

Examining the link between competition and negative co-occurrence patterns

Authors: Hannah A. Brazeau, Brandon S. Schamp
Department of Biology,
Algoma University
1520 Queen St. East,
Sault Ste. Marie, Ontario, Canada
P6A 2G4

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Abstract

Negative species co-occurrence patterns have long intrigued ecologists because of their potential link to competition. Although manipulative field experiments have consistently revealed evidence of competition in natural communities, there is little evidence that this competition produces negative co-occurrence patterns. Evidence does suggest that abiotic variation, dispersal limitation, and herbivory can contribute to patterns of negative co-occurrence among species; it is possible these influences have obscured a link with competition. Here, we test for a connection between negative co-occurrence and competition by examining a small-scale, relatively homogeneous old-field plant community where the influence of abiotic variation was likely to be minimal and we accounted for the impact of herbivory with an herbivore exclosure treatment. Using three years of data (two biennial periods), we tested whether negatively co-occurring pairs of species, when occasionally found together, experienced asymmetric abundance decline more frequently than positively co-occurring pairs, for which there is no such expectation. We found no evidence that negatively co-occurring pairs consistently suffered asymmetric abundance decline more frequently than positively co-occurring pairs, providing no evidence that competition is a primary driver of negative co-occurrence patterns in this community. Our results were consistent across control and herbivore exclosure treatments, suggesting that herbivores are not driving patterns of negative species co-occurrence in this community. Any influence of competition or herbivory on co-occurrence patterns is small enough that it is obscured by other factors such as substrate heterogeneity, dispersal, and differential species responses to climatic variation through time. We interpret our results as providing evidence that competition is not responsible for producing negative co-occurrence patterns in our study community and suggest that this may be the case more broadly.

Keywords: species association, asymmetric competition, plant community

Introduction

The past several decades have seen considerable effort directed toward identifying deterministic patterns of species co-occurrence, with the goal of linking these patterns to specific underlying mechanisms. Given the preponderance of evidence that competition is an important force in minimally or infrequently disturbed natural plant communities (Grime 1979, Schoener 1983, Goldberg and Barton 1992, Aarssen and Epp 1990, Gurevitch et al. 1992), it is of particular interest whether patterns of negative co-occurrence represent a signature of antagonistic interactions among species (Diamond 1975, Connor and Simberloff 1979). Despite the progress made in the development of reliable methods to identify and quantify species co-occurrence patterns at both the community level (Hastings 1987, Gotelli 2000,

Gotelli and McCabe 2002) and at the level of species pairs (Sfenthourakis et al. 2004, Gotelli and Ulrich 2010, Veech 2013), evidence of a relationship between negative co-occurrence and competition has been elusive.

A large number of communities have been examined with respect to co-occurrence patterns. Thus far, evidence indicates that negative co-occurrence patterns are relatively common (Gotelli and McCabe 2002), although they are not ubiquitous (Bar-Massada 2015) and some evidence suggests that positive co-occurrence patterns may be more common in alpine systems (Götzenberger et al. 2012). Researchers have also made progress in recognizing that several mechanisms can contribute to co-occurrence patterns. For example, in a hypothetical field that has wet soil conditions at one

end and dry conditions at the other, we would find some species only at the wet end of the field and others only at the dry end. Consequently, a co-occurrence test including samples from both ends of the field would result in strong negative co-occurrence for these species. It is therefore unsurprising that several studies have linked negative co-occurrence patterns to variation in abiotic components of the environment, including elevation (Choler et al. 2001, Callaway et al. 2002), temperature (Dullinger et al. 2007), rainfall, and soil quality (Tirado and Pugnaire 2005). At large scales, abiotic variation leads to negative co-occurrence when different sites contain species that are differentially adapted to local conditions. Götzenberger et al. (2012), in a review of the literature, determined that spatial variation in the abiotic environment is the predominant driver of co-occurrence patterns in the studies they examined.

Other researchers have found evidence that dispersal is likely to play a role in governing significant patterns of species co-occurrence (Bell 2005, Schamp et al. 2015, D'Amen et al. 2017). At large scales, dispersal limitation may restrict some species from reaching particular sites, leading to negative co-occurrence patterns. Furthermore, sampling units that are too large will not capture the grain at which biotic interactions occur (McNickle et al. 2018). At smaller scales, abiotic variation related to mineral nutrients and water in the soil may be too limited or transient to drive strong patterns of negative co-occurrence. In these smaller, more abiotically homogeneous communities, all species should be capable of dispersing to all potential sites and suited to the conditions within those sites. For these reasons, it is best to conduct research into the influence of competition on negative co-occurrence in smaller samples, within relatively homogeneous communities.

Even if it is possible to control or minimize abiotic variation by examining small communities, careful effort is required to be confident that any observed negative co-occurrence patterns are actually linked to competition. At smaller scales, other processes can also contribute to or add noise to co-occurrence patterns. For example, noise can result from local dispersal delivering seeds of a species into an area where it will eventually be outcompeted by residents (Boulangéat et al. 2012). In such circumstances, the newly arrived species may still be included in survey data as a small plant that will never reach maturity. At least one study has demonstrated that this can contribute strongly to observed negative co-occurrence patterns (Schamp et al. 2016). Disturbance can reduce the impact of competition on co-occurrence patterns by

maintaining local biomass at low levels such that resource supply exceeds demand (Taylor et al. 1990). Herbivory can be a common source of disturbance that leads either to plant mortality or changes in interspecific competitive dynamics (Gurevitch et al. 2000). As such, herbivores have the potential to influence the distribution and abundance of species within the community (Soliveres et al. 2012). In communities where herbivores are active, it may be important to control for their influence when testing for a link between co-occurrence patterns and competition.

Thus far, researchers have generally investigated the mechanisms underpinning patterns of co-occurrence using composition data from multiple samples taken during a single growing season, relying on this snapshot to reveal the products of competition. Because competition plays out over time, it may be beneficial to examine how patterns change across multiple growing seasons. Some evidence already suggests that competition is a significant contributor to community-level turnover (Bengtsson et al. 1994), with pairwise competition showing a tendency to restrict growth of the competitively inferior species (Freckleton and Watkinson 2001). As such, one way to determine whether negative co-occurrence patterns are influenced by competition is to test whether negatively co-occurring species pairs are more likely to experience asymmetric decline in abundance (decline for one of the two species) when they are occasionally found together, compared to positively co-occurring species pairs. As far as we are aware, there is no reason to expect competition to result in asymmetric decline in abundance for positively co-occurring species pairs, particularly as positive co-occurrence has previously been associated with facilitation (Long et al. 2015).

Here, we examine negative co-occurrence in the context of plot-level changes in species abundances across seasons as a means of testing for evidence of a link between negative co-occurrence and antagonistic interactions between species. Specifically, we test whether significantly negatively co-occurring species pairs, when found together, subsequently experience asymmetric decline in abundance more frequently than pairs of positively co-occurring species. We test this for two biennial periods (three growing seasons) using vegetation plots belonging to control and herbivore exclusion treatments, to also examine whether small mammal herbivores influence these patterns within the community.

Methods

Study site

We conducted this research at the Ontario Forest Research Institute's Arboretum in Sault Ste. Marie, Ontario (46°32'34.1" N 84°27'37.4" W). Our study site is an old-field community that has remained unmown and untilled for more than 10 years; prior to that, it was mown yearly and shallow tilled irregularly. In 2009, we set up a grid of 1.5 x 1.5 m plots separated by 1 m laneways within a 25 x 70 m section of the field. From the plots in the grid, we randomly assigned 75 plots to the control group, and 75 plots to an herbivore exclusion treatment (150 plots in total). At the centre of our 1.5 x 1.5 m plots, we set out circular plots measuring 0.5 m in diameter. Recent research has identified that smaller plot sizes such as these are most appropriate for testing the influence of competition on co-occurrence patterns (McNickle et al. 2018) while reducing the effects of abiotic variation and dispersal limitation (Bar-Massada et al. 2018). While we do not have direct evidence that our study field is homogeneous with respect to abiotic resources, we present soil mapping here for undisturbed plots in an adjacent part of the field located 5 m away (70 plots, 0.5 m diameter). Soil maps illustrate the distribution of soil nitrogen, phosphorus, and moisture (Supplementary material Appendix 1, Fig. A1-1), providing some information about the nature of soil resource variation in our study field. We also include an aerial photograph of the locations of our field and the adjacent mapped field to illustrate their juxtaposition (Supplementary material Appendix 1, Fig. A1-2).

In 2009, we surrounded herbivore exclusion plots with 1 cm gauge fencing that extended approximately 45 cm above ground and 15 cm below ground. We left fencing open on top during growing seasons to allow vertical plant growth and covered them during the winter to prevent small mammals from entering the plots by vertically tunneling through the snowpack. Small mammals are known to eat seedlings of several species in this community; in a separate experiment, over 90% of seedling transplants of six species were eaten (personal observation). Consequently, the purpose of the exclusion treatment was primarily to limit herbivory from small mammals. Thus, co-occurrence patterns in the herbivore exclusion treatments should not be subject to noise from herbivore activity. The community is composed of a total of 39 species, primarily herbaceous perennials, including grasses and sedges, forbs, and nitrogen fixing forbs. Common species include *Poa pratensis*, *Symphotrichum lanceolatum*, *Phalaris arundinacea*, *Lotus corniculatus*, and *Carex pallescens*. A table quantifying mean plot-level abundance of each species can be found in Supplementary material Appendix 2, Tables A2-1 and A2-2.

Data collection

We conducted annual plot censuses from May through September, for three consecutive years (2013-15). During each census, the abundance of each species in each 0.5 m diameter plot was determined through weekly surveys. We conducted weekly surveys of each plot to accurately determine the abundance of species in plots each year and reduce sampling error. This repeated sampling also ensured that we accurately measured abundance for species that flowered early in the season and then died back (e.g., flowering members of *Poa pratensis*). We calculated abundance per plot as the maximum number of rooted units observed per species across weekly surveys. A rooted unit is a unique transition from above-to-belowground tissues (Schamp et al. 2013, Schamp et al. 2016). This measure of abundance allows us to quantify changes in the plot-level abundance of each species across years. For these three years of data, we examined compositional changes during two consecutive biennial periods that represent transitions over two growing seasons (2013-14, 2014-15).

Analysis

We identified significantly co-occurring pairs of species using two methods to test the sensitivity of our results to the pairwise test used. First, we used Veech's pairwise co-occurrence method (Veech 2013), which we executed with the "cooccur" package in R (Griffith et al. 2016, R Core Team 2018). This method employs a probabilistic approach to determine which species pairs co-occur more (positive co-occurrence) or less (negative co-occurrence) often than is likely by chance. Second, we used the randomization method of Sfenthourakis et al. (2004) with the C-Score co-occurrence metric (Stone and Roberts 1990) to assess pairwise co-occurrence. For each species pair, we tested whether observed co-occurrence patterns are more extreme than would be expected when the community matrix is shuffled using the fixed-fixed swap algorithm with 5000 matrices per null distribution, and 30,000 independent swaps per null matrix. If the C-Score was higher than expected under the null model, then the pair was significantly negatively co-occurring, and if the C-Score was smaller than expected, the pair was identified as positively co-occurring. We ran this pairwise test using code developed by M. Lavender in the Scala programming language (Scala 2.11.12). These two pairwise co-occurrence tests performed better than other available pairwise co-occurrence tests in a recent analysis (Lavender et al. 2019). For the first two years of community data (third year co-occurrence would be linked to

subsequent turnover), we independently subjected control and herbivore exclusion plots to these pairwise co-occurrence tests and collected the identities of pairs identified as significantly negatively co-occurring ($\alpha = 0.1$) as well as those identified as positively co-occurring ($\alpha = 0.1$). This cut-off allowed us to examine a reasonable sample size of pairs with a strong tendency towards negative or positive co-occurrence, allowing for the fact that co-occurrence data generally contain noise (Schamp et al. 2016). We chose to compare negatively co-occurring pairs to positively co-occurring pairs rather than comparing negative pairs to any pair that wasn't negatively co-occurring (i.e., random and positively co-occurring pairs). Using positively co-occurring species pairs served two purposes. First, it ensured that these pairs were not simply negatively co-occurring pairs that the two pairwise methods incorrectly categorized due to noise. Second, there is no a priori expectation that competition should result in asymmetric abundance decline for positively co-occurring species pairs.

Importantly, pairs of species that each of our two methods identified as negatively co-occurring were occasionally found growing together in some plots. This was critical for our study because we assumed that if competition was keeping pairs of species apart, logic dictates that when dispersal occasionally brings them together, they should compete. As such, we identified plots where negatively co-occurring pairs of species were found together and determined whether the abundance of one member of a pair declined in that plot in the subsequent year. Incidences of asymmetric abundance decline included the four possible combinations that see one of the two species decline in that plot in the subsequent year (Fig. 1). For a given biennial period, any reduction in abundance by one species in a pair that was not also experienced by the other species was characterized as asymmetric abundance decline.

We focused on asymmetric abundance decline because competition between two species should produce negative co-occurrence patterns as individuals of the inferior competitor are excluded. We also identified plots in which significantly positively co-occurring pairs were found together and again determined the frequency of asymmetric abundance decline for these pairs across two biennial periods. Each significantly co-occurring pair found in a given plot represents the independent observational unit we considered in our analyses. Because some species were involved in multiple co-occurrences within a given plot, we randomly selected independent instances of these pairs in plots such that no species was involved in more than one pair per

plot. Multiple pairs from a given plot could be included in this random selection as long as they were independent. For example, if a plot contained two significantly co-occurring pairs that spanned three species (i.e., Species 1 and 2, as well as Species 2 and 3), only one pair in that plot could be selected to ensure sample independence. A particular species pair that significantly co-occurred (e.g., Species 1 and 2), could be selected from multiple plots where they were found together. For example, in the herbivore exclusion treatment for the first biennial period, there were 184 instances in which significantly co-occurring pairs of species (both positive and negative) were found together in at least one of our 75 plots. Random selection to ensure independence allowed us to select 122 of those instances for analysis (66.3%). Because this selection process, although random, is subject to sampling error, we performed the selection 25 times to examine the sensitivity of our results to this sampling process.

To test whether negatively co-occurring pairs of species experienced more asymmetric abundance decline than did positively co-occurring pairs, we used a generalized linear mixed model with asymmetric abundance decline (yes/no) as the binomial dependent variable. These tests examined the influence of co-occurrence of the focal pair (negative/positive), while accounting for treatment (control/herbivore exclusion), biennial period (1st/2nd), as well as conflicting co-occurrence patterns. Conflicting patterns occur when a species that is part of a negatively co-occurring pair in a plot is also part of a positively co-occurring pair in that same plot, or vice versa. The conflicting pair was not included in the analysis – to ensure independence – but a conflict variable (conflict present/conflict absent) was included to understand whether this influenced our results. Some species pairs were more commonly represented in analyses; for this reason, species pair was included as a random effect within these analyses. These models were run for each of the 25 replicates resulting from our two co-occurrence methods (50 models in total). Models were run using the `glmer` function in the `lme4` package for R (Bates et al. 2015, R Core Team 2018).

To explore compositional differences between our two treatments (control and enclosure), we compared them in terms of several measures of community structure. We compared treatments with respect to plot species richness and evenness, (E_{var} ; Smith and Wilson 1996) using t -tests, and we tested whether the treatments were different with respect to composition using Bray-Curtis dissimilarity in combination with a PERMANOVA using the `adonis` function within the `vegan` package in R (Oksanen et

al. 2017, R Core Team 2018). Species richness and how evenly species are distributed across samples are particularly relevant here because differences in these characteristics can impact co-occurrence tests (Schamp et al. 2015, 2016).

Results

Both pairwise co-occurrence tests found positively and negatively co-occurring pairs of species in both control and herbivore exclusion; however, the pairwise method of Sfenthourakis et al. (2004) generally identified slightly more pairs than did the Veech's probabilistic method (Veech 2013; Table 1). Both pairwise methods also revealed more pairs in control plots than in herbivore exclusion plots (Table 1). A summary of the number of positive and negative pairings each of the two pairwise methods identified for each species in each treatment and biennial period can be found in Supplementary material Appendix 3, Table A3-1.

Binomial mixed models revealed no evidence that negatively co-occurring species pairs experience significantly more asymmetric abundance decline (model result for one replicate in Table 1; model results for all replicates for both pairwise methods are presented in Supplementary material Appendix 4). Negatively co-occurring species pairs, when found growing together, were no more likely to experience asymmetric abundance decline than were positively co-occurring pairs of species across our two treatments or biennial periods (Table 1 and Supplementary material Appendix 4). The presence of conflicting co-occurrence patterns did not significantly influence asymmetric abundance decline (Table 2). Mean asymmetric decline in relation to co-occurrence across treatments and our two biennial periods, for both co-occurrence methods, is visualized graphically in Fig. 2.

There was no difference in mean plot species richness or evenness (E_{var}) between control and herbivore exclusion treatments in any of the three growing seasons (t -tests, $DF = 148$, all $p > 0.05$). Finally, treatments differed significantly in composition in the third year (2015: PERMANOVA, 999 permutations, $DF = 1$, $p = 0.023$), but differed only at $\alpha = 0.1$ for the first two years (2013: $p = 0.069$; 2014: $p = 0.088$).

Discussion

We explored the long-standing question of whether patterns of negative species co-occurrence are influenced by competition (e.g., Diamond 1975, Connor and Simberloff 1979, Gotelli and McCabe 2002). Specifically, we examined whether negatively co-occurring species pairs experienced asymmetric abundance decline during biennial periods, in plots

where they were found growing together in the first year of the period. We compared this to the proportion of positively co-occurring species that experienced asymmetric abundance decline to determine if competitive exclusion was more common for negatively co-occurring species pairs. Using binomial mixed-models, we found no evidence linking asymmetric abundance decline to negative co-occurrence patterns (Table 2). These findings are not consistent with a competitive explanation for negative co-occurrence patterns in this community. Our results contribute to the longstanding debate in the ecological literature concerning whether negative co-occurrence patterns reflect competitive assembly in natural communities (e.g., Diamond 1975, Connor et al. 2013, Korňan and Korňan 2016).

Our results are of particular interest because of the nature of our approach, which differs from previous efforts. As far as we are aware, this is the first time co-occurrence has been examined in relation to changes in species abundance within samples over time. Rather than inferring process from spatial patterns, we tested whether patterns of co-occurrence in a given year were predictive of specific changes in abundance across years. Our focus on small sample plots within a small plant community reduces the likelihood that the influence of competition on co-occurrence patterns was obscured by influences that primarily manifest at larger scales, such as dispersal limitation (D'Amen et al. 2017, Bar-Massada et al. 2018) and substrate variation (Tirado and Pugnaire 2005). As such, if competition were the primary driver of negative co-occurrence patterns and asymmetric abundance decline, this should have been clear in our results. Other researchers have inferred that co-occurrence patterns observed among small-scale vegetation plots are likely explained by species interactions (e.g., Reitalu et al. 2008). Our results do not support this interpretation and suggest that researchers should avoid inferring competition from co-occurrence patterns, even at small scales.

Importantly, our tests identified significantly negatively co-occurring, as well as positively co-occurring species pairs in our focal community. Our results suggest that competition does not drive these patterns, or that other influences overwhelm any impact of competition. As such, the nature of these significant co-occurrences remains unresolved. A number of possible explanations exist. First, it remains possible that small-scale soil heterogeneity is influencing these patterns. While we see this as unlikely given the small scale of our study site, it remains a possibility. While we do not have data to directly address this question, we have relevant data for the adjacent part of the focal field (5 m away;

Supplementary material Appendix 1, Fig. A1-2). We conducted a posthoc analysis on plot data from this adjacent part of the field (70 plots, 50 cm diameter), focusing on those species that were part of significantly co-occurring pairs in our study field. We tested whether plot-level variation in soil nitrogen (nitrate + ammonia), phosphorus, and soil moisture was predictive of variation in the abundance of those species. Species that were part of significantly co-occurring pairs were not responsive to the degree of spatial variation in resources present in the field; details of these analyses can be found in Supplementary material Appendix 5. While this evidence is indirect, it is suggestive that abiotic variation is not driving changes in the abundance of these species, and is therefore unlikely to be driving patterns of negative co-occurrence in our field.

It is also possible that co-occurrence patterns are reflective of changes in climatic conditions across growing seasons that lead to species-specific abundance declines that are unrelated to, or act in concert with, other contributors to co-occurrence patterns. Exploring this will require a data set with plot-level abundance recorded across many years, from which species-specific responses to climatic change can be developed, and then accounted for in further efforts to test for a link between competition and co-occurrence patterns. We have some limited data to address this, including climatic data for five years in our target field. In a post-hoc test, we assessed, again for species that were part of significantly co-occurring pairs, whether abundance varied significantly by year with mean growing season temperature, and mean growing season precipitation (May-Oct in this region). Using Pearson correlations, we found no evidence of a correlation for any of our species. The timeframe examined includes the three years we explored in our main tests, suggesting that during that time, species abundances were not responding to temporal variation in these important abiotic conditions. Analyses are further detailed in Supplementary material Appendix 6, Table A6-1. After correcting for multiple tests using the false discovery rate method (Benjamini and Hochberg 1995), no q-values (adjusted p-values) are less than 0.3 – there is no clear evidence that the abundance of these species are responsive to climatic changes. Our tests also produced no evidence of significant treatment effects on the link between negative co-occurrence and asymmetric abundance decline. Therefore, we conclude that herbivory is not responsible for negative co-occurrence patterns in this system.

A strong candidate for explaining patterns of co-occurrence in this community is local dispersal. In previous work, local dispersal has been identified

both experimentally (Schamp et al. 2015) and using field data (Zalewski and Ulrich 2006, Heino 2013, Schamp et al. 2016) as having the capacity to contribute to co-occurrence patterns. Dispersal can ensure that pairs of species that compete asymmetrically are sometimes found growing together, at least temporarily, until competitive interactions lead to the exclusion of the inferior competitor (Vilá and Weiner 2004, Schamp and Aarssen 2010). Contrastingly, dispersal can also ensure that pairs of positively co-occurring species are sometimes found growing apart, contributing noise to co-occurrence patterns (Schamp et al. 2016). If competitive exclusion proceeds more slowly, it is possible that the impacts of dispersal dominate, filling gaps generated not only by competitive exclusion, but by mortality in general.

Any factor contributing to mortality or instability within the community can influence the relative importance of dispersal in driving compositional changes in plant communities. For example, some species may experience relatively high mortality rates (e.g., Sarukhán and Harper 1973), leaving frequent gaps open for dispersal. Mortality rates will vary with a number of factors. They may be the result of basic population demography or a variety of sources of disturbance. Several other influences on community instability have been observed, including functional diversity (Cadotte et al. 2011, Mason et al. 2013, Laureto et al. 2015), and phylogenetic diversity (Cadotte et al. 2012, Potter and Woodall 2014, Pu et al. 2014). So while competitive exclusion itself opens up vegetation gaps for dispersal to fill, our results suggest that other contributors to mortality have a stronger impact on asymmetric abundance decline, obscuring any link between competition and co-occurrence patterns (see also Pinto et al. 2014). If asymmetric abundance decline is driven principally by factors other than competition, it is clear that negative co-occurrence patterns in our focal community are not shaped by asymmetric competition.

Conclusions

We found no evidence supporting a link between pairwise negative co-occurrence patterns and asymmetric abundance decline, which we expected if competition is the principle driver of these patterns. We also found that positively co-occurring species pairs generally suffered asymmetric abundance decline as much as negatively co-occurring pairs, which suggests that positive co-occurrence may not reflect positive species interactions, at least those that contribute to reduced mortality. We used a methodology and study system that greatly reduced

the likely impact of dispersal limitation, abiotic variation, and herbivory on co-occurrence patterns, which may obscure the relationship between competition and negative co-occurrence. While it does not appear that climatic variation is a significant driver of abundance change in species in this system, this remains a possible explanation for the disconnect between co-occurrence patterns and asymmetric abundance decline across years. Our results suggest that previous assertions that co-occurrence patterns reflect species interactions may not be warranted. Other causes of mortality and asymmetric abundance decline within the community, and subsequent

dispersal into gaps created by this mortality, appear to be more important in driving asymmetric abundance declines. At this time, the driver of abundance decline is unclear – we openly invite readers who may be in possession of long-term data sets with abiotic soil variables and long-term weather data, to contact us to collaborate. Further research should also examine these patterns across systems that differ in productivity and degree of disturbance, to test whether species interactions are related to co-occurrence patterns under specific conditions.

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Tables

Table 1: A summary of the number of significantly co-occurring species pairs that the two pairwise co-occurrence methods identified for each of the two biennial periods considered, and for each treatment.

Biennial Period	Treatment	Sfenthourakis		Veech	
		Negative	Positive	Negative	Positive
2013-2014	Control	21	27	21	20
	Herbivore exclusion	19	14	16	12
2014-2015	Control	12	35	11	24
	Herbivore exclusion	9	23	8	10

Table 2: The results of a binomial mixed effects model (generalized linear model framework) – one of the 25 replicate samples explored for each of the two pairwise co-occurrence methods used. Models test whether variation in asymmetric abundance decline is significantly impacted by co-occurrence pattern (negative vs. positive), treatment (control vs. herbivore enclosure), biennial period (1st vs. 2nd), conflict (whether a member of a given pair of co-occurring species is also part of conflicting co-occurrence patterns in that plot). Models include all interactions and species pair were included as random effects.

Replicate Sample 1 (Veech Pairwise Co-occurrence method)

Fixed effects	Estimate	Z value	P value
Intercept	0.6931	1.132	0.258
Co-occur	-0.6931	-1.063	0.288
Treatment	-0.55	-0.764	0.445
Biennial	-1.3863	-1.013	0.311
Conflict	-1.0296	-1.215	0.224
Co-occur*Conflict	0.822	0.863	0.388
Co-occur*Treatment	0.1332	0.168	0.866
Treatment*Conflict	0.5988	0.498	0.618
Co-occur*Biennial	1.118	0.799	0.424
Biennial*Conflict	0.9343	0.59	0.555
Treatment*Biennial	1.3973	0.916	0.36
Co-occur*Treatment*Conflict	-0.5339	-0.37	0.712
Co-occur*Biennial*Conflict	-0.7461	-0.41	0.682
Co-occur*Treatment*Biennial	-0.6794	-0.427	0.669
Treatment*Biennial*Conflict	-2.044	-1.001	0.317
Co-occur*Treatment*Biennial*Conflict	2.4357	1.01	0.313

Std. Dev. Species Pair = 0

Figure 1: A visual representation of the potential outcomes of asymmetric pairwise competitive interactions. In outcome a, species 1 maintains its initial abundance while species 2 decreases in abundance, or vice versa. In outcome b, species 1 increases in abundance while species 2 decreases in abundance, or vice versa.

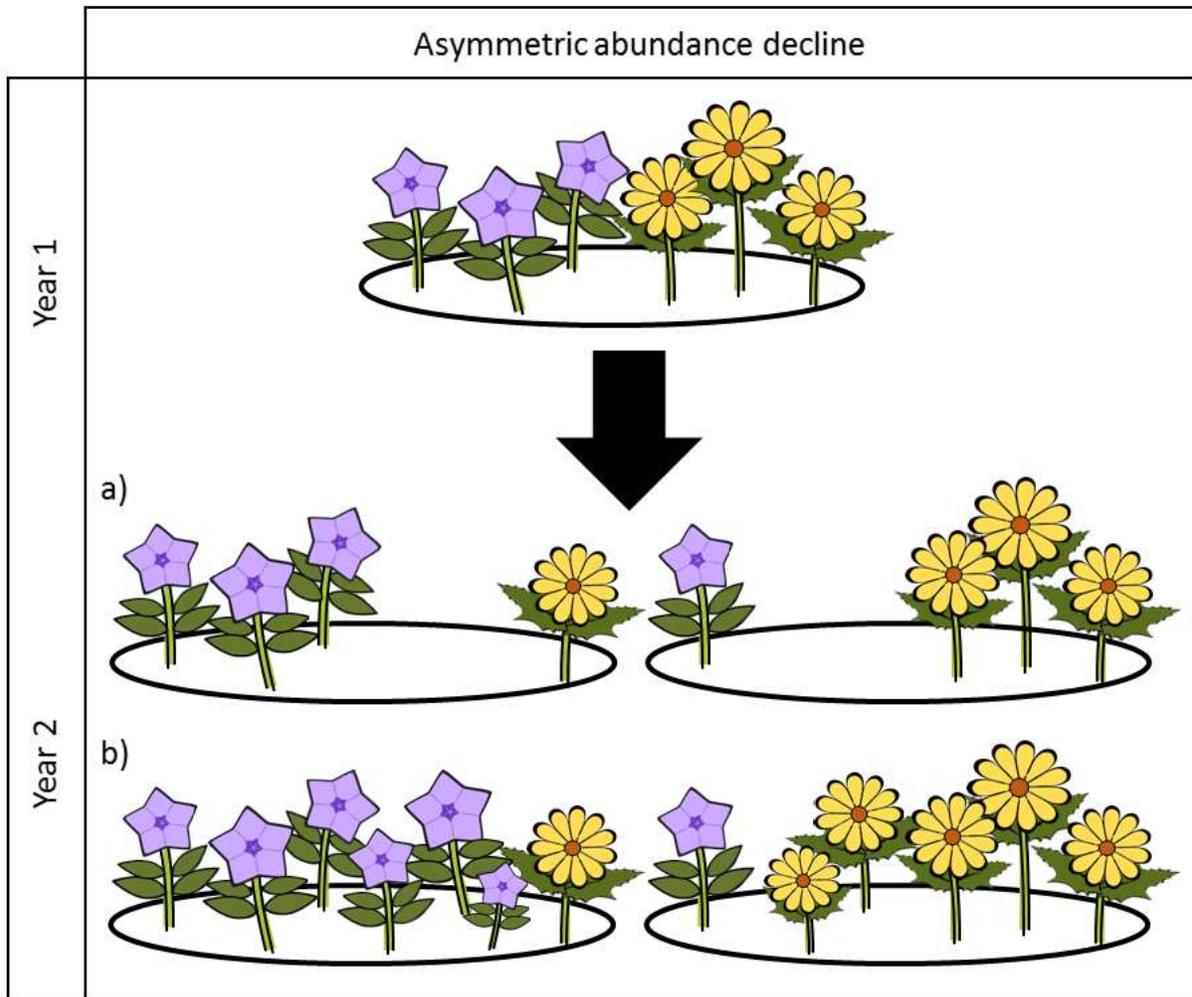


Figure 2: The mean proportion of instances of pairwise asymmetric abundance decline for negatively and positively co-occurring species pairs in control and herbivore exclusion treatments from 25 random samples of co-occurring pairs in plots. Proportions for co-occurring pairs identified by the randomization method of Sfenthourakis et al. (2004) are given by grey bars, and proportions for pairs identified by the probabilistic approach of Veech (2013) are given by white bars. Error bars indicate standard error. Panels (a) and (b) compare the proportions observed in the 2013-14 biennial period, panels (c) and (d) compare the proportions observed in the 2014-15 biennial period.

