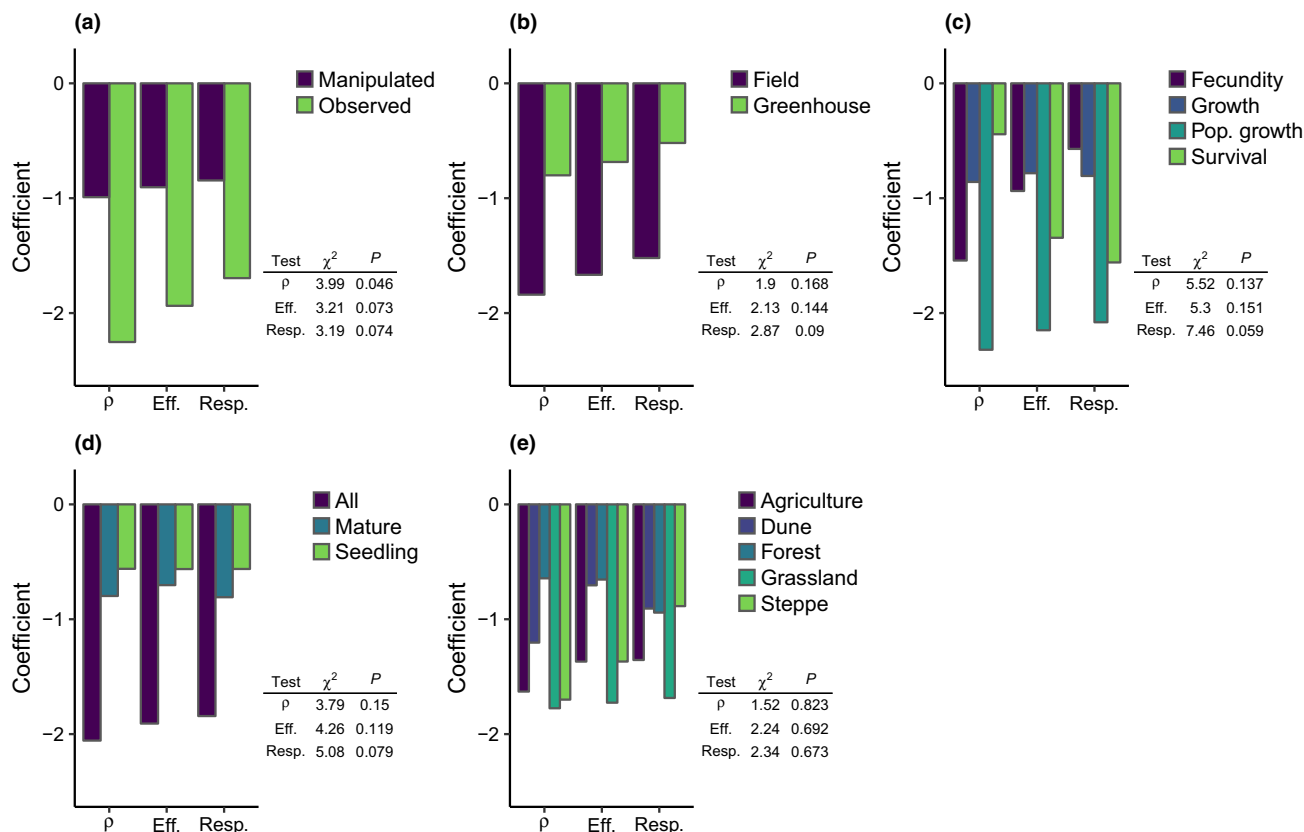


Figure 3 Tests of additional factors influencing $\log \rho$ and the log ratios of competitive effects ("Eff.") and responses ("Resp."). Each panel shows the influence of a different set of categorical covariates on the responses: (a) experimental design, (b) research setting, (c) fitness component studied, (d) life stage studied, and (e) vegetation type. Bars show fixed effect coefficients for each level of the covariate. The inset tables show the results of a likelihood ratio test comparing a model accounting for covariates to a simpler model that ignores the covariates. $P < 0.05$ indicates significant support for the more complex model.

Johnson *et al.* (2012) conducted a similar analysis of seedling recruitment in US forests and found very similar results. Kunstler *et al.* (2016) analysed the effects of neighbourhood

competition on the growth of individual forest trees in a global data set and found that intraspecific effects were roughly two-fold stronger than interspecific effects, pooling across

species, even before accounting for effects of differences in functional traits which drive additional, slight reductions in niche overlap.

An important caveat is that our results primarily reflect interactions among locally common species. Although most species in a community are locally rare, their rarity makes them difficult to study using observational approaches, and we suspect they are seldom included in manipulative competition experiments either. It is possible that differences between intra- and interspecific competition might be smaller when common and rare species interact. However, Yenni *et al.* (2017) found that locally rare, persistent species are even less sensitive to interspecific competition than common species, suggesting that the pattern we found in our review might not be limited to common species.

Our results, and those from recent studies, provide strong evidence that niche differences play an important role in community dynamics at neighbourhood spatial scales. The next step is to identify the mechanisms causing intraspecific limitation to be so much stronger than interspecific limitation. Our literature search focused on phenomenological competition because relatively few empirical studies have quantified the strength of particular coexistence mechanisms. However, the pace of such research is accelerating. Many recent studies have focused on species-specific herbivores and pathogens in general, and Janzen–Connell effects in particular (Kulmatiski *et al.* 2008; Bever *et al.* 2010; Bagchi *et al.* 2014; Comita *et al.* 2014). The role of spatial and temporal environmental variation in promoting coexistence is also receiving increasing attention (Adler *et al.* 2006; Sears & Chesson 2007; Angert *et al.* 2009; Usinowicz *et al.* 2017). In fact, new tools for quantifying the stabilising effects of environmental variation in space and time are becoming available (Ellner *et al.* 2016; Hart *et al.* 2017). Work on resource partitioning deserves equal treatment (e.g., Dybzinski & Tilman 2007). Over the next decade, we may accumulate enough case studies to quantify and compare the strength of different coexistence mechanisms in different communities.

What factors affect variation in the relative strength of intra- and interspecific competition?

Putting together our quantitative analyses of ρ and competitive effects and responses data sets provided some evidence that the difference between inter- and intraspecific competition is larger in observational than in experimental studies. Consistent with this trend, a recent meta-analysis showed stronger effects of biodiversity on primary productivity in nature than in experiments (Duffy *et al.* 2017). One explanation for this difference is that experiments are typically conducted at small spatial and short temporal scales, excluding coexistence mechanisms that only operate in the presence of coarser scale environmental variation. The issue of scale was also invoked by Kraft *et al.* (2015) to explain why their models, based on one-year experiments, predict competitive exclusion for many species pairs which appear to coexist at their study site. Short-term experimental manipulations may also prevent the build-up of plant-soil feedbacks, which are a likely source of intraspecific competition in mature communities (e.g. Mangan *et al.* 2010).

A second explanation involves the “ghost of competition past” (Connell 1980). Observational studies are often conducted in mature, relatively undisturbed communities where it is possible that local competitive exclusion has largely played out. Experimental manipulations may effectively push these communities into an earlier stage of community assembly where pairs of species that compete intensely are put into close proximity at densities that are not stable over the long term, resulting in stronger interspecific competition (Kokkoris *et al.* 1999). Similarly, we might expect stronger interspecific interactions following colonisation by new species or when environmental perturbations alter competitive interactions (Urban *et al.* 2012). However, the hypothesis that we are less likely to observe strong interspecific interactions when a community is close to equilibrium does not explain why we still find strong *intraspecific* competition in observational studies. Perhaps local dispersal overwhelms the tendency of competition to generate overdispersed (regular) spatial patterns and instead creates high local conspecific densities and a stronger signal of competition.

We found much weaker statistical support for other sources of variation in the relative strength of intra- and interspecific competition. The difference between intra- and interspecific competition was greater in the field than in the greenhouse and greater in studies of population growth across the full life cycle than in studies of individual fitness components. Although the statistical support for most of these contrasts was marginal, the patterns are consistent with our intuition: the opportunities for species to exploit different niches and avoid interspecific competition should be greater in the field than the greenhouse and when integrated over the full life cycle. Similarly, we found no evidence that the ratio of inter- to intraspecific competition varies among vegetation types, giving us confidence that a key condition necessary for stable, pairwise coexistence is likely common and strong at local scales in terrestrial plant communities worldwide.

CONCLUSIONS

Our results resolve a long-standing mismatch between theory and data. We found that intraspecific competition is often much stronger than interspecific competition, an important condition for local-scale stable coexistence. A second important finding is that just 39 of the more than 5400 papers on plant competition that we reviewed provided the information we needed to compare intra- and interspecific effects. We are aware that our literature search did not capture all relevant studies (e.g. Levine & HilleRisLambers 2009; Kunstler *et al.* 2016; we chose not to include these because we did not want to bias our random sample). However, the fact that such a small fraction of papers on “competition” rigorously quantify the strength of intra- and interspecific competition reflects weak links between theoretical and empirical research in ecology. We hope that future work on competition will follow the empirical approaches of the studies we included in our review, or even simpler designs (Hart *et al.* 2018), to estimate the per capita competitive effects central to theory, as opposed to indices of competition that come from replacement series or

additive designs which provide little inference about the population-level outcomes of competition.

Our work also has implications for future coexistence research. Empirical evidence that interspecific competition is often much weaker than intraspecific competition in many plant communities is also evidence that stabilising coexistence mechanisms operating at neighbourhood scales are common and consequential. Understanding local-scale patterns of biodiversity will require careful consideration of the strength of these stabilising forces and the mechanisms generating them.

ACKNOWLEDGEMENTS

We thank Simon Hart and Jonathan Levine for comments that improved an early version of the manuscript. PBA was supported by the National Science Foundation (DEB-1054040 and DEB-1655522). ATT was supported by a National Science Foundation Postdoctoral Research Fellowship (DBI-1400370). This research was supported by the Utah Agricultural Experiment Station, Utah State University, and approved as journal paper number 9065.

AUTHORSHIP

All authors designed the study and collected the data; PBA and AT analysed the data; PBA drafted the manuscript and all authors contributed to editing.

DATA ACCESSIBILITY STATEMENT

All data and computer code used in this study are available for download from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.q5mg97b>).

REFERENCES

- Adler, P.B. (2004). Neutral models fail to reproduce observed species-time and species-area relationships in Kansas grasslands. *Ecology*, 85, 1265–1272.
- Adler, P.B., HilleRisLambers, J., Kyriakidis, P.C., Guan, Q. & Levine, J.M. (2006). Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proc. Natl Acad. Sci.*, 103, 12793–12798.
- Adler, P.B., HilleRisLambers, J. & Levine, J.M. (2007). A niche for neutrality. *Ecol. Lett.*, 10, 95–104.
- Adler, P.B., Ellner, S.P. & Levine, J.M. (2010). Coexistence of perennial plants: an embarrassment of niches. *Ecol. Lett.*, 13, 1019–1029.
- Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proc. Natl Acad. Sci. USA*, 106, 11641–11645.
- Bagchi, R., Gallery, R.E., Gripenberg, S., Gurr, S.J., Narayan, L., Addis, C.E. *et al.* (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*, 506, 85–88.
- Baribault, T.W. & Kobe, R.K. (2011). Neighbour interactions strengthen with increased soil resources in a northern hardwood forest. *J. Ecol.*, 99, 1358–1372.
- Bates, D., Machler, M. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.*, 67, <http://dx.doi.org/10.18637/jss.v067.i01>.
- Bell, G. (2000). The distribution of abundance in neutral communities. *Am. Nat.*, 155, 606–617.
- Bever, J.D., Dickie, I.A., Facelli, E., Facelli, J.M., Klironomos, J., Moora, M. *et al.* (2010). Rooting theories of plant community ecology in microbial interactions. *Trends Ecol. Evol.*, 25, 468–478.
- Boivin, F., Paquette, A., Papaik, M.J., Thiffault, N. & Messier, C. (2010). Do position and species identity of neighbours matter in 8–15-year-old post harvest mesic stands in the boreal mixedwood? *For. Ecol. Manag.*, 260, 1124–1131.
- Call, L.J. & Nilsen, E.T. (2005). Analysis of interactions between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*). *Plant Ecol.*, 176, 275–285.
- Chesson, P. (1994). Multispecies competition in variable environments. *Theor. Popul. Biol.*, 45, 227–276.
- Chesson, P. (2000a). General theory of competitive coexistence in spatially-varying environments. *Theor. Popul. Biol.*, 58, 211–237.
- Chesson, P. (2000b). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.
- Chesson, P. (2013). Species Competition and Predation. In *Ecological Systems*. Springer, New York, NY, pp. 223–256.
- Chu, C. & Adler, P.B. (2015). Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. *Ecol. Monogr.*, 85, 373–392.
- Chu, C., Kleinhesselink, A.R., Havstad, K.M., McClaran, M.P., Peters, D.P., Vermeire, L.T. *et al.* (2016). Direct effects dominate responses to climate perturbations in grassland plant communities. *Nat. Commun.*, 7, 11766.
- Clark, J.S. & MacLachlan, J.S. (2003). Stability of forest biodiversity. *Nature*, 423, 635–638.
- Collet, C., Ningre, F., Barbeito, I., Arnaud, A. & Piboule, A. (2014). Response of tree growth and species coexistence to density and species evenness in a young forest plantation with two competing species. *Ann. Bot.*, 113, 711–719.
- Comita, L.S. & Hubbell, S.P. (2009). Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology*, 90, 328–334.
- Comita, L.S., Queenborough, S.A., Murphy, S.J., Eck, J.L., Xu, K., Krishnadas, M. *et al.* (2014). Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *J. Ecol.*, 102, 845–856.
- Connell, J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of Populations*. (eds Den Boer, P.J., Gradwell, G.R.). PUDOC, Wageningen, pp. 298–312.
- Connell, J.H. (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 35, 131–138.
- Coomes, D.A., Rees, M., Turnbull, L. & Ratcliffe, S. (2002). On the mechanisms of coexistence among annual-plant species, using neighbourhood techniques and simulation models. *Plant Ecol.*, 163, 23–38.
- DeCesare, N.J., Hebblewhite, M., Robinson, H.S. & Musiani, M. (2010). Endangered, apparently: the role of apparent competition in endangered species conservation. *Anim. Conserv.*, 13, 353–362.
- Duffy, J.E., Godwin, C.M. & Cardinale, B.J. (2017). Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature*, 549, 261–264.
- Dybziński, R. & Tilman, D. (2007). Resource use patterns predict long-term outcomes of plant competition for nutrients and light. *Am. Nat.*, 170, 305–318.
- Ellner, S.P., Snyder, R.E. & Adler, P.B. (2016). How to quantify the temporal storage effect using simulations instead of math. *Ecol. Lett.*, 19, 1333–1342.
- Farrer, E.C., Goldberg, D.E. & King, A.A. (2010). Time lags and the balance of positive and negative interactions in driving grassland community dynamics. *Am. Nat.*, 175, 160–173.
- Forrester, D.I., Vanclay, J.K. & Forrester, R.I. (2011). The balance between facilitation and competition in mixtures of Eucalyptus and Acacia changes as stands develop. *Oecologia*, 166, 265–272.
- Forrester, D.I., Kohnle, U., Albrecht, A.T. & Bauhus, J. (2013). Complementarity in mixed-species stands of *Abies alba* and *Picea abies* varies with climate, site quality and stand density. *For. Ecol. Manag.*, 304, 233–242.

- Francis, M.G. & Pyke, D.A. (1996). Crested wheatgrass-cheatgrass seedling competition in a mixed-density design. *J. Range Manag.*, 49, 432–438.
- Freckleton, R.P., Watkinson, A.R., Dowling, P.M. & Leys, A.R. (2000). Determinants of the abundance of invasive annual weeds: community structure and non-equilibrium dynamics. *Proc. Biol. Sci.*, 267, 1153–1161.
- Freckleton, R.P., Watkinson, A.R., Green, R.E. & Sutherland, W.J. (2006). Census error and the detection of density dependence. *J. Anim. Ecol.*, 75, 837–851.
- Gause, G.F. (1932). Experimental studies on the struggle for existence: 1. Mixed populations of two species of yeast. *J. Exp. Biol.*, 9, 389–402.
- Gazol, A. & Julio Camarero, J. (2012). The performance of Mediterranean shrubs depends more on microsite than on regional climate conditions. *J. Veg. Sci.*, 23, 1062–1070.
- Geijzendorffer, I.R., van der Werf, W., Bianchi, F.J.J.A. & Schulte, R.P.O. (2011). Sustained dynamic transience in a Lotka-Volterra competition model system for grassland species. *Ecol. Model.*, 222, 2817–2824.
- Godoy, O. & Levine, J.M. (2014). Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology*, 95, 726–736.
- Godoy, O., Kraft, N.J.B. & Levine, J.M. (2014). Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.*, 17, 836–844.
- Goldberg, D.E. & Barton, A.M. (1992). Patterns and consequences of interspecific competition in natural communities - a review of field experiments with plants. *Am. Nat.*, 139, 771–801.
- Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. (1992). A meta-analysis of competition in field experiments. *Am. Nat.*, 140, 539–572.
- Harpole, W.S., Sullivan, L.L., Lind, E.M., Firn, J., Adler, P.B., Borer, E.T. *et al.* (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, 537, 93–96.
- Hart, S.P., Usinowicz, J. & Levine, J.M. (2017). The spatial scales of species coexistence. *Nat. Ecol. Evol.*, 1, 1066.
- Hart, S.P., Freckleton, R.P. & Levine, J.M. (2018). How to quantify competitive ability. *J. Ecol.*, <https://doi.org/10.1111/1365-2745.12954>.
- Hartnett, D.C., Hetrick, B.A.D., Wilson, G.W.T. & Gibson, D.J. (1993). Mycorrhizal influence on intra- and interspecific neighbour interactions among co-occurring prairie grasses. *J. Ecol.*, 81, 787–795.
- Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Inouye, B.D. (2001). Response surface experimental designs for investigating interspecific competition. *Ecology*, 82, 2696–2706.
- Janzen, D.H. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat.*, 104, 501–528.
- Johnson, D.J., Beaulieu, W.T., Bever, J.D. & Clay, K. (2012). Conspecific negative density dependence and forest diversity. *Science*, 336, 904–907.
- Kim, T.N., Underwood, N. & Inouye, B.D. (2013). Insect herbivores change the outcome of plant competition through both inter- and intraspecific processes. *Ecology*, 94, 1753–1763.
- Kokkoris, G.D., Troumbis, A.Y. & Lawton, J.H. (1999). Patterns of species interaction strength in assembled theoretical competition communities. *Ecol. Lett.*, 2, 70–74.
- Kraft, N.J.B., Godoy, O. & Levine, J.M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl Acad. Sci.*, 112, 797–802.
- Kubota, Y. & Hara, T. (1996). Allometry and competition between saplings of *Picea jezoensis* and *Abies sachalinensis* in a sub-boreal coniferous forest, northern Japan. *Ann. Bot.*, 77, 529–538.
- Kulmatiski, A., Beard, K.H., Stevens, J.R. & Cobbold, S.M. (2008). Plant-soil feedbacks: a meta-analytical review. *Ecol. Lett.*, 11, 980–992.
- Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C. *et al.* (2016). Plant functional traits have globally consistent effects on competition. *Nature*, 529, 204–207.
- LaManna, J.A., Mangan, S.A., Alonso, A., Bourg, N.A., Brockelman, W.Y., Bunyavechewin, S. *et al.* (2017). Plant diversity increases with the strength of negative density dependence at the global scale. *Science*, 356, 1389–1392.
- Lebrija-Trejos, E., Wright, S.J., Hernández, A. & Reich, P.B. (2013). Does relatedness matter? Phylogenetic density-dependent survival of seedlings in a tropical forest. *Ecology*, 95, 940–951.
- Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–257.
- Levine, J.M., Bascompte, J., Adler, P.B. & Allesina, S. (2017). Beyond pairwise mechanisms of species coexistence in complex communities. *Nature*, 546, 56–64.
- Lin, L., Comita, L.S., Zheng, Z. & Cao, M. (2012). Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. *J. Ecol.*, 100, 905–914.
- Lotka, A.J. (1925). *Elements of Physical Biology*. Williams and Wilkins, Baltimore.
- MacDougall, A.S., Gilbert, B. & Levine, J.M. (2009). Plant invasions and the niche. *J. Ecol.*, 97, 609–615.
- Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K.M.L., Valencia, M.C., Sanchez, E.I. *et al.* (2010). Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, 466, 752–755.
- Martorell, C. & Freckleton, R.P. (2014). Testing the roles of competition, facilitation and stochasticity on community structure in a species-rich assemblage. *J. Ecol.*, 102, 74–85.
- McGill, B.J. (2003). A test of the unified neutral theory of biodiversity. *Nature*, 422, 881–885.
- Medina-Roldán, E., Paz-Ferreiro, J. & Bardgett, R.D. (2012). Grazing-induced effects on soil properties modify plant competitive interactions in semi-natural mountain grasslands. *Oecologia*, 170, 159–169.
- Moloney, K.A. & Chiariello, N. (1998). Yield-density functions as predictors of community structure in a serpentine annual grassland. *J. Ecol.*, 86, 749–764.
- Nanami, S., Kawaguchi, H. & Yamakura, T. (2011). Spatial pattern formation and relative importance of intra- and interspecific competition in codominant tree species, *Podocarpus nagi* and *Neolitsea aciculata*. *Ecol. Res.*, 26, 37–46.
- Ngo Bieng, M.A., Perot, T., de Coligny, F. & Goreaud, F. (2013). Spatial pattern of trees influences species productivity in a mature oak-pine mixed forest. *Eur. J. For. Res.*, 132, 841–850.
- Osunkoya, O.O., Othman, F.E. & Kahar, R.S. (2005). Growth and competition between seedlings of an invasive plantation tree, *Acacia mangium*, and those of a native Borneo heath-forest species, *Melastoma beccarianum*. *Ecol. Res.*, 20, 205–214.
- R Development Core Team. (2017). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Rees, M., Grubb, P.J. & Kelly, D. (1996). Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *Am. Nat.*, 147, 1–32.
- Sears, A.L.W. & Chesson, P. (2007). New methods for quantifying the spatial storage effect: an illustration with desert annuals. *Ecology*, 88, 2240–2247.
- Sheley, R.L. & James, J.J. (2014). Simultaneous intraspecific facilitation and interspecific competition between native and annual grasses. *J. Arid Environ.*, 104, 80–87.
- Sheley, R. & Larson, L. (1994). Comparative growth and interference between cheatgrass and yellow starthistle seedlings. *J. Range Manag.*, 47, 470–474.
- Sheley, R.L. & Larson, L.L. (1995). Interference between cheatgrass and yellow starthistle at 3 soil depths. *J. Range Manag.*, 48, 392–397.
- Siepielski, A.M. & McPeck, M.A. (2010). On the evidence for species coexistence: a critique of the coexistence program. *Ecology*, 91, 3153–3164.
- Suter, M., Ramseier, D., Guesewell, S. & Connolly, J. (2007). Convergence patterns and multiple species interactions in a designed plant mixture of five species. *Oecologia*, 151, 499–511.
- Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey.
- Turkington, R. & Jolliffe, P.A. (1996). Interference in *Trifolium repens*-*Lolium perenne* mixtures: short- and long-term relationships. *J. Ecol.*, 84, 563–571.

- Turnbull, L.A., Coomes, D., Hector, A. & Rees, M. (2004). Seed mass and the competition/colonization trade-off: competitive interactions and spatial patterns in a guild of annual plants. *J. Ecol.*, 92, 97–109.
- Urban, M.C., Tewksbury, J.J. & Sheldon, K.S. (2012). On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proc. R. Soc. B Biol. Sci.*, 279, 2072–2080.
- Uriarte, M., Condit, R., Canham, C.D. & Hubbell, S.P. (2004). A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *J. Ecol.*, 92, 348–360.
- Uriarte, M., Hubbell, S.P., John, R., Condit, R. & Canham, C.D. (2005). Neighborhood effects on sapling growth and survival in a neotropical forest and the ecological equivalence hypothesis. In *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity*. (eds Burslem, D.F.R.P., Pinard, M.A., Hartley, S.E.). Cambridge University Press, Cambridge, United Kingdom, pp. 89–106.
- Usinowicz, J., Chang-Yang, C.-H., Chen, Y.-Y., Clark, J.S., Fletcher, C., Garwood, N.C. *et al.* (2017). Temporal coexistence mechanisms contribute to the latitudinal gradient in forest diversity. *Nature*, 550, 105–108.
- Vasquez, E., Sheley, R. & Svejcar, T. (2008). Nitrogen enhances the competitive ability of cheatgrass (*Bromus tectorum*) relative to native grasses. *Invasive Plant Sci. Manag.*, 1, 287–295.
- Vellend, M. (2016). *The Theory of Ecological Communities*. Princeton University Press, Princeton, United States.
- Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. *Nature*, 118, 558–560.
- Webb, C.O., Gilbert, G.S. & Donoghue, M.J. (2006). Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology*, 87, S123–S131.
- Yenni, G., Adler, P.B. & Ernest, S.K.M. (2017). Do persistent rare species experience stronger negative frequency dependence than common species? *Glob. Ecol. Biogeogr.*, 26, 513–523.
- Zarnetske, P.L., Gouhier, T.C., Hacker, S.D., Seabloom, E.W. & Bokil, V.A. (2013). Indirect effects and facilitation among native and non-native species promote invasion success along an environmental stress gradient. *J. Ecol.*, 101, 905–915.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Liza Comita

Manuscript received 30 January 2018

First decision made 11 March 2018

Manuscript accepted 16 May 2018