
Article:
Tuck, S.L., Porter, J., Rees, M. orcid.org/0000-0001-8513-9906 et al. (1 more author) (2018) Strong responses from weakly interacting species. Ecology Letters, 21 (12). pp. 1845-1852. ISSN 1461-023X

https://doi.org/10.1111/ele.13163

ECOLOGY LETTERS

Ecology Letters, (2018) doi: 10.1111/ele.13163

LETTER

Strong responses from weakly interacting species

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Abstract

The impact of species loss from competitive communities partly depends on how populations of the surviving species respond. Predicting the response should be straightforward using models that describe population growth as a function of competitor densities; but these models require accurate estimates of interaction strengths. Here, we quantified how well we could predict responses to competitor removal in a community of annual plants, using a combination of observation and experiment. It was straightforward to fit models to multi-species communities, which passed standard diagnostic tests and provided apparently sensible estimates of interaction strengths. However, the models consistently underpredicted the response to competitor removal, by a factor of at least 50%. We argue that this poor predictive ability is likely to be general in plant communities due to 'the ghost of competition present' that confines species to parts of the environment in which they compete best.

Keywords

Community assembly, community dynamics, niches, non-manipulative method, plant competition, population dynamics, sand-dune annuals, species coexistence.

Ecology Letters (2018)

INTRODUCTION

As communities lose species, they will lose ecological function (Balvanera *et al.* 2006; Cardinale *et al.* 2012), although the extent of this loss depends on which species are lost and how the surviving members of the community respond (Smith & Knapp 2003; Zavaleta & Hulvey 2004; Isbell *et al.* 2008). At first glance, predicting how each species will respond to the loss of others in competitive communities seems straightforward. We simply need to parameterise models that describe how competition impacts the population growth of each species in a community and then use these models to predict how species will respond to the loss of any (or all) of their competitors (Rees *et al.* 1996; Adler *et al.* 2010; Martorell & Freckleton 2014; Chu & Adler 2015). However, good prediction first requires good estimates of the interaction strengths between community members.

Unfortunately, while any farmer or gardener can confirm that competition depresses plant performance, the best way to estimate the strength of competition has always been controversial (Damgaard & Weiner 2017). Various direct methods, e.g. removal experiments (Silander & Antonovics 1982) and simple competition experiments in pots or common gardens (Goldberg & Barton 1992; Gurevitch *et al.* 1992) have revealed that competition between species can be strong and that competitive hierarchies are common; but the methods have been criticised, either as methodologically flawed (Putwain & Harper 1970), or because they take place under unrealistic ecological conditions (Freckleton & Watkinson 2000; Damgaard & Weiner 2017).

Partly in response to these criticisms, ecologists have instead tried to measure competition between species embedded within natural communities (Weiner 1982; Pacala & Silander 1990; Rees *et al.* 1996; Law *et al.* 1997; Freckleton & Watkinson 2000; Adler *et al.* 2010; Chu & Adler 2015). Rather than manipulating the system, these methods exploit natural variation in density and species composition to estimate competitive effects. For example, neighbourhood modelling requires detailed spatial maps that allow target plant size or fecundity to be modelled as a function of the number and identity of close neighbours (Mack & Harper 1977; Pacala & Silander 1990; Turnbull *et al.* 2004; Stoll & Newbery 2005; Kunstler *et al.* 2016). Alternatively, counting the numbers of plants in subdivided permanent quadrats allows changes in population sizes from year to year to be modelled as a function of competitor densities (Rees *et al.* 1996; Martorell & Freckleton 2014). Both methods yield interaction matrices consisting of pairwise competitive effects.

A recent meta-analysis has summarised the results of competition studies in which pairwise interaction coefficients are available (Adler *et al.* 2018b). It concludes that, while it is common to find that the strength of intraspecific competition exceeds the strength of interspecific competition – at least when interactions are exclusively competitive – this effect is greatly enhanced in unmanipulated field settings. We suggest an explanation for this unexpected pattern and conjecture that it will impact our ability to predict how species respond to competitor removal in natural communities.

We suggest that, in unmanipulated field settings, species are pushed by competition into realised niches – i.e. to parts of the environment where they compete best (Rees *et al.* 1996; Turnbull *et al.* 2007). Once this spatial sorting has taken place, we expect to estimate higher values of the intraspecific competition coefficient relative to interspecific effects. But, we also expect that any model parameterised using this data will underpredict the response to competitor removal (Rees *et al.* 1996; Adler *et al.* 2010; Martorell & Freckleton 2014; Chu & Adler 2015) because the removal of competitors allows species to expand their realised niche. This effect could be dubbed 'the ghost of competition present' (although this term has

been used to mean other things (Miller *et al*. 2009)), as it parallels 'the ghost of competition past', which is thought to shape fundamental niches over evolutionary time (Connell 1980). The ghost of competition present shapes realised (rather than fundamental) niches, but might lead to a similar underestimate of the importance of competition among species.

A logical procedure to detect the ghost of competition present is: (1) parameterise a model in an unmanipulated setting; (2) use it to predict how a species responds to the removal of competitors; and (3) compare those predictions to an appropriate experimental manipulation. Here, we present results from an experiment conducted under semi-natural conditions using a simplified community of sand-dune annuals that had been established for 3 years. We parameterised models in an unmanipulated setting (using mixture plots) and tested the predicted effect of species removals against observations of monoculture plots established at the same time.

We found strong evidence for a ghost of competition present. Models parameterised solely from mixture plots underpredicted the response to competitor removal by a factor ranging from 1.5 to 2.5 in four out of five species, and overpredicted the response for the competitive dominant. Our results are consistent with the operation of a 'ghost of competition present' that confines species to realised niches in an unmanipulated setting and hence underestimates their response to competitor removals.

MATERIALS AND METHODS

Outline of approach

Our community was a well-studied system of sand-dune annuals (Mack & Harper 1977; Rees *et al*. 1996; Turnbull *et al*. 1999, 2004). We used replicate semi-natural communities and fitted population growth models to five common species (see 'Experiment'), which included terms to describe the impact of competitors (see 'Models'). The models were fitted to data on population size garnered in years 3 and 4 from both monoculture and mixture plots.

To determine the predictive ability of our models, we followed the same logic as Adler *et al*. (2018a). Models were fitted to the combined data set, but in monocultures the population sizes of competitor species were set to zero. The models included further modifying terms to describe any effects of the monoculture 'treatment' above and beyond the simple absence of competitors (see 'Predicting the effect of competitor removals'). If the modifying terms are estimated to be non-zero, it suggests that the impact of competitor removal cannot be predicted from a model fitted only to the full community. To estimate the impact of these additional terms on population growth in monoculture, we compared predictions using a model in which we included the modifying terms, to those from a model in which these effects were ignored.

Experiment

Seven species of sand-dune annuals were grown for 4 years (2010–2013) in a common garden experiment in Zürich, Switzerland (Fig. S1). The study species and their seed sizes were: *Saxifraga tridactylites* L. (0.006 mg), *Arabidopsis thaliana* [L.] Heynh. (0.025 mg), *Cerastium diffusum* Pers. (0.045 mg), *Arenaria serpyllifolia* L. (0.088 mg), *Veronica arvensis* L. (0.112 mg), *Myosotis discolor* Pers. (0.213 mg), and *Valerianella locusta* [L.] Laterr. (0.851 mg). They germinate in autumn and flower in spring. We analysed five of these species, because *Veronica* and *Valerianella* were too rare to provide sufficient data.

The experiment comprised 80 (1×1 m^2) plots. Plots were constructed in the following way: a pre-formed concrete lattice consisting of 56 (6×6 cm^2) individual cells was placed in each plot on top of a weed-proof liner and filled with a low-nutrient mixture of sand and compost to a depth of 10 cm (Fig. S2). The lattice walls were sufficiently thick (4 cm) that plants in adjacent cells rarely overlapped aboveground. Thus, we assumed that plants only competed for resources within (and not between) cells. Plants could disperse seeds freely within plots, but metal barriers prevented significant seed movement among plots. Subdividing the plots into cells provided the fine-grained information necessary for parameterising the models. We grew eight monocultures of each species and 24 mixtures containing all seven species.

The experiment was established from seed at the end of August 2009 using a constant total density per plot in a substitutive design. In all plots, seeds were distributed evenly among cells by counting the required number of seeds per cell: 21 seeds per cell in the case of monocultures ($21 \times 56 = 1176$), and three seeds per species per cell in the case of mixtures ($3 \times 7 \times 56 = 1176$). The experiment ran for four generations of adult plants: 2010–2013 inclusive. The data presented here are from the final 2 years: 2012–2013, following two generations of natural dispersal and establishment (Fig. S1) which should allow spatial sorting to occur. In 2012 and 2013, a full census of each cell was carried out in each year at the start of April and these are the data used to fit the models. It is available on Dryad (https://doi.org/10.5061/dryad.m7r60n0).

To facilitate the fitting of nonlinear population models, which is often hampered by lack of information at low density (Law & Watkinson 1987; Rees *et al*. 1996), we tried to create a gradient of plant density across plots by imposing a series of disturbance treatments designed to reduce seed production. To reduce the plot-level seed set (and hence, we hoped, the density of adult plants), we removed all plants from a subset of cells before they set seed. Plants were cut at ground level and did not regrow. In mixture plots, we applied five levels of disturbance by removing plants from 12.5, 25, 50, 75 or 87.5% of cells. There were only eight monoculture plots per species, so we imposed only three levels of disturbance: 12.5, 50 and 87.5%. To spread the manipulations evenly across the plots, we selected cells in a stratified random way: removing all plants from a fixed number of randomly selected cells from each row in a plot grid. The disturbance treatment was imposed every year of the experiment, from 2010 to 2012. In 2012 and 2013, there was a highly significant negative relationship between the proportion of cells removed and average density per cell, although this was mainly driven by an effect on *Myosotis*, the competitive-dominant (interaction between species and percentage of cells disturbed: $F_{6,21} = 5.4$,

$P = 0.0017$; Fig. S3). The hierarchy for average cell biomass in mixture was *Myosotis* > *Arenaria* > *Cerastium* > *Saxifraga* > *Arabidopsis* – broadly in decreasing order of seed size.

Models

To ensure that conclusions were not dependent on model choices and to bracket the types of models used in previous work, we fitted three different models, which incorporated a range of assumptions about the nature of species interactions and dispersal within plots. The first two models assume that either: (1) all seeds remain in their natal cells, or (2) some fraction of seeds remain in the natal cell (m), while the rest join a global seed rain ($1 - m$).

The general form of model 1 is:

$$N_{t+1,i,c} = mr_i F_c + (1-m)\langle r_i F_k \rangle_k \quad N_{t,i,c} > 0, \tag{1}$$

where $N_{t+1,i,c}$ is the population size in year $t + 1$ of target species i in cell c. The population growth rate of species i in the absence of competition, r_i, is modified by density-dependent interactions in the following way:

$$F_c = \left[\frac{N_{t,i,c}}{1 + \sum_{j=1}^{5} \alpha_{ij} N_{t,j,c}} \right], \tag{2}$$

where α_{ij} is the per capita effect of species j on species i. Thus, the first term in eqn 1 describes the expected number of individuals of species i in year $t + 1$ that originated in the natal cell. Similarly, the average value of F_c among the cells within a plot can be calculated using:

$$\langle F_k \rangle_k = \left[\frac{1}{p} \sum_{k=1}^{p} \frac{N_{t,i,k}}{1 + \sum_{j=1}^{5} \alpha_{ij} N_{t,j,k}} \right] \tag{3}$$

where p is the total number of cells within a plot. Thus, the second term in eqn 1 describes the expected number of immigrants arriving from other cells within the plot.

Model 2 (eqn 4) contains only the first, within-cell-growth term from eqn 1, and thus assumes that no seeds disperse outside their natal cells:

$$N_{t+1,i,c} = \left[\frac{r_i N_{t,i,c}}{1 + \sum_{j=1}^{5} \alpha_{ij} N_{t,j,c}} \right] = r_i F_c \quad N_{t,i,c} > 0, \tag{4}$$

Model 3 (eqn 5) has a different structure. In this case, we assume that within cells population growth is density-dependent, but is only sensitive to the density of conspecifics:

$$N_{t+1,i,c} = \left[\frac{r_i N_{t,i,c}}{1 + \alpha_{ii} N_{t,i,c}} \right] q_{t+1,i,c} \quad N_{t,i,c} > 0, \tag{5}$$

where q is an index of cell quality. Other species affect the target species by modifying the quality of cells:

$$q_{t+1,i,c} = \frac{e^{(\beta_0 + \sum_{j \neq i}^{5} \beta_j N_{t+1,j,c})}}{1 + e^{(\beta_0 + \sum_{j \neq i}^{5} \beta_j N_{t+1,j,c})}}, \tag{6}$$

This cell quality index is a logistic function of the densities of other species in year $t + 1$ and their *per capita* effects on the target species, β_j. For each target species, we estimate a basal cell quality, β_0, but the quality of each cell can deviate above or below this value depending on the density of other species present in the same year. Model 3 allows species interactions to be positive as well as negative (eqn 6) – in contrast to models 1 and 2 where they are constrained to be negative. Positive interaction coefficients might indicate facilitation. Alternatively, they might simply indicate that the seedling densities of both the neighbour and target species tend to be positively correlated, perhaps because they share a preference for the same types of cells.

All models were fitted using the R package *rjags v4-6* (Plummer 2003) in *R v3.5.0* (R Development Core Team 2018) and the complete code is available in the supplementary analysis. We assumed that N_{t+1} was Poisson distributed. To estimate the competition coefficients, we specified uninformative priors, assuming they had a normal distribution ($\mu = 0$, $\sigma^2 = 1000$). Competition coefficients were constrained to be positive – that is competitive – by applying an exponential transformation. A common concern when parameterising such models is that the competition coefficients (α_{ij}) and the population growth rates in the absence of competition (r_i) can be correlated, because they trade off against each other (Rees *et al*. 1996). This can produce an unstable estimation process, because as one parameter increases the other decreases, yielding an equally good model fit. To avoid this instability, we used informative priors for the species-specific r_i values. We specified these informative priors by assuming a gamma distribution with an expected value equal to the average 2012–2013 population growth observed in monocultures with the highest fraction of cells removed (gamma: *shape* = mean 2012–2013 growth; *rate* = 1; E[X] = *shape*/*rate*). In a single case (fitting model 3 to *Myosotis*), we fixed β_0 at zero (basal cell quality = 0.5) to stabilise the estimation process, because there were significant trade-offs between r_i and β_0.

We ran all models with three sampling chains. We ensured each model had sufficiently converged on the target distribution by running an adaptation period of 10 000 samples (plus 10 000 burn-in). Following adaptation, we monitored 10 000 samples from the chains, thinning to every 10th sample to reduce autocorrelation – giving us 1000 samples from each posterior distribution. We checked that the chains had converged by plotting the sampling chains, posterior densities and chain autocorrelation. We used Gelman-Rubin plots to check that chains had converged on the same target distribution (Brooks & Gelman 1998). We also checked models by: (1) testing that they can recover known parameters from simulated data, (2) examining residual diagnostic plots, and (3) comparing simulated and observed data to look for systematic differences between models and observations (Gelman & Hill 2007). Predicted data qualitatively resembled the respective

observed data, although the observed data often showed a longer tail of right skewness. To have the same sample size for each model, all models were fitted only to cells where N_t was positive. Generally, the three models produced similar fits with qualitatively similar results and to simplify presentation we show detailed output from Model 2 only (additional output from Models 1 and 3 are available in the supplementary analysis). A comparison of the predictive accuracy of all models is also shown.

Predicting the effect of competitor removal

To test whether we could predict the extent of competitive release, we fitted a modified model to both monoculture and mixture data. In the monoculture data, the population sizes of all competitor species are set to zero. We also included two additional terms in the model to capture the ghost of competition present. The effect of the ghost could be to change the intensity of intraspecific competition or to change the fundamental population growth rates in monocultures relative to mixtures, as the realised niches of species expand. To accommodate these potential changes, the population growth rate of species i in monoculture, $r_{i,mono}$, is specified as:

$$r_{i,mono} = r_{i,mix} + dr$$

Similarly, the strength of intraspecific competition in monoculture, $\alpha_{ii,mono}$ is modelled as:

$$\alpha_{ii,mono} = \exp\left(\rho_{ii,mix} + da\right)$$

where $\alpha_{ii,mix} = \exp\left(\rho_{ii,mix}\right)$. If the distributions of the modifying parameters, dr and da, are not significantly different from zero, then we can assume that the model parameters in monocultures and mixtures are similar and we would expect to make a good prediction without the modifiers. We can assess the impact of modifiers on the predicted response to competitor removal by examining predictions generated at the cell level in monocultures from models that do or do not include these additional modifying terms. For Models 1 and 3, this parameterisation did not converge well and so we fitted these two models with separate parameters in mixtures and monocultures (e.g. $r_{i,mono}$ and $r_{i,mix}$) and then compared the predictions made.

Plot-level data

As an additional test of whether monocultures and mixtures have different population growth rates, we also analysed average population sizes for each plot. We regressed average population sizes in 2013 on average population sizes in 2012 for both mixtures and monocultures. The slope of the regression line through the origin is therefore the population growth rate and we tested whether slopes were different using linear regression. If the regression slope in monoculture is steeper than in mixture, then there is a clear positive effect of removing competitors on population growth and this is the effect that we should be able to capture using the models parameterised in mixture plots.

RESULTS

The matrix of interaction coefficients shows that intraspecific competition was strong for all species (Fig. 1). However, not all interspecific effects are weak. There is evidence of a competitive hierarchy based on seed size: some species with large seeds had a strong competitive effect on those with smaller seeds (e.g. *Myosotis* had a strong negative effect on all other species, while the reciprocal effect was usually weak). When we allowed for positive interactions (Model 3), the pattern disappeared: instead all interactions were scattered around zero, with similar numbers of positive and negative interactions (Fig. S4). Broadly speaking, all models estimated interactions coefficients with high precision.

When fitting Model 2 to both monoculture and mixture data, at least one of the modifying parameters, dr or da, was non-zero for each species, as all of the 3000 posterior samples were either positive or negative (Fig. 2). This strongly suggests that there are additional changes when switching to monoculture over and above the simple absence of competitor species. The effect of including these additional terms when estimating population growth rates is large: for four out of five species, cell-level population growth rates in monoculture are much higher when these terms are included (Fig. 3). Thus, using models parameterised only from mixture plots will greatly underestimate the response to competitor removal. The exception is *Myosotis*: the competitive-dominant, which is predicted to respond more strongly to the removal of competitors than it actually does (Fig. 3). All models on average miss-predicted the response to competitor removal although the magnitude of the under or overprediction varied (Fig. 4).

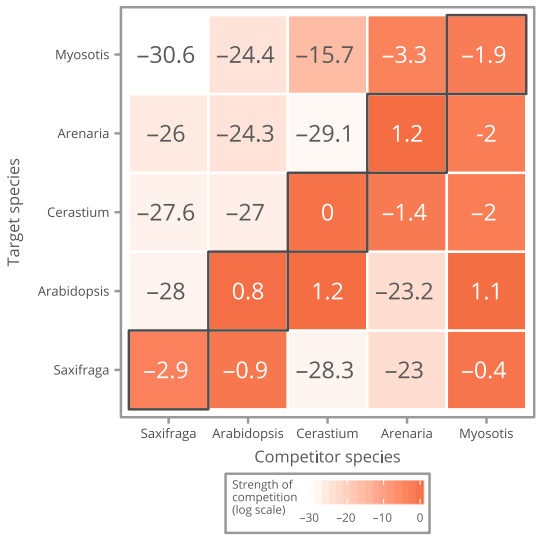

Figure 1 Competition is asymmetric and related to seed size. The effects of competitor species (columns) on the population size of each target species (rows). The diagonal shows intraspecific competitive effects, which are generally strong. Weak competitive effects are shown in pale orange and stronger effects are darker (effects are log-scaled, so large negative values describe very weak effects). Species are ordered left to right and bottom to top by increasing seed size. Broadly speaking, competitive effects are linked to seed size, with large-seeded species exerting stronger competitive effects on smaller seeded species.

For the plot-level data, when comparing average population growth rates in monocultures vs. mixtures, we observed a significant three-way interaction between species identity, treatment (mixture vs. monoculture) and density ($F_{4,140} = 3.4$, $P = 0.01$). Inspection of the slopes revealed that for four of the five species, population growth rate in monocultures was roughly twice that in mixtures (Fig. 5) an effect that clearly could not be captured by models parameterised using only data from mixture plots. The exception was *Myosotis*, whose population growth rate was higher in mixture plots (although when we used biomass data, rather than population sizes, *Myosotis* showed no difference in population growth rate between monoculture and mixture plots: Fig. S5).

DISCUSSION

Given the current extinction crisis, we tested whether we could predict how species within semi-natural plant communities would respond to the loss of their competitors. In line with previous studies, we used standard techniques to fit population models to mixture plots that included estimates of interaction strengths within the community. The models revealed that intraspecific competitive effects were strong for all species but there was also evidence of a competitive hierarchy linked to seed size, consistent with previous work in this community (Rees 1995; Turnbull *et al.* 1999, 2004).

Once fitted, population models can be used to predict the response of each species to the removal of its competitors, but normally there is no independent test. Our experiment included monoculture plots, which were sown with only one species, and the models should therefore be able to predict the population growth rate in these plots, by simply setting the population sizes of competitor species to zero.

Following Adler *et al.* (2018a), we fitted models to both mixture and monoculture plots but included additional modifying parameters, to capture any additional effect of monoculture, over and above the simple absence of competitors. At least one of these parameters was estimated to be non-zero for all species. When we compared predictions with and without these modifiers, we saw that the response to competitor removal was severely underpredicted without them. This requires further explanation.

Why did observational models underpredict the response to species loss?

The first possibility is that we fitted poor models and that our estimates of competitive interactions were flawed – hence the poor predictions; but this seems unlikely for a number of reasons. First, the competition coefficients had small standard errors and were estimated using independent sampling chains that converged on the same posteriors. Second, model uncertainty was low, reflected by the narrow intervals in Fig. 4; hence the models were a good fit to the observed data, as judged by normal criteria. Third, distributions of cell population sizes in data simulated from the models closely resembled that of the observed data, further indicating that there was no systematic bias. Fourth, the three models included different assumptions about the nature of species interactions and dispersal, yet all models made poor predictions about the response to the removal of competitors. Fifth, our test was fair, as it expressed the same effect as our predictions – the mean change in population size in response to competitor removal – and did so for the same data. Sixth, the large range in observed densities meant that we avoided potential underestimation due to observing species only at high densities (Law & Watkinson, 1989). Taken together, we do not therefore believe that the problem stems from poor model choices. Our results also echo those of Adler *et al.* (2018a) who discovered a near-identical problem, when using removal experiments to test the predictions of a model fitted to observational data; hence it seems that our problem might be a general one.

The alternative is that there is nothing wrong with the models or the estimates. Rather, the problem lies in using models parameterised in natural communities to predict what happens when competitors are removed. Our suggestion is that species in natural communities are confined by competition to realised niches (hence we estimate weak interactions). However, once competitors are removed, species are free to expand their niches. The concept of realised niches was introduced by

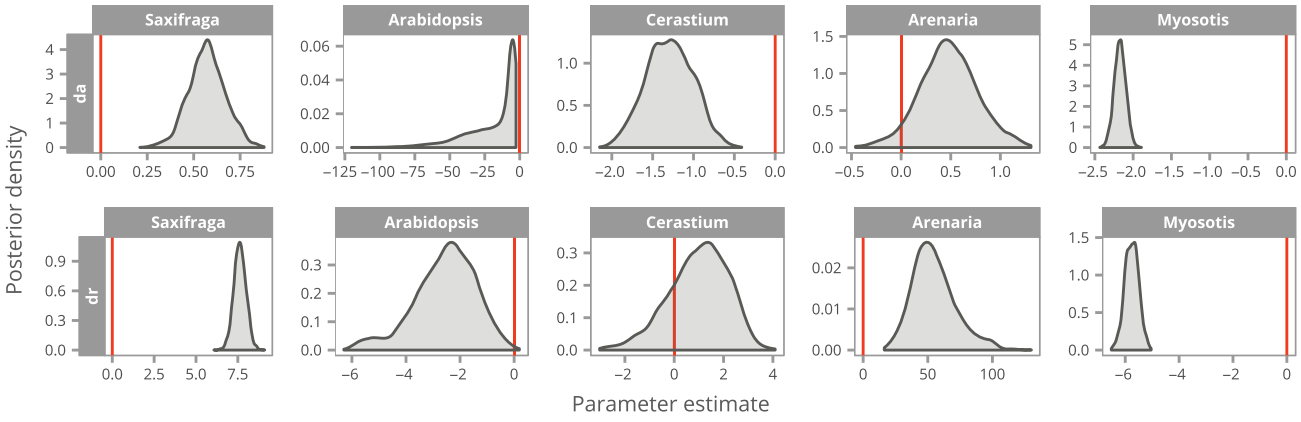

Figure 2 The distribution of parameters that describe any additional effect of growing in monoculture, which is not captured by simply setting population sizes of competitor species to zero. In Model 2, the parameter *da* modifies the effect of intraspecific competition, and the parameter *dr* modifies the fundamental population growth rate. In each case, 3000 samples from the posterior distribution are shown.

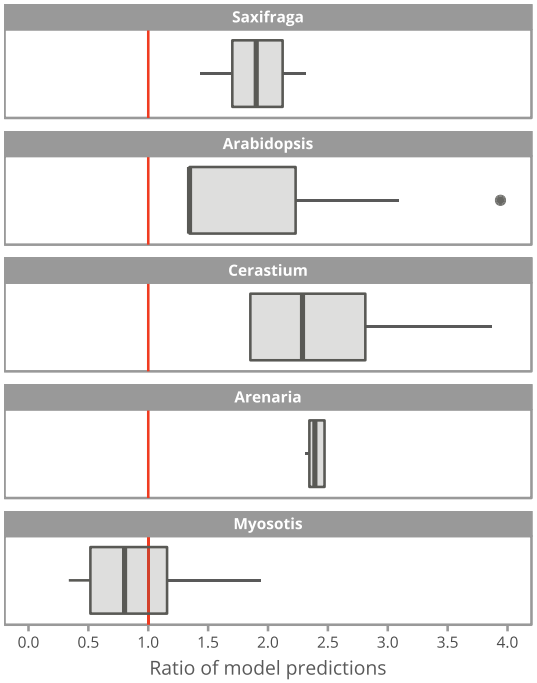

Figure 3 The ratio of monoculture predictions with and without the modifying parameters. Setting the modifying parameters to zero in Model 2 causes the change in population size to be underpredicted in four species and slightly overpredicted in *Myosotis*. The boxplots represent the population of monoculture cells for each species. Ratios are calculated using the average parameter values for each model. Boxes show the median and interquartile range (IQR); the whiskers extend to any points within 1.5 × IQR. For clarity, any ratios > 4 were omitted (< 2% of cells).

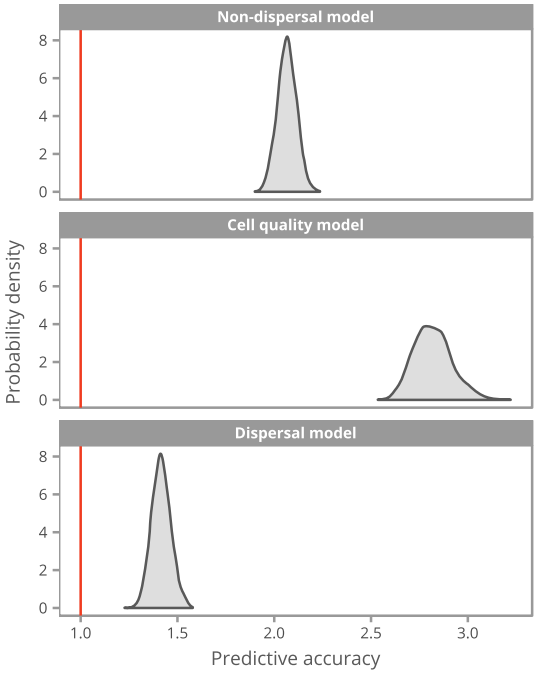

Figure 4 All models underpredict the response to competitor removal in monoculture. Plots show the average mismatch in the predictive ability of models fitted to mixture data when compared to models fitted to monoculture data (or with and without modifying parameters in the case of the non-dispersal model). The distribution is sampled from the full posterior distribution in each case, propagating model uncertainty, and then averaged across cells and species. A predictive accuracy of two means the models fitted to mixture data underpredicted the effect of competition by one half.

Hutchinson (1957) and stems from the idea that most species can tolerate a broader range of ecological conditions than those in which they are actually found in nature. The full range of conditions tolerated by the species is called the fundamental niche and is naturally broader (Chase & Leibold 2003).

In order to coexist, species must have different realised niches. For example, each species might compete best for a limited range of soil conditions; e.g. each species might grow best at a given soil moisture level (Silvertown *et al.* 1999). This specialisation, if coupled with micro-heterogeneity in environmental variables, can strongly favour coexistence, although it might be extremely hard to measure directly. If species are confined to parts of the habitat where they tend to compete best, then models will correctly identify that the current strength of interspecific competition in the community is weak. Indeed, fitting neighbourhood competition models to the same species embedded in a natural community produced a very similar conclusion (Turnbull *et al.* 1999). However, as shown here, a strong response to competitor removal may still occur. Our suggested explanation is that species are able to expand out of their realised niches once the competitor is removed. This interpretation would also predict that the competitive-dominant – in this case *Myosotis* – would experience the least compression of its fundamental niche by competitors. We would therefore expect to be able to make a better prediction about its response to competitor removal; which does indeed seem to be the case (Fig. 3).

Adler *et al.* (2018a) showed that removal experiments in the field seemed to reveal a stronger response to competitor removal than that predicted by their previously fitted population models (Adler *et al.* 2010; Chu & Adler 2015). As they note, removal experiments in the field fall into a grey area between observational studies and randomised, controlled experiments as they rely on natural spatial variation in composition. Establishing experimental communities, as we have done here, might be the only way to get around this problem. Given the wide range of communities where this pattern has been observed (Adler *et al.* 2018b), we believe that this is likely to be a very general problem, and not some peculiarity of the community described here.

What are the implications?

Ecologists have argued long and hard about the best way to measure competition. The reason for this argument is partly intellectual but it has real implications if we are to use community models to make good predictions. Certainly, it is intriguing that direct experimental work generally reveals a different balance between intraspecific and interspecific competition than those carried out in unmanipulated field settings (Adler *et al.* 2018b). Our study offers a resolution to this debate. In experiments, the experimenter chooses which plants to grow where, whereas species in natural communities often display strong spatial structure (Stoll & Prati 2001; Turnbull *et al.* 2004). This structure may result from micro-habitat specialisation; i.e. species are found where they compete best.

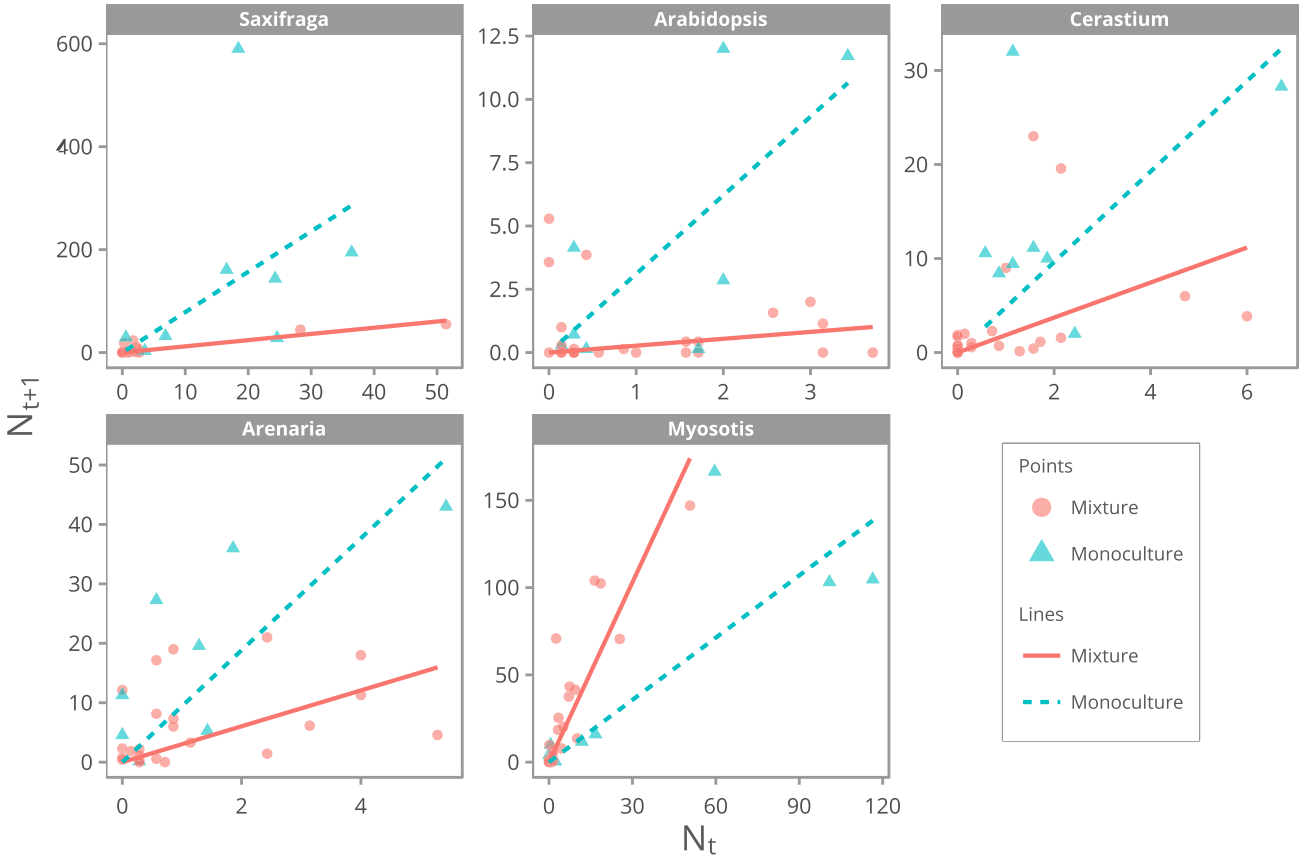

Figure 5 Population growth rates in monoculture and mixture plots. The average cell-level population size for each plot in 2013 (N_{t+1}) vs. 2012 (N_t). Blue dots show monoculture plots, red dots show mixture plots. The regression lines, fitted through the origin, show the average population growth rate. Species are shown in order of increasing seed size. Population growth rates were significantly higher on average in monocultures than mixtures for four species. The exception was *Myosotis*, which was competitively dominant. In terms of population size, *Myosotis* performed better in mixtures, but biomass data show no difference between diversity treatments for this species (Fig. S4).

Unfortunately, this means that we cannot use any model that relies on estimates of the strength of competition *currently experienced* to make predictions about how species will respond to competitor removal in the future. We suggest that this phenomenon could be dubbed 'the ghost of competition present', as like the ghost of competition past, its operation means that the impact of competition is underestimated.

Coexisting species in natural communities may thus appear to interact weakly, because they have been confined to realised niches by competition. If so, then paradoxically, they might respond strongly to the removal of competitors. When weak interactions are found, it is therefore unreasonable to claim that communities are only loosely structured by competition (Martorell & Freckleton 2014). Much of the competition simply goes undetected.

Future directions

If we want to predict how communities will respond to species loss, we need to develop new methods. These should be guided by theory and coupled with manipulations in real or experimental communities to test and refine predictions. For example, species could be removed singly to see whether models can predict which of the remaining species will show the strongest response. Alternatively, we might need more detailed data on how species are affected by competition during specific life-history stages, rather than the more common observations of adult–adult transitions. Current observational data and methods are valuable tools, but we will need a greater combination of approaches to fully understand the role of competition between species in natural plant communities.

The increasing prevalence of new diseases (Pautasso *et al.* 2013) and the continued exploitation of high-value species means that extinction rates are unlikely to drop in the near future. Given that ecosystem properties depend on species richness (Balvanera *et al.* 2006), predicting how natural communities will respond to the loss of competitors is key to understanding how extinctions will affect communities. In particular, we need to know whether, and to what extent, competitor species can 'fill the gap' left by their competitors. In competitive communities, current methods appear to be inadequate. Refining or replacing current techniques is therefore an urgent priority.

ACKNOWLEDGEMENTS

We thank the many people who helped with counting and weighing plants in the experiment. The work was supported by a grant from the Swiss National Science Foundation SNSF: 31003A_133082 to LAT. SLT was funded by a UK Natural Environment Research Council studentship.

AUTHORSHIP

LAT designed the experiment. JP collected the data. All authors were involved in discussion and design of analyses. SLT performed all analyses. The paper was drafted by SLT and LAT with input from all authors.

DATA ACCESSIBILITY STATEMENT

The data used here are available in Dryad (https://doi.org/10.5061/dryad.m7r60n0).

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Editor, Robin Snyder
Manuscript received 17 May 2018
First decision made 21 June 2018
Manuscript accepted 7 August 2018