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Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences

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Abstract. Intransitive competition is often projected to be a widespread mechanism of species coexistence in ecological communities. However, it is unknown how much of the coexistence we observe in nature results from this mechanism when species interactions are also stabilized by pairwise niche differences. We combined field-parameterized models of competition among 18 annual plant species with tools from network theory to quantify the prevalence of intransitive competitive relationships. We then analyzed the predicted outcome of competitive interactions with and without pairwise niche differences. Intransitive competition was found for just 15–19% of the 816 possible triplets, and this mechanism was never sufficient to stabilize the coexistence of the triplet when the pair-wise niche differences between competitors were removed. Of the transitive and intransitive triplets, only four were predicted to coexist and these were more similar in multidimensional trait space defined by 11 functional traits than non-coexisting triplets. Our results argue that intransitive competition may be less frequent than recently posed, and that even when it does operate, pairwise niche differences may be key to possible coexistence.

Key words: *California grasslands; competitive networks; functional traits; intransitive competition; rock-paper-scissors dynamics; stabilizing processes; trait dispersion patterns.*

INTRODUCTION

Ecologists have long attributed the maintenance of species diversity to the stabilizing effect of niche differences. Differences in phenology, resource uptake and efficiency, or pathogen pressure have all been shown to reduce the likelihood of competitive exclusion by causing intraspecific competition to exceed interspecific competition (MacArthur and Levins 1967, Angert et al. 2009, Kraft et al. 2015, Parker et al. 2015). The demographic mechanisms by which niche differences promote diversity (i.e., growth rate advantage when species are at low relative abundance) are well understood for species pairs (Chesson 2000, Adler et al. 2007). However, in natural communities, species interact with many others simultaneously. This fact has led research over the last decade to explicitly consider the mechanisms of species coexistence that only arise when species are embedded

within a larger network of competitive interactions (e.g., Kerr et al. 2002, Reichenbach et al. 2007, Castillo et al. 2010, Allesina and Levine 2011, Metlen et al. 2013, Soliveres et al. 2015, Ehlers et al. 2016).

Under diffuse competition, competition by a constellation of species, the structure of interactions within a network determines the opportunities for coexistence (Fig. 1; Case 1990). The simplest competitive network, that with three species, can be arranged in several ways. If all species compete for single limiting resource, generating a simple competitive hierarchy (Fig. 1a), species will have indirect benefits on one another via the suppression of shared competitors (Miller 1994). However, the net effect of the superior on the inferior should still be negative if its suppressive effect on the inferior outweighs the indirect benefit of a lower density intermediate competitor. A different outcome emerges when species are still hierarchically arranged, but the superior has little effect on the inferior (due to competition for different resources, for example; Fig. 1b). Now, the superior can have a net positive effect on the inferior via the

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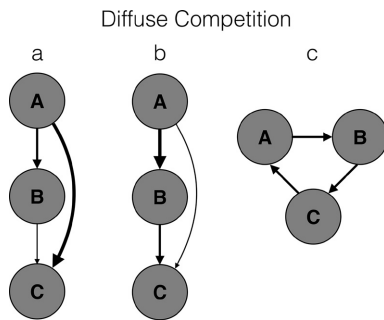


FIG. 1. Three examples showing the architecture of species interactions under diffuse competition. (a) Indirect effects of species A on C can mitigate the competitive effect species B on C, and under certain conditions, (b) generate a net positive effect of A on C. (c) Intransitive competition (right side) is a particular case of indirect competitive effects where there is no universally weak or universally strong competitor species. Arrow width shows the strength of competitive dominance of the superior over the inferior (to which the arrow head points).

suppression of the intermediate competitor, an effect strong enough to determine the persistence of the inferior (Levine 1976). A final and well-studied case emerges when there is no longer a transitive competitive hierarchy (Fig. 1c). With such intransitive networks of competitors, the maintenance of diversity can be achieved in a way analogous to the game of rock-paper-scissors: species A excludes B, B excludes C, but C excludes A (Fig. 1c; Gilpin 1975, May and Leonard 1975).

Many theoretical studies have explored how intransitive competition benefits diversity maintenance (Huisman et al. 2001, Laird and Schamp 2006, Reichenbach et al. 2007, Allesina and Levine 2011), but empirical support for this coexistence mechanism is sparse. Rock-paper-scissor games have been noted in evolutionary and laboratory contexts (Jackson and Buss 1975, Sinervo and Lively 1996, Kerr et al. 2002, Lankau and Strauss 2007). Meanwhile, field studies have inferred intransitive competition from co-occurring patterns (Ulrich et al. 2014, Soliveres et al. 2015). However, because these approaches assume intransitive competition is the only mechanism maintaining diversity, they cannot be used to evaluate its empirical prevalence. As a consequence, ecologists lack a clear understanding of the prevalence and importance of intransitive competition in nature.

One limitation of past empirical and theoretical work on intransitive competition is its emphasis on the effects of intransitivity in isolation of pairwise mechanisms that can stabilize coexistence. Yet, real ecological communities are composed of species with pairwise niche differences, driven for example, by species differences resource limitation, and susceptibility to stress, pathogens, and herbivores (Pianka 1974, McKane et al. 2002, Borer et al. 2007, Harpole and Tilman 2007, Levine and HilleRisLambers 2009). Thus, rather than independently studying the effects of indirect competitive effects, intransitive competition, and pairwise niche differences in promoting diversity, we believe great progress can be made

by exploring how these three mechanisms interact in nature. Progress, however, requires overcoming two hurdles. First, one needs the full matrix of interactions within a diverse guild of competitors. Few field systems present the opportunity to feasibly obtain such information. Second, we require methods that disentangle the individual and combined effects of pairwise niche differences and intransitive competition on coexistence.

Due to the logistical challenges of estimating all competitive interactions in a diverse network, trait-based approaches may provide a valuable alternative to directly measuring all interactions. However, we lack clear expectations for how trait differences relate to pairwise niche differences, indirect competitive effects and intransitive competition. Under “rock-paper-scissors” intransitive competition, each of the component species must differ from one another along different trait axes to generate the competitive imbalances necessary for the operation of the mechanism (Allesina and Levine 2011). We might therefore expect trait dissimilarity to promote coexistence via intransitive competition. A similar prediction comes from classic theory where pairwise niche differences that stabilize coexistence arise from the functional trait differences between the competitors (Cavender-Bares et al. 2004). Alternatively, trait similarity among the coexisting species in a competitive network might be expected if large trait differences increase the chance that one species will be a competitive dominant against all others, and therefore break the symmetry necessary for coexistence in intransitive loops. If the measured functional traits are most associated with niche differences and intransitive competition, we might expect more trait dissimilarity among species in coexisting vs. non-coexisting competitive networks; alternatively, if the measured traits are most associated with competitive fitness differences along a single axis of dominance, then we might expect trait similarity in the coexisting triplets.

Here, we test how empirically measured competitive networks determine species coexistence in an annual plant community, focusing on three questions: (1) What is the prevalence of transitive vs. intransitive competition? (2) What is the role of intransitive competition in promoting coexistence in the presence and absence of pairwise stabilizing niche differences? (3) How do these interactions relate to trait dispersion patterns?

To address these questions, we field parameterized a plant-competition model for 18 annual California grassland species by quantifying species’ vital rates and interaction coefficients. We then used these parameters to estimate the network of competitive dominance between all species pairs (Question 1). We next predicted the competitive outcome for all combinations of three species (the simplest multispecies “network”), four species, five species, etc., in models that allowed for pairwise niche differences between species and simpler models that set niche differences to zero (Question 2). Finally, we quantified the dispersion of the coexisting and non-coexisting triplets in multidimensional trait space defined by 11

functional plant traits associated with variation in leaves, root, seeds, and whole plant characteristics (Question 3).

METHODS

Experimental quantification of niche and fitness differences between species pairs

In 2011–2012, we conducted a field experiment with 18 annual plant species in a grassland in Santa Barbara County, California, USA to field-parameterize a mathematical model of competition. The climate is Mediterranean with cold wet winters (298 mm in the study year) and hot dry summers. The competitive dynamics of a community of annual plant species can be modeled as follows:

$$N_{i,t+1} = (1 - g_i)s_i N_{i,t} + \frac{\lambda_i g_i N_{i,t}}{1 + \sum_{j=1}^S \alpha_{ij} g_j N_{j,t}} \quad (1)$$

where $N_{i,t}$ is the number of individuals of species i in year t , and λ_i is the per individual seed production in the absence of neighbors, g_i is the germination rate, and s_i is the survival of seeds in the seed bank. The decline in population growth due to neighbors is described by the term in the denominator, where α_{ij} is the per capita effect of a germinant of species j on the seed production of a germinant of species i (the summation includes the intraspecific interaction as well). All parameters were estimated in field plots in which each focal species i was sown into a density gradient (2–16 g seed/m²) of each competitor species. Two previous papers give extensive details of the experimental set up, estimation of species' vital rates and interaction coefficients, and formal definitions of niche and fitness differences in this model (Godoy et al. 2014, Kraft et al. 2015). The fitted interaction coefficients and vital rates in these two prior papers are the same as those used here.

Scaling up from species pairs to a network of competition

In past work, we have found that the pairwise niche differences quantified between these competitors are typically insufficient to explain species coexistence (Godoy et al. 2014, Kraft et al. 2015), suggesting a potentially key role for mechanisms that only emerge with more than two species. Therefore, with the empirically estimated vital rates and interaction coefficients, we built a competitive network to assess the frequency of transitive (i.e., species arranged along a competitive hierarchy) vs. intransitive competition (i.e., species arranged in a non-hierarchical loop) among the 18 focal species considered (Question 1). Due the complexity of assessing competitive dominance between to species when they can also coexist via pairwise niche differences, we used several approaches to determine dominance in a pair.

The first approach involved evaluating the competitive fitness differences between all pairs to determine the

superior species in the absence of pairwise niche differences. To do this, following Godoy and Levine (2014), we calculated the competitive fitness difference between species j and i (κ_j/κ_i) as

$$\frac{\kappa_j}{\kappa_i} = \frac{\eta_j - 1}{\eta_i - 1} \frac{\sqrt{\alpha_{ij}\alpha_{ii}}}{\sqrt{\alpha_{ji}\alpha_{jj}}} \quad (2)$$

where η_j is the annual seed production per seed lost from the seed bank due to death or germination ($\lambda_j g_j$)/ $1 - (1 - g_i)s_i$ and α_{ji} and α_{ij} are the per capita effects of a germinant of species i and species j , respectively, on the seed production of a germinant of species j . The species with the higher value of this expression (either κ_j or κ_i) is predicted to displace the other in the absence of pairwise niche differences (Godoy and Levine 2014). A second approach for determining pairwise dominance involved using the equilibrium abundances of the two species (Appendix S1) to assess which persists and which is excluded in pairwise competition. Pairs with an equilibrium where both species have non-zero abundance were simply removed from all subsequent analyses since an intransitive loop based on pairwise competitive exclusion cannot contain pairs of species that coexist in isolation. This approach has the advantage of matching prior theoretical work on how intransitive competition operates (Allesina and Levine 2011).

For each approach, we calculated an adjacency matrix assigning the superior competitor within each pair a value of 1 and the inferior competitor a value of 0 (and coexisting pairs a NA [non available] for the second approach). We then calculated the proportion of transitive and intransitive triplets for all combinations of three species (a total of 816 triplets). We then compared our proportion of intransitivity to that predicted by a binomial distribution when the competitive dominant within a pair is randomly assigned (which generates an expectation of 75% of triplets being transitive and 25% of triplets being intransitive; Shizuka and McDonald 2012).

To assess the combined effect of indirect competitive effects and pairwise niche differences on diversity maintenance within transitive and intransitive networks (Question 2), we algebraically solved for the unique equilibrium species abundances for all combinations of 3, 4, 5, ..., 17, 18 species (a total of 261,972 assemblages). Specifically, we used a matrix inversion approach (Yodzis 1988) applied to the model in Eq. 1 parameterized with the empirically observed vital rates and interaction coefficients. Then, we estimated which of the feasible species assemblages (i.e., assemblages showing positive abundances of all members at equilibrium) were also locally stable by deriving the Jacobian matrix for the annual plant model, and assessing whether the maximal eigenvalue (in absolute value terms) of the Jacobian was less than one (Appendix S1).

In addition, we repeated the analysis of predicted equilibrium abundances and local stability for all assemblages, but this time modified the interaction coefficients

to remove pairwise stabilizing niche differences. We did so following the methodology of Chu and Adler (2015), which involves rescaling the two interspecific competition coefficients for each pair with the inverse of niche overlap ($\sqrt{\frac{\alpha_{ij} \cdot \alpha_{ji}}{\alpha_{ij} \alpha_{ji}}}$). The result of this rescaling is that no two species can coexist with one another in isolation (as the pairwise niche difference = 0), yet their pairwise competitive imbalance (fitness difference) matches that parameterized from the experimental data.

Finally, we evaluated whether the number of feasible and locally stable species assemblages obtained with our field-parametrized demography and competition data was significantly greater or less than expected by chance. Specifically, we randomized the matrix of interaction coefficients estimated from field observations 999 times, including both the intra- and interspecific interaction coefficients as these did not differ in magnitude. After each randomization, we calculated the number of species assemblages that were both feasible and stable. The distribution of this number was then compared to the actual number of feasible and stable triplets based on the observed arrangement of interaction coefficients in our data.

Species functional traits and multidimensional assembly analysis

Eleven plant functional traits were measured on replicate individuals of each species (Appendix S2), as detailed in Kraft et al. (2015). Given this information, we followed several steps to assess how the multidimensional trait space occupied by the species in each network related to the likelihood of their coexistence (Question 3). First, we ran a principal component analysis to condense trait information into a reduced set of unrelated axes using the Kaiser-Guttman criterion (Yeomans and Golder 1982). This criterion selected the first five principal component axes, which accounted for the 84.31% of the trait variance (Appendix S2); this number of axes is comparable to that identified in other studies (Blonder et al. 2014). We then used the species scores for these five axes to characterize the multidimensional trait space occupied by each network.

Because most of the networks with predicted coexistence were composed of just three species (see *Results*), we computed three measures of triangle centrality to describe the multidimensional trait dispersion of the three species. Specifically, we computed distance to centroid as the average Euclidian distance from each species of the triangle (vertex) to the triangle centroid, triangle area as the Euclidian area in our multidimensional trait space delimited by the three species (vertices), and triangle length as the sum of the three sides of the triangle. Finally, we ran a permutation test and a bootstrap analysis to statistically evaluate whether each of these three metrics differed between coexisting and non-coexisting triplets. All analyses were conducted in R (version 3.3.1) (R Development Core Team 2016).

RESULTS

We found that intransitive competition was not prevalent in our system. Of 816 possible triplets, only 126 (15.44%) showed intransitivity based on the pairwise fitness differences, a proportion significantly less than expected if competitive dominance were randomly assigned to each pair ($P < 0.0001$). If we instead used predicted competitive exclusion to build the competitive network (excluding all triplets with pairs that coexist in isolation), 18.93% of triplets proved intransitive. This percentage was also significantly less ($P = 0.0002$) than expected if randomly assigning pairwise dominance.

The proportion of triplets with positive equilibrium abundances of all three species (termed “feasible”) did not significantly differ between the transitive and intransitive triplets ($df = 1, \chi^2 = 0.68, P = 0.411$). Specifically, three of the 126 intransitive triplets (2.38%) and seven of the 690 transitive triplets (1.01%) produced a feasible equilibrium. Three quadruplets were also predicted to be feasible, but for 5, 6, 7, ..., 17, 18 species assemblages, we never predicted an equilibrium with all members at positive abundance. Of the quadruplets predicted to coexist, two of them showed transitive competition and one showed a mixture of transitive and intransitive competition. In all, just 13 assemblages of species out of a possible 261,972 combinations (0.0046%) from 3 to 18 species were predicted to have a feasible equilibrium. Moreover, of these 13 assemblages, only four possessed a locally stable equilibrium, and only one of these four possessed an intransitive loop. This low degree of predicted coexistence found for our system was significantly less than that found when the observed interaction coefficients were randomized across the species pairs (Appendix S3). When we used a simpler model of competition that removed the stabilizing effect of pairwise niche differences, we never found an assemblage with a feasible equilibrium. Thus, the presence of pairwise niche differences in both transitive and intransitive triplets proved key to predicted coexistence in the multispecies assemblages (Fig. 2).

Finally, we found that the four triplets with a feasible and stable equilibrium were significantly more clustered in multidimensional trait space than would be expected by 999 random draws of four triplets from the total pool of 816. Specifically, clustering (a mean dispersion value falling within the lower 5% of dispersion values obtained from the random draws) was significant for triangle area (mean = 3.47, 95% CI = 3.70–9.38) and length of sides (mean = 10.04, 95% CI = 10.15–14.66) and non-significant for average distance to the centroid (mean = 1.61, 95% CI = 1.58–2.79).

DISCUSSION

Sparse empirical evidence that pairwise niche differences explain multispecies coexistence has motivated many ecologists to suggest that intransitive competition may contribute significantly to the maintenance of species diversity (Laird

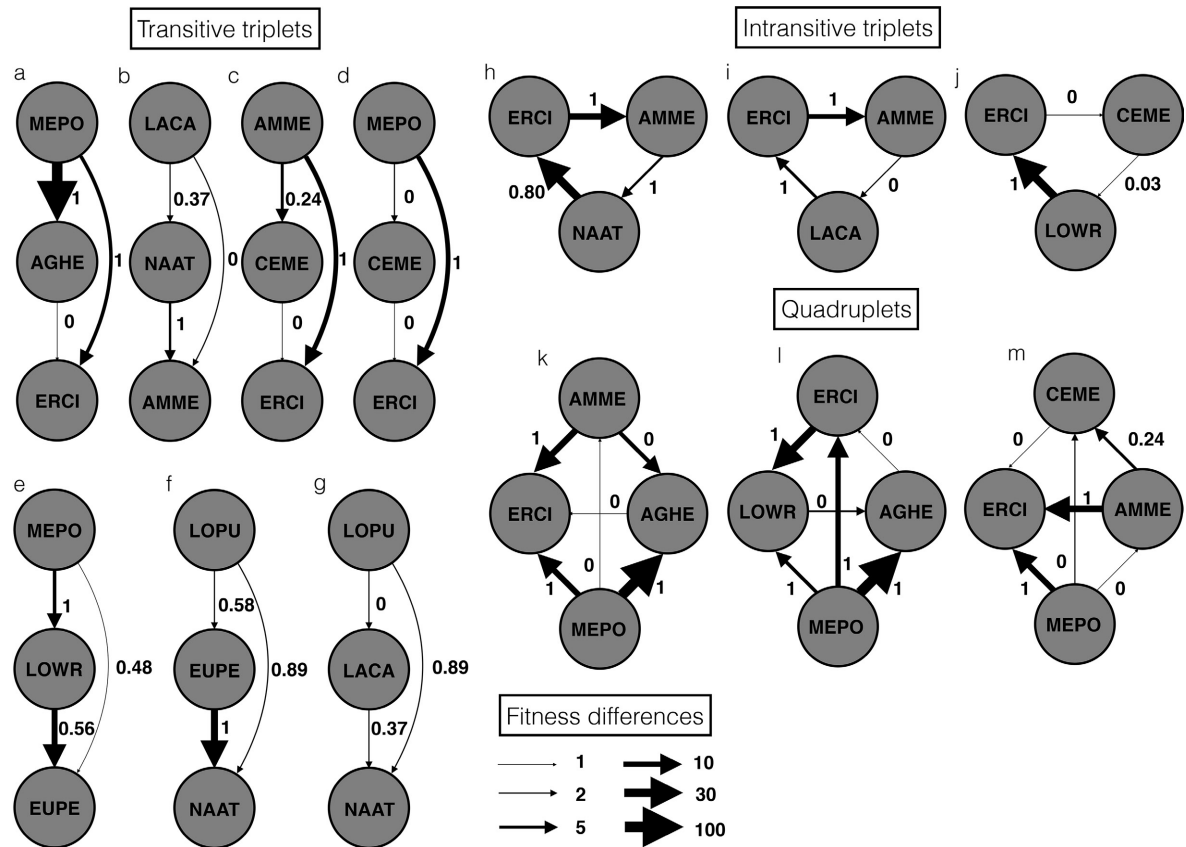


Fig. 2. Illustration of the 10 triplets (7 transitive and 3 intransitive) and 3 quadruplets that produce a feasible equilibrium. Of the 13 feasible assemblages, only 3 transitive triplets (cases c, e, and f), and 1 intransitive triplet (case h) have a locally stable equilibrium. Note that some quadruplets can contain transitive and intransitive competitive relationships simultaneously: in case (l), ERCI outcompetes LOWR, LOWR outcompetes AGHE, AGHE outcompetes ERCI, and these three species shared a common dominant competitor (MEPO). Black arrows denote the magnitude of fitness differences, and the pairwise niche differences (between 0 and 1) are provided numerically for each species pair. Species codes are AGHE (*Agoseris heterophylla*), AMME (*Amsinckia menziesii*), CEME (*Centaurea melitensis*), ERCI (*Erodium cicutarium*), EUPE (*Euphorbia peplus*), LACA (*Lasthenia californica*), LOPU (*Lotus purshianus*), LOWR (*Lotus wrangelianus*), MEPO (*Medicago polymorpha*), and NAAT (*Navarretia atractyloides*).

and Schamp 2006, Allesina and Levine 2011). Yet, few empirical studies have amassed the field data necessary to rigorously quantify the competitive dynamics between the many species pairs found in diverse communities. In one of the first studies to do so, we found modest prevalence of intransitive competition, between 15% and 19% of all triplets in our annual plant community, depending on the method for determining pairwise competitive dominance. Moreover, only one of these intransitive triplets possessed a feasible and locally stable equilibrium, and this was only true with the inclusion of pairwise niche differences (simulation also showed no coexistence, cyclical or otherwise). Our results therefore suggest a limited role for intransitive competition in maintaining species diversity in our system.

Prevalence and importance of intransitive competition in natural communities

Whether less than 20% of triplets showing intransitivity, as found here, should be considered a high or low value is unclear. Although this percentage is less than one

would expect under randomly assigned pairwise competitive dominance (Shizuka and McDonald 2012), whether random assignment of competitive dominance provides a good null expectation is debatable. Moreover, while the observed 15–19% of triplets exhibiting intransitivity is more than Shipley (1993) finds in his review of experiments conducted largely in the greenhouse, it is seemingly less than would be suggested by the important role for intransitivity in grasslands and drylands suggested by Soliveres et al. (2015). Nonetheless, beyond case studies of intransitivity in an individual triplet (e.g., Kerr et al. 2002, Lankau and Strauss 2007, Reichenbach et al. 2007), there are almost no comprehensive field studies directly quantifying the numerous pairwise competitive interactions necessary to properly evaluate the prevalence of this process in nature.

Separate from the prevalence of intransitive competition is whether it strongly promotes species diversity in natural systems, as previous theoretical and observational work suggest (Kerr et al. 2002, Laird and Schamp 2006, Vandermeer and Yitbarek 2012, Soliveres et al. 2015).

Results found here suggest that intransitive competition effects on coexistence are weaker than commonly posed. We believe the major difference between our empirical results suggesting a limited role for intransitivity and the more optimistic suggestions of theory relate to the unevenness of competitive dominance in empirical intransitive networks. Intransitive competition is most stabilizing when each of the species pairs shows comparable competitive dominance (A beats B to the same extent as B beats C, and C beats A). However, with our empirically measured competitive interactions, the degree of competitive dominance differed considerably among the pairs composing each triplet. The pairwise fitness differences (the Eq. 2 values) ranged from a minimum of 1.03 to a maximum of $64,876.69 \pm 6,839.55$ (mean \pm SD). This variation should counteract the stabilizing effect of the intransitivity (May and Leonard 1975). More generally, our results suggest that rather than viewing networks as transitive or intransitive, it may be fruitful to consider how balanced are the pairwise competitive dominances that make up a given network (see examples of this balance in Fig. 2).

Our results are seemingly at odds with recent suggestions of widespread and important intransitivity in natural communities (Soliveres et al. 2015). However, rather than directly measuring intransitivity from an empirically measured network of competitive interactions, these prior studies infer the intransitive competition from observed abundance patterns following the assumptions of low spatial environmental heterogeneity and density-independent probabilities of species replacement (Ulrich et al. 2014). While the underlying mechanics of this approach are elegant and the geographic scope of the work impressive, these studies should not be interpreted as evidence for the prevalence of intransitivity because the inferred competition matrix does not allow for pairwise niche differences, and therefore intransitivity is not compared to alternative explanations for controls over abundance. Our approach, which directly measures the pairwise niche differences and then overlays the competitive network should give a better estimate of the prevalence and importance of intransitive competition on species coexistence compared to pairwise mechanisms.

Assembly of competitive networks in multidimensional trait space

As laid out in the introduction, trait differences are required for both pairwise niche differences and intransitive competitive loops, and thus we might expect coexisting triplets to contain species more different from one another in multivariate trait space than those in triplets that fail to generate coexistence. Instead we found modest evidence that the four triplets predicted to coexist from our models (a feasible and locally stable equilibrium) were more functionally similar than the triplets not predicted to coexist. This result would be expected if species trait differences predicted the fitness differences that drive competitive dominance more than pairwise niche

differences. Unfortunately, the small number of coexisting triplets and only one with intransitive competitive loops did not allow us to test for significant differences in trait dispersion between triplets showing transitive vs. intransitive competition. One avenue for future research involves better characterizing how the multidimensional trait space in which species are embedded relates to the arrangement of interactions in a competitive network.

Limitations

One limitation of our work is that we assume that the interactions between species are fundamentally pairwise. In our framework, the outcome of competition between two species can be affected by the presence of a third species through effects it has on the abundance of the first two, but not through changes in their per capita effects on one another. Such “higher order interactions” have great potential to alter coexistence dynamics (Bailey et al. 2016), but quantifying them in empirical systems is prohibitively challenging (but see Ehlers et al. 2016 for a three-species system). A second limitation is that our approach is phenomenological and therefore we can not determine the mechanistic drivers of the limited intransitivity we found.

Finally, our approach does not measure coexistence, but instead predicts coexistence based on empirically measured model parameters. Importantly, these parameters are measured during a single year in a rather homogeneous field plot, which limits the number and type of interactions possible between our focal species. In past work, we have argued that this aspect of the study, necessary for practical reasons, likely explains the rarity of even pairwise coexistence in the system (Kraft et al. 2015), but it also may contribute to the rarity of coexistence via intransitive competition for several reasons. First, the greater the number of limiting factors in a system, the more likely it is for intransitive competition to emerge (Huisman et al. 2001, Allesina and Levine 2011). Second, the stronger pairwise niche differences expected with more heterogeneous environments could bolster coexistence not possible with intransitivity alone. Regardless of the causes of infrequent coexistence in the multispecies assemblages, it remains surprising that the observed interaction structure permits even less coexistence than randomizations of the interaction coefficient matrix (Appendix S3).

CONCLUSIONS

Over the last several decades, ecologists have debated whether indirect competitive effects provide important mechanisms for the maintenance of species diversity (Pianka 1974, May and Leonard 1975, Shipley 1993, Kerr et al. 2002, Laird and Schamp 2006, Allesina and Levine 2011, Soliveres et al. 2015). Nevertheless, empirical progress has been limited by the availability of experimental data and mathematical approaches that allow one

to quantify the prevalence and importance of intransitive competition in natural communities. In our study, we found only a modest prevalence of intransitive competitive, and more importantly, its presence was never sufficient to generate a prediction of stable coexistence without the stabilizing effects of pairwise niche differences. Finally, although our results suggest that functional traits may be useful for predicting coexistence in competitive networks that combine pairwise niche differences and indirect competitive effects, further studies exploring how traits predict coexistence in competitive networks are needed.

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