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Multi-species interactions in competitive hierarchies: New methods and empirical test

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Abstract

Question: Are competitive hierarchies, which are typically based on the results of pair-wise competition experiments, sensitive to the level of species interaction in the underlying competition experiments?

Location: Controlled greenhouse study using vegetation typical of old-fields in East Tennessee, USA.

Methods: We extend traditional competitive effect/response methods to incorporate data from competition experiments featuring any level of species interaction (i.e., 2, 3,…, *n* species interacting simultaneously) and develop an ordinal technique that makes hierarchies more robust to variation in the numerical values of relative yield. We apply these methodological techniques to empirical data from a greenhouse experiment wherein four old-field plant species were grown in pair-wise and tri-wise combination. We also demonstrate how resampling can be used to determine the variability of data and its consequences for development of competitive hierarchies.

Results: Different hierarchies were produced when we used different evaluation methods, different levels of species interaction, and different levels of replication. More acute resampling distributions and wider ranges of target/neighbor scores revealed that higher levels of species interaction lead to more distinct hierarchies.

Conclusions: Hierarchies developed from interactions among subsets of species may inadequately characterize relationships among the full community because of indirect or higher-order interactions within multi-species assemblages. Different evaluation methods can yield different hierarchies, and resampling is an effective tool to determine the sensitivity of resultant hierarchies to the level of replication. In sum, our new methodology can be used to control uncertainty in poorly-replicated experiments.

Keywords: Indirect interaction; Interspecific competition; Old-field species; Resampling; Relative yield.

Abbreviations: AOM = Alternative Ordering Methodology; CE = Competitive effect; CR = Competitive response.

Nomenclature: Terrell (1967); Wofford & Kral (1993).

Introduction

Investigations of interspecific competition within ecological communities have traditionally focused on pair-wise interactions between two potentially competing species (e.g. Volterra 1926). Competitive hierarchies, which seek to rank species according to relative competitive ability, construct rankings based on the outcome of pair-wise competition experiments in which individuals are grown in all possible combinations of species taken two at a time (Keddy 2001). Such hierarchies have been constructed for many biological systems, including sessile invertebrate communities in artificial reefs (Lam 2003), ant communities (Morrison et al. 2000; Gibb & Hochuli 2004), and many types of plant communities (Panetta & Randall 1993; Zamfir & Goldberg 2000; Bigelow & Canham 2002). It has been hypothesized that the results of relatively simple pair-wise competition experiments can be extrapolated to explain competition among members of natural communities (Keddy & Shipley 1989; Shipley & Keddy 1994), making competitive hierarchies useful for gaining insight into the structure and composition of communities (Miller & Werner 1987; Goldberg & Barton 1992).

However, competition among members of ecological communities, especially plants (Keddy & Shipley 1989), is highly local and thus is dependent on the conditions that arise from heterogeneity in many factors. To account for this, studies in plant communities often focus on the effects of abiotic variables on relative competitive ability (Silvertown & Dale 1991; Gurevitch et al. 1990; Goldberg et al. 1999; Novoplansky & Goldberg 2001; Suding & Goldberg 2001). Such studies less often consider how the arrangement of competitors within the immediate neighborhood of an individual may affect competitive performance; for example, individuals in nature often compete with several species simultaneously (Connell 1983; Schoener 1983). Without proper consideration of the determinants of relative competitive ability among individuals, it is difficult to make generalizations about

competition throughout a community (Stoll & Weiner 2000). Consequently, determinations of competitive ability using pair-wise interactions fail to consider localized competitive interactions, which may complicate predictions of the outcome of competitive interactions in more complex communities.

To overcome the limitations of competitive hierarchies developed from pair-wise competition experiments, we developed a new technique to construct competitive hierarchies based on the outcomes of experiments that consider higher order interactions. First, we extended traditional competitive effect/response methods to incorporate higher order interactions mathematically. Second, we implemented a technique to assign ordinality to the interactions between species and rank them accordingly. Both approaches construct competitive hierarchies based on the outcomes of any possible level of competitive interactions that exist in a natural community (i.e. 2, 3,..., *n* species interacting simultaneously), making these approaches more robust to indirect interactions. We tested these methods using an empirical greenhouse experiment with four herbaceous plant species, wherein we compared the competitive hierarchy derived from experiments wherein individuals of three different species were grown in all possible combinations (hereafter referred to as tri-wise competition). Although this study features only a single application of this method to a four-species community, our analytical method is capable of constructing competitive hierarchies for communities of any richness.

In addition, we developed and applied a resampling routine to determine the robustness of the use of mean values in determining relative yields. Although various tests of concordance have been devised to help quantify the differences between hierarchies derived from different methods (Kendall & Gibbons 1990; Zar 1996), the variability of data collected from ecological experiments could potentially cause different ordering methods to yield different hierarchies. Worse, all methods could produce the same hierarchy, even when resampling reveals that a second hierarchy is nearly as dominant. Our use of a resampling method, which is applicable to any ordering methodology that employs relative yield values, is capable of determining whether a single distinct hierarchy exists for a given community. This resampling technique can be used with pair-wise-methodologies such as competitive effect/response rankings, as well as the technique for assessment of higher order interactions presented herein.

Methods

Greenhouse experiment

We conducted a competition experiment in a greenhouse at the University of Tennessee to evaluate the relative competitive abilities of four common old-field species: two grasses, *Dactylis glomerata* and *Festuca pratensis*, and two herbaceous dicots, *Plantago lanceolata* and *Trifolium pratense*. Two weeks after we propagated plants from seed in the greenhouse, we transplanted seedlings into 20 cm diameter pots containing a 1:1 mix of commercial potting medium and field soil collected at a depth of 8-20 cm in a nearby old-field. Experimental treatments consisted of one individual of each species in two-species and three-species polycultures, resulting in six and four planting permutations, respectively ($n = 6$). The control, or monoculture, treatment consisted of a single individual of each species ($n = 6$). We used plastic liners in the monoculture treatment pots to constrain the available soil volume of each plant to that in the corresponding experimental treatments. Limiting the soil resources of plants in control treatments allowed for direct comparison of competitive yields between control and experimental treatments and thereby isolated the effect of density-dependent below-ground competition between plants in experimental treatments.

Pots were watered daily for the first three weeks, and as necessary thereafter to prevent wilting; pots were re-randomized on greenhouse benches on a weekly basis. One month after transplanting we began recording monthly measurements of the maximum height of all plants. We terminated the experiment after 100 days because the incremental change in maximum height measurements slowed and because most plants were entering their reproductive stages. At experiment termination we destructively harvested the plants and recorded above-ground biomass after drying them at 60 °C for 72 hours.

Competitive effect/response

The most basic procedure for constructing competitive hierarchies begins with calculating the relative yield ${}_{b}r_{a}$ of species *a* in pair-wise competition with species *b*, represented mathematically by the equation

$$ {}_{b}r_{a} = \frac{Y_{ab}}{Y_{a}} \qquad (1) $$

where Y_{ab} is the yield of species *a* in competition with species *b* and Y_{a} is the yield of species *a* grown in isolation (Keddy 2001). If ${}_{b}r_{a} > {}_{a}r_{b}$ then species *a* is considered competitively superior to species *b*.

Once the competitive relationship between all pairs of

competing species is established one can rank species in a hierarchical fashion provided two assumptions are met: 1. The competitive relationship between the species in each pair must be asymmetric (*sensu* Keddy & Shipley 1989), which means that the procedure is disrupted when ${}_br_a = {}_ar_b$. 2. A hierarchy only exists when the competitive relationship among species is transitive, in which case the very possible result of ${}_br_a > {}_ar_b$, ${}_cr_b > {}_br_c$, and ${}_ar_c > {}_cr_a$ fails to yield a competitive hierarchy.

The limitations of the basic procedure can be overcome by constructing a relative yield matrix in which ${}_jr_i$ is the entry in row *i*, column *j*. The sum of entries in the *j*th column is the neighbor score for species *j*, which represents the ability of species *j* to affect or suppress the other species in the community (Wilson & Keddy 1986). Likewise, the sum of entries in the *i*th row is the target score for species *i*, which represents the ability of species *i* to withstand the competitive effects of other species in the community (Wilson & Keddy 1986). These scores represent the competitive effect (CE) and competitive response (CR) methods, respectively (Miller & Werner 1987). The advantage of these methods is that the assignment of numerical values to each species allows for evaluation of the entire community on a standardized scale. However, CE and CR methods are typically applied in the case of pair-wise, but not higher-order, interactions.

To extend the CE and CR methods to data from experiments where tri-wise or higher-order interactions are considered, we first define ${}_{bc}r_a$ as the relative yield of species *a* in competition with species *b* and *c*. To isolate the competitive effect of species *b* on species *a* – while also taking into consideration the additive competitive effects of the other species – we introduce a new term, *effective relative yield*, denoted by ${}_bR_a$. The effective relative yield of species *a* in competition with species *b* is defined as the sum of all relative yields of *a* in which species *b* and any other species *x* are present. Although we assume additivity to maintain the simplicity of our approach, particularly for speciose communities, assumptions regarding other competitive interactions (e.g. non-additive, higher-order) could be incorporated in future applications. Mathematically, effective relative yield is represented by the equation

$$ {}_bR_a = \sum_{x \in \{c,d,\ldots\}} {}_{bx}r_a \qquad (2) $$

A relative yield matrix can then be constructed using the effective relative yield values. Target and neighbor scores are calculated in the same fashion as in the previous paragraph. By analogue, this technique can be applied to data from experiments featuring any number of competing species.

Alternative Ordering Methodology

Instead of relying on the precise values of relative yields to construct rankings, we here present the Alternative Ordering Methodology (AOM), which separates species into categories based on their performance relative to their competitors. Whereas the CE and CR methods are based on numerical relationships, AOM emphasizes ordinal relationships. Further, this method is amenable to the use of the effective relative yield values ${}_jR_i$ used to describe relative competitive ability among multiple interacting species.

The first step in ordering the relative competitive ability of all species relies on an ordinal relationship based on effective relative yields. Each species is grouped according to its ordinal index, which is defined by

$$ W_a = \sum_{x \in \{b,c,\ldots\}} {}_xW_a \qquad (3) $$

where the ordinality for species *a* in competition with species *x* is defined by the piecewise function

$$ {}_xW_a = \begin{cases} 1, & {}_xR_a \geq {}_aR_x + \varepsilon \\ 0, & {}_aR_x \geq {}_xR_a + \varepsilon \\ 0.5, & otherwise \end{cases} \qquad (4) $$

The constant ε is a positive value that defines to what extent the relative yields must differ for the species to be regarded as having different relative competitive abilities. Choosing ε = 0 effectively makes AOM and CR equivalent procedures, whereas choosing $\varepsilon > \max\{|{}_iR_j - {}_jR_i|\}$ produces no hierarchies, as every species interaction is deemed a tie. To avoid either of these undesirable outcomes, we recommend choosing a value of ε for which the user is confident that differences in effective relative yield greater than ε reflect differences in competitive ability and not errors in either experimental procedure or data collection. In our demonstration of AOM on experimental data, we chose ε = 0.05.

Groups are then ranked in descending order of ordinal index because this index correlates with competitive superiority. This step is similar to the construction of a CR hierarchy in that one can think of creating a matrix where ${}_jW_i$ replaces each matrix element ${}_jR_i$. In this sense, the ordinal index W_i is a sum across the columns of the matrix, analogous to the target scores produced in the CR method. Also similar to the CR method, assigning values of 1, 0, and 0.5 (Eq. 4) groups species according to the results of pair-wise interactions. However, unlike methods based solely on pair-wise interactions, a defining feature of AOM is that it allows the assignment of equivalences in the event that the difference between effective relative yields is numerically small (i.e. less than ε). By assigning species to groups with equivalent

ordinal indices, AOM reduces the possibility that error in experimental measurements will influence the outcome of the hierarchy.

To further separate species into a transitive ranking, the second step of AOM utilizes magnitudes of effective relative yields to order the ordinally-equivalent species within each group. To accomplish this tie-breaking step, all species are ordered within their respective groups based on their target scores, which are computed in the same manner as in the CR method. The ranking order produced in this manner is both transitive and asymmetric for any set of relative yield values.

Resampling

As described above, relative yield is calculated by using mean yield for polyculture and monoculture treatments. However, using means in the calculation of relative yield ignores variation in replicate polyculture and monoculture experimental units (i.e., experimental and control pots, respectively), including potential losses of experimental units for any reason. Such uncontrolled variability can be constrained by using a resampling technique when calculating relative yield. To explore the potential for resampling relative yield, we subjected data from pair-wise and tri-wise experiments described above to both 'one-replicate' and 'four-replicate' resampling, though any number of replicates could be employed. For an introduction to the use of resampling methods in ecology, see Crowley (1992).

In the one-replicate case each relative yield was produced using single values for both the numerator and denominator. To reduce the effect of variation among experimental units on the outcome of the resampling procedure, relative yields for species *a* and *b* were taken from individuals from the same experimental unit. In addition, for each resampling event the same monoculture yield value was used in the calculation of relative yield for a given species. Similar considerations were used when calculating tri-wise effective relative yields. In the four-replicate case, the mean yield values of four individuals were used in both the numerator and denominator of each relative yield value. The CE, CR and AOM methods were each used to execute 1000 resampling events for both the one- and four-replicate cases using both pair-wise and tri-wise competition data. The result of interest in each set of 1000 resampling events was the frequency distribution of the 24 possible ranking orders.

Results

Hierarchies derived from competition experiments

The CR and AOM methods resulted in the same hierarchies but were different from the hierarchy produced by the CE method (Table 1). For the CR and AOM methods, hierarchies were different when calculations were based on data collected from pair-wise or tri-wise experiments (Table 2). Whatever the method or interaction level, *D. glomerata* was competitively superior to the other species.

Data resampling

Of 24 possible rankings, one-replicate resampling of data collected from pair-wise competition experiments produced 23, 24, and 22 different ranking orders at least once using the CR, CE, and AOM methods, respectively (Fig. 1a). The frequency distribution of ranking orders differed from a uniform distribution ($\chi^2_{CE} = 1027$, $\chi^2_{CR} = 1033$, $\chi^2_{AOM} = 1315$; $P < 0.0001$; Fig. 2) for the one-replicate resampling procedure using the CR, CE, and AOM methods on data collected from pair-wise competition experiments. The most frequently produced ranking was *D>P>F>T*, which was produced 128, 126, and 150 times in 1000 resampling events using the CR, CE, and AOM methods, respectively (Fig. 1a).

Four-replicate resampling of data collected from pair-wise competition experiments produced 8 different ranking orders at least once for all methods (Fig. 1b). The frequency distribution of ranking orders differed from a uniform distribution for the four-replicate resampling procedure using the CR, CE, and AOM methods on data collected from pair-wise competition experiments ($\chi^2_{CE} = 3785$, $\chi^2_{CR} = 3806$, $\chi^2_{AOM} = 4402$; $P < 0.0001$; Fig. 2). The most frequently produced ranking was *D>P>F>T*, which was produced 470, 469, and 399 times in 1000 resampling events using the CR, CE, and AOM methods, respectively (Fig. 1b).

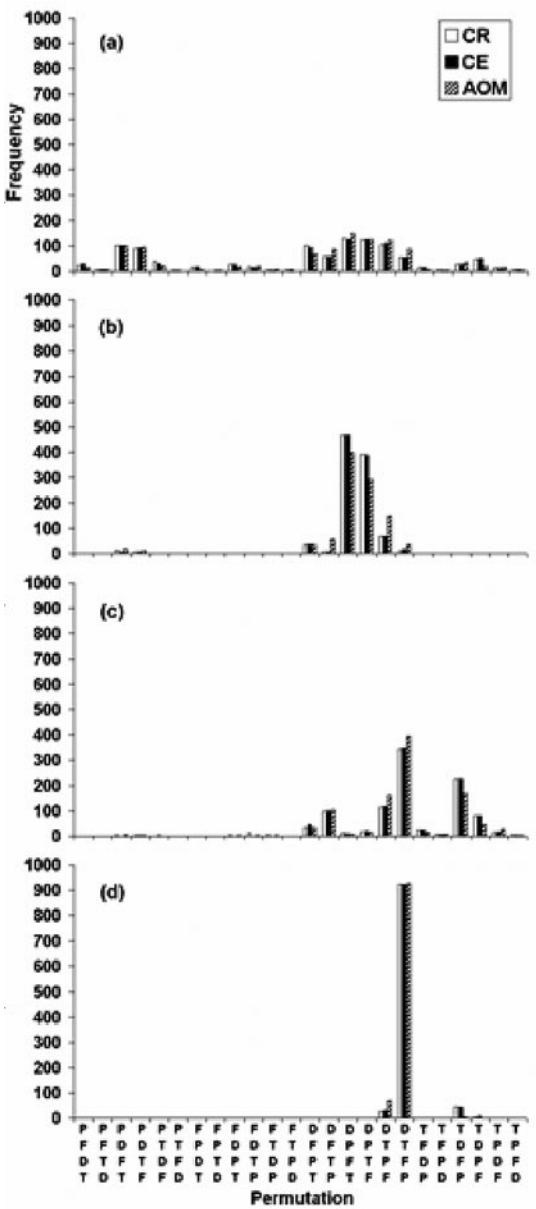
One-replicate resampling of data collected from tri-wise competition experiments produced 20, 15, and 19 different ranking orders at least once using the CR, CE, and AOM methods, respectively (Fig. 1c). The frequency

Table 1. Ranking permutations produced by using competitive response (CR), competitive effect (CE), and alternative ordering methodology (AOM) methods on data from pair-wise and tri-wise competition experiments. Each species is referred to by the first letter of its genus name.

	CR	CE	AOM
Pair-wise	*D > P > T > F*	*D > T > P > F*	*D > P > T > F*
Tri-wise	*D > T > F > P*	*D > T > P > F*	*D > T > F > P*

Table 2. a. Relative yields, target scores (competitive response) and neighbor scores (competitive effect) calculated from pair-wise competition experiments. **b.** Effective relative yields, target neighbor scores calculated from tri-wise competition experiments.

	Trifolium	*Dactylis*	*Festuca*	*Plantago*	Target Score
a.					
Trifolium	1.00	0.38	0.73	0.65	2.77
Dactylis	0.84	1.00	0.78	0.79	3.41
Festuca	0.56	0.38	1.00	0.61	2.56
Plantago	0.66	0.53	0.68	1.00	2.87
Neighbor score	3.05	2.30	3.20	3.06	
b.					
Trifolium	1.00	0.83	1.08	0.92	3.83
Dactylis	1.01	1.00	1.13	0.97	4.11
Festuca	0.59	0.53	1.00	0.61	2.73
Plantago	0.42	0.45	0.48	1.00	2.35
Neighbor score	3.03	2.80	3.69	3.50	



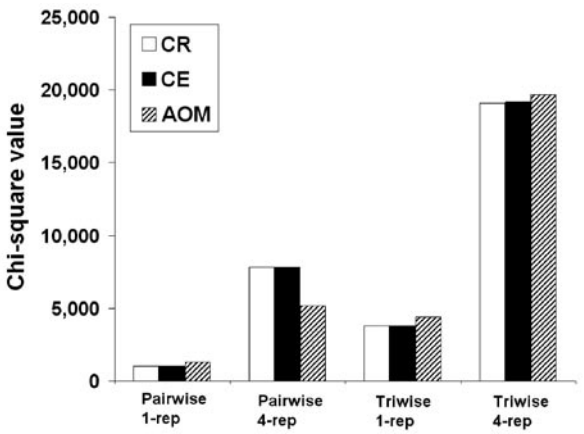


Fig. 2. Test statistic values from χ^2 Goodness of Fit tests to determine whether resampling data were uniformly distributed for pair-wise and tri-wise experiments considering one replicate or four replicates. For all test statistic values, $P < 0.0001$.

Fig. 1. Frequencies of rankings in 1000 resampling events calculated by applying competitive response (CR), competitive effect (CE), and alternative ordering methodology (AOM) methods. Frequencies are reported according to the following data resampling classifications: (**a**) one-replicate and (**b**) four-replicate resampling of data collected from pair-wise competition experiments, (**c**) one-replicate and (**d**) four-replicate resampling of data collected from tri-wise competition experiments. Permutations reflect each possible competitive hierarchy; letters represent initials for each genus.

distribution of ranking order differed from a uniform distribution ($\chi^2_{CE} = 7796$, $\chi^2_{CR} = 7817$, $\chi^2_{AOM} = 5172$; $P < 0.0001$; Fig. 2); the most frequently produced ranking of *D>P>F>T* was produced 344, 349, and 396 times in 1000 resampling events using the CR, CE, and AOM methods, respectively (Fig. 1c).

Four-replicate resampling of data collected from tri-wise competition experiments produced four different ranking orders at least once for all methods (Fig. 1d). The frequency distribution of ranking orders differed from a uniform distribution for each method ($\chi^2_{CE} = 19095$, $\chi^2_{CR} = 19182$, $\chi^2_{AOM} = 19691$; $P < 0.0001$; Fig. 2). The most frequently produced ranking was *D>P>F>T*, which was produced 925, 921, and 926 times in 1000 resampling events using the CR, CE, and AOM methods, respectively (Fig. 1d).

Discussion

Hierarchies from the greenhouse experiment

The results of all ranking procedures indicate that *Dactylis* was competitively superior to the other three species in both pair-wise and tri-wise competition experiments (Table 1). This result held when the numerator and denominator of relative yield was calculated using all replicates, four replicates, or even a single replicate (Fig. 1) and when rankings were based on target or neighbor scores (Table 1). Thus, *Dactylis* seems to defy the classical trade-off between competitive effect and competitive response exhibited by other species (Goldberg 1987; Miller & Werner 1987).

While the ranking for *Dactylis* is unambiguous, it still remains unclear how *Trifolium*, *Festuca*, and *Plantago* fit into the competitive hierarchy. Application of the CE method was consistent in ranking *Trifolium*, *Festuca*, and *Plantago* in descending order after *Dactylis* for both pair-wise and tri-wise competition data (Table 1). CR and AOM, though concordant, yielded different hierarchies than CE and also yielded different hierarchies when utilizing pair-wise and tri-wise data (Table 1). The fact that CR and AOM were in agreement is not surprising because AOM employs the same target scores as CR, although the two methods apply the scores differently as described in the methods.

One possible explanation for differences in the rankings between CE and CR/AOM is that these two groups of methods are based on different measures of competitive ability: CE considers competitive effects exerted by the focal species onto its neighbors, whereas CR/AOM indicate how well species withstand competitive pressure from neighbors (Miller & Werner 1987). Hence, in the case of pair-wise competition, it may be that *Plantago* is better able to withstand competitive pressure than *Trifolium* but that the opposite is true with regard to its ability to suppress performance of its neighbors. Likewise, in the case of tri-wise competition, *Festuca* appears better able to withstand competitive pressure than *Plantago*, and *vice versa* with regard to its ability to suppress performance of its neighbors.

While CR/AOM produced different hierarchies for pair-wise and tri-wise data, the hierarchies produced by CE were consistent across levels of interaction. This result mirrors the observation of Keddy et al. (1994) that hierarchies produced by CE were consistent across environmental treatments, while those produced by CR were not. Although our data offer no insight into a mechanism for this pattern, it remains possible, as Keddy et al. (1994) first noted, that CE may be more robust because of its dependence on species traits, which are invariant across environments or levels of interaction. On the other hand, CR is more likely to be sensitive to abiotic or biotic conditions that influence the amount of stress an organism experiences (and consequently how well it withstands competition).

Replication

Resampling the data from our greenhouse experiment revealed that the frequency distribution among ranking orders was much more tightly centered around a single value (or related set of values) when we used a four-replicate resampling procedure as opposed to sampling only a single datum (Figs. 1 and 2). This finding is intuitive, as single-replicate resampling is analogous to conducting an experiment with only a single replicate. The results of such an experiment are likely to be idiosyncratic and require confirmation by additional replicates. The results of the four-replicate resampling method are therefore better estimates of the mean outcome because they are more robust to the inclusion of outliers.

Although it is preferable to perform experiments with high replication, doing so is not always feasible because of limitations of space or time. Moreover, increasing the number of species (e.g. to better resemble the richness of natural communities) would require additional experimental units. In field situations, the number of replicates may be further constrained by the abundance of a rare species or other factors. The use of AOM as described herein offers a potential solution to the dilemma of limited replication. First, since the addition of replicates will typically lead to mean relative yield values with less variation (as in our greenhouse experiments) and thus greater confidence in the true mean relative yield for each species, one could use a lower value of ε in the execution of AOM, where $\varepsilon \rightarrow 0$ as the number of replicates increases. Conversely, in the more likely situation of low

replication, the value of ε could be increased to account for uncertainty in the mean relative yield for each species, though this will increase the incidence of ties between species, with the possibility that no hierarchy emerges when taken to the extreme. Nonetheless, the freedom to choose and manipulate values of ε gives researchers some alleviation from the problems traditionally faced in studies evaluating competitive hierarchies with low replication.

Level of species interaction

In this study, competitive hierarchies were influenced not only by evaluation method and number of replicates, but also by the level of species interaction (i.e. pair-wise vs. tri-wise competition). These differences were manifest in hierarchies calculated from full-mean relative yield values (Table 1), as well as in the data resampling procedure (Fig. 1). In the resampling procedure, the frequency distribution among ranking orders was much more tightly centered around a single ranking for the resampling of tri-wise data than for the analogous pair data (Figs. 1 and 2). This result suggests that differences with respect to relative competitive ability were more pronounced in tri-wise competition experiments because there was less uncertainty about which hierarchy was most probable. Further, in hierarchies calculated from full mean relative yield values, the range of target scores in tri-wise competition experiments was considerably wider than in pair-wise experiments, as were differences between the target scores of each species in the hierarchy (Table 2). Hence, our results indicate that species may perform differently when faced with different numbers or identities of competing species, and that higher numbers of competing species may result in more distinct differences in relative competitive ability.

One hypothesis as to why different hierarchies emerged from the pair-wise and tri-wise experiments is that indirect species interactions could alter the competitive pressure on the focal species. Indirect interactions occur when the addition of a competitor disproportionately weakens one of the original species, conferring an advantage to the other (Miller 1994). In our greenhouse experiment, the addition of a third competitor in tri-wise experiments in triplets benefited the previously dominant species. While this indicates the presence of negative indirect interactions in our system, positive indirect interactions (e.g. Levine 2000), in which the dominant species is weakened by the addition of more competitors, could also be a mechanism for inconsistencies in competitive hierarchies across levels of species interaction in other communities.

Conclusions

Ranking species according to relative competitive ability has been attempted in many types of communities and appeals to researchers as a way of neatly classifying interspecific competition in complex communities. Contrary to their appeal as a general classification scheme, we demonstrate that different hierarchies are produced when evaluated with different hierarchy evaluation methods, with different levels of replication, and with different numbers of interacting species. Previous work has demonstrated that competitive hierarchies are also sensitive to a number of environmental factors like nutrient levels and disturbance (Grubb 1985; Tilman 1988; Aerts et al. 1990; Keddy et al. 2000; Novoplansky & Goldberg 2001; Tripler et al. 2005) and depend on what type of measure of competitive ability is being considered (Carlyle & Fraser 2006). These results bring into question the usefulness of competitive hierarchies in describing communities but also highlight their potential use in other areas of research, such as investigating how indirect interactions affect competition in complex communities.

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