Predicting community persistence based on different methods of species ranking

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Different species in a community can be ranked according to the strength of their effect on the dynamics of the entire community. Despite a considerable research effort on community structure and the "keystone" species concept, there are still unresolved issues in this area. This work addresses the suitability of different methods of characterising community members, either by relative abundance, or different measures of competitive ability. Multi-species competitive communities were simulated to allow comparison of methods that rank community members by either their abundance or competitive ability. Results indicate that characterising species according to their relative density, rather than competitive ability, provides a more refined measure of the importance of each community member. The analysis is extended by assessing which species are most likely to be involved with cascading extinction events, showing that the species with the lowest abundance is most likely to face extinction. Here it is also shown that removal of the most abundant species, i.e. that with the greatest relative density within the community, leads to the highest probability of community collapse, with further loss of community members through cascading extinctions. The asymmetry and non-linearity of between species interactions mean that species' ranking can change unexpectedly following species loss. These results can lead to practical recommendations in management decisions for conservation and other species management problems, e.g. harvesting in marine food-webs, where it may be difficult to assess relative competitive ability between species in the ecosystem.

Introduction

Studies of community interactions have generated a variety of interesting results. Historically, there has been a divide between the findings of empirical and theoretical studies on the stability of multi-species systems (MacArthur 1955, Elton 1958, Hutchinson 1959, May 1972, Frank & McNaughton 1991, Pimm 1991, Haydon 1994, Putman 1994, Johnson *et al*. 1996, de Grandpre & Bergeron 1997). Theoretical findings have tended to point to a reduction in stability in increasingly complex systems, while empirical work has traditionally suggested the opposite. Recently, however, some models have predicted an increase in stability with increasing complex-

ity (Harding 1999, Borrvall *et al.* 2000, Lehman & Tilman 2000, Rozdilsky & Stone 2001, Fowler & Lindström 2002, Fussman & Heber 2002). Theory that addresses the effects of species number in multispecies assemblages at the population level has generally focused on the indirect effects across different trophic levels (Bender *et al.* 1984, Yodzis 1989, Pimm 1991). More recently, Abrams (1996) reviewed the opportunity for evolutionary change to arise following alteration in food webs (species insertion or deletion), predicting major differences in population-level processes through effects on traits of other species, while Wilmers *et al.* (2002) showed that simulated ecological species assembly processes can result in patterns of co-existence that show reduced community variation with increasing complexity. What is of undoubted importance in studies such as these, and their practical implications, is the ability to assess the importance of each species in their respective assemblages.

A keystone species is a species with a disproportionately large influence on some specific community trait, e.g. species diversity or biomass (Paine 1966, Menge 1995, Gaston 1996, Power *et al.* 1996). The idea of keystone species is also related to the notion of ecosystem or community engineers, i.e. species that influence, for example, either habitat structure or nutrient flow such that other species are greatly affected (Lawton 1994, Coleman & Williams 2002, Reichman & Seablom 2002). Generally the keystone concept hinges on the assumption (and at times observation) that interspecific interactions in the community are reasonably strong, at least between the keystone species and other community members. That is why, for example, model communities where interaction strength can be specifically modified may produce strong cascading effects on different community traits. Such cascades can be either trophic cascades (indirect effects across trophic levels) or extinction cascades; the removal of one species is accompanied by additional extinctions from the community (e.g. Borrvall *et al.* 2000, Lundberg *et al.* 2000, Fowler & Lindström 2002, Wilson *et al.* 2003, Wilson & Lundberg 2004). Cascading extinctions are difficult to detect in natural systems. It either requires large-scale and long-term experimental manipulations, or, when such

manipulations are not possible, control for other changes than solely the loss of a particular species. Therefore, extinction cascades have largely remained a theoretical construct, with some notable exceptions (Paine 1966, Fritts & Rodda 1998, Berger *et al.* 2001, Carr *et al.* 2002, Pauly *et al.* 2002). Previous works on extinction cascades have generally only paid attention to the identity of the species responsible for cascades. One exception is Borrvall *et al.* (2000), who looked at food webs properties that influenced the risk of cascading extinctions.

In the present study, I address the question of cascading extinction events in a competitive community by systematically removing species from a community, and compare the effects of defining those community members by either their relative density (abundance), or their competitive ability within the community. I ask whether predictions about community persistence following disturbance (in terms of cascading extinction events and species removal respectively) should be based on the rather complicated methods required to establish interspecific competitive relationships (both mathematically and under natural conditions), or a more simple measure of interspecific relationships, in this case, relative abundance within the community.

The model

To simulate a multi-species community I applied a Ricker-type growth model with Lotka-Volterra competitive interactions between *m* species. This is a commonly used function in ecological models (e.g. Levins 1968, May 1973, Lundberg *et al.* 2000, Fowler & Lindström 2002) allowing a wide range of biologically relevant deterministic dynamical behaviours to arise. Thus the population size N of any species i in an m species community was calculated for successive generations ($t + 1$), given knowledge of the present population size ($N_{i,t}$) as follows:

$$N_{i,t+1} = N_{i,t} \exp\left[r\left(1 - \frac{\sum_{j=1}^{m} \alpha_{i,j} N_{j,t}}{K_i} \right) \right] \quad (1)$$

The intrinsic growth rate for each species

is represented by r, which was held constant at 1.75 in all simulations. (Varying r between species has previously been shown to have no qualitative effect in this system, within the stable dynamical region (Fowler & Lindström 2002), and preliminary investigations showed no relationship between relative population growth rate and cascading extinction probability.) The species-specific carrying capacity, K_i, was scaled to unity. This means all species densities are expressed as a fraction of their equilibrium density in the absence of interspecific competitors. Species densities were initiated by each being drawn independently from a uniform random distribution with limits [0,1]. Using this method of community assembly, all communities that were subsequently tested for robustness to extinction events are insensitive to varying the initial densities of the species.

All species in the community competed with each other over some shared resource, while intraspecific competition was set to unity in all cases, all interspecific interaction values were scaled accordingly. Fryxell and Lundberg (1998) highlighted the importance of horizontal (competitive) interactions in ecological systems. In this model, interspecific interaction strengths (α values) were asymmetric, being drawn from a uniform random distribution with limits [0,1]. This represents a purely competitive community, however, using different forms of random distributions for selecting $\alpha_{i,j}$ values does not qualitatively change the results presented here. Collectively, all pairwise species interactions can be expressed in an m by m community matrix, $\mathbf{A}$, as follows:

$$\mathbf{A} = \begin{bmatrix} \alpha_{1,1} & \alpha_{1,2} & \cdots & \alpha_{1,m} \\ \alpha_{2,1} & \alpha_{2,2} & \cdots & \alpha_{2,m} \\ \vdots & \vdots & \ddots & \vdots \\ \alpha_{m,1} & \alpha_{m,2} & \cdots & \alpha_{m,m} \end{bmatrix} \quad (2)$$

The nature of these asymmetric interactions means that species i might have a more negative influence on species j than species j has on species i. For each new model iteration, a new $\mathbf{A}$ matrix was constructed.

Community size was varied between four and ten species. Although these represent relatively small ecological communities, this approach makes it possible to address important

community processes between strongly interacting species. The majority of most between-species interactions are likely to be weak (McCann 2000), and therefore likely to be difficult to assess in real communities. By focusing on relatively strong between-species interactions here, I attempt to study those that are most likely to be of interest to ecologists in the field or lab.

Each separate community with its corresponding $\mathbf{A}$ matrix was then run for 1000 generations to reveal instabilities. The purpose of this was to remove transients and allow the community dynamics some time to settle to a steady state. The community was considered stable if the number of species present after 1000 generations was equal to the initial community size. A species was considered extinct if its population size fell below a critical threshold value (in all cases presented here this critical value was $N_{i,t} < 1 \times 10^{-6}$, a conservative limit for a species density). This method was used as the model in this form will not give explicit extinction events, with population densities approaching a zero value asymptotically, but never hitting 0. Here it is assumed that demographic or environmental effects will lead to species loss if they do drop below such a critical low density, which represents one millionth of each species' maximum sustainable density in the absence of other species.

It is also possible to derive the equilibrium stable state for such communities analytically, using vectors to represent the equilibrium population density of all species in the community (May 1973). It is known that the species specific carrying capacity (K) can be derived from the equilibrium density of each species (N^*), and the interaction matrix ($\mathbf{A}$). In vector notation, this becomes $\mathbf{A}N^* = K$. By setting K as a column vector of length m filled with ones, it then becomes possible to rearrange this to determine the equilibrium densities of each species.

$$N^* = \mathbf{A}^{-1}K \quad (3)$$

Thus, the matrix multiplication of the inverse of matrix $\mathbf{A}$ and column vector K will result in a vector N of length m which contains the new species specific equilibrium densities for all species in the community. In this way, it is possible to have an $\mathbf{A}$ matrix that will produce equilibrium

densities smaller than zero, known as unfeasible communities. Following derivation of the community steady state, communities where any elements of the vector N^* are smaller than the extinction threshold (1×10^{-6}) were discarded. If this was the case, a new **A** matrix was again randomly generated, and the process was repeated until a suitable community was found.

At this point, each species was selected and removed from the community sequentially, in an order described below. This was done by renewing the interaction matrix by simply removing the row and column that related to the removed species. This gave a new $m - 1$ by $m - 1$ interaction (**A**) matrix. Once again, the community steady state was derived from Eq. 3. This time, however, any species with a corresponding element in the new N^* vector below the extinction threshold (1×10^{-6}) was considered to have become a victim of a cascading extinction event, and these were noted. These $m - 1$ species communities were then simulated over a further 1000 generations to test for any further cascading extinction events. This process was repeated 500 times, to allow the probabilities of cascading extinctions to be calculated after the removal of each community member.

Ranking community members

Community members were ranked according to either their relative equilibrium density (abundance) within the community, or relative competitive ability. Three different methods were initially used to characterise competitive ability. Pairwise interaction strengths were summed across the **A** matrix either in its original form ($\sum$**A**), to assess the effect of each species on all other species in the community, or summed across the transpose of the **A** matrix ($\sum$**A**´) to assess the competitive effect of all other species on each focal species. Finally, the difference between these two measures was used to characterise competitive ability ($\sum$**A** $-$ $\sum$**A**´). This represents the difference between the feedback each focal species exerts on all other community members and the feedback all other community members exert on the focal species. If these were symmetric communities, these values would always sum to zero, however the asymmetric community interactions used here will lead to differences in the competitive effects the species have on each other.

This information was used for ranking the species in the community in its original state, and again when analyzing the outcome following the sequential removal of each species. Thus, every one of the species in the community is removed, and the new community (with one species less) is allowed to renew for a further 1000 generations. Again, as described above the structure is controlled for further extinctions according to the densities of the remaining species. The lower density limit of any species to be considered extant was again set to 1×10^{-6}, all species with densities below that were treated as extinct.

All of the following results are based on 500 iterations of the community model, unless otherwise stated.

Results

Different sized multi-species communities were simulated to determine the relationship between species abundance and different measures of competitive ability. Correlations of the raw data from all interactions in 500 iterations of ten species communities showed a relatively low relationship between actual abundance (N^* = equilibrium density for each species) and the summed impact of the focal species on all others in the community ($\sum$**A**; Pearson's $r = 0.0580$), while abundance against the summed effects of all other species on the focal species ($\sum$**A**´; Pearson's $r = -0.5226$) and abundance against the difference between these two measures ($\sum$**A** $-$ $\sum$**A**´, Pearson's $r = 0.3631$) had much closer relationships, although in opposite directions.

Species characteristics in the community were then ranked according to relative abundance or the different competitive measures as described above (in all cases, species ranked 1 had the lowest relative numeric value of the characteristic of interest, e.g. abundance rank 1 had the lowest relative density of all species in the community, competitive ranks were according to the lowest summary values taken from the **A** matrix). Abundance rank was then compared with the
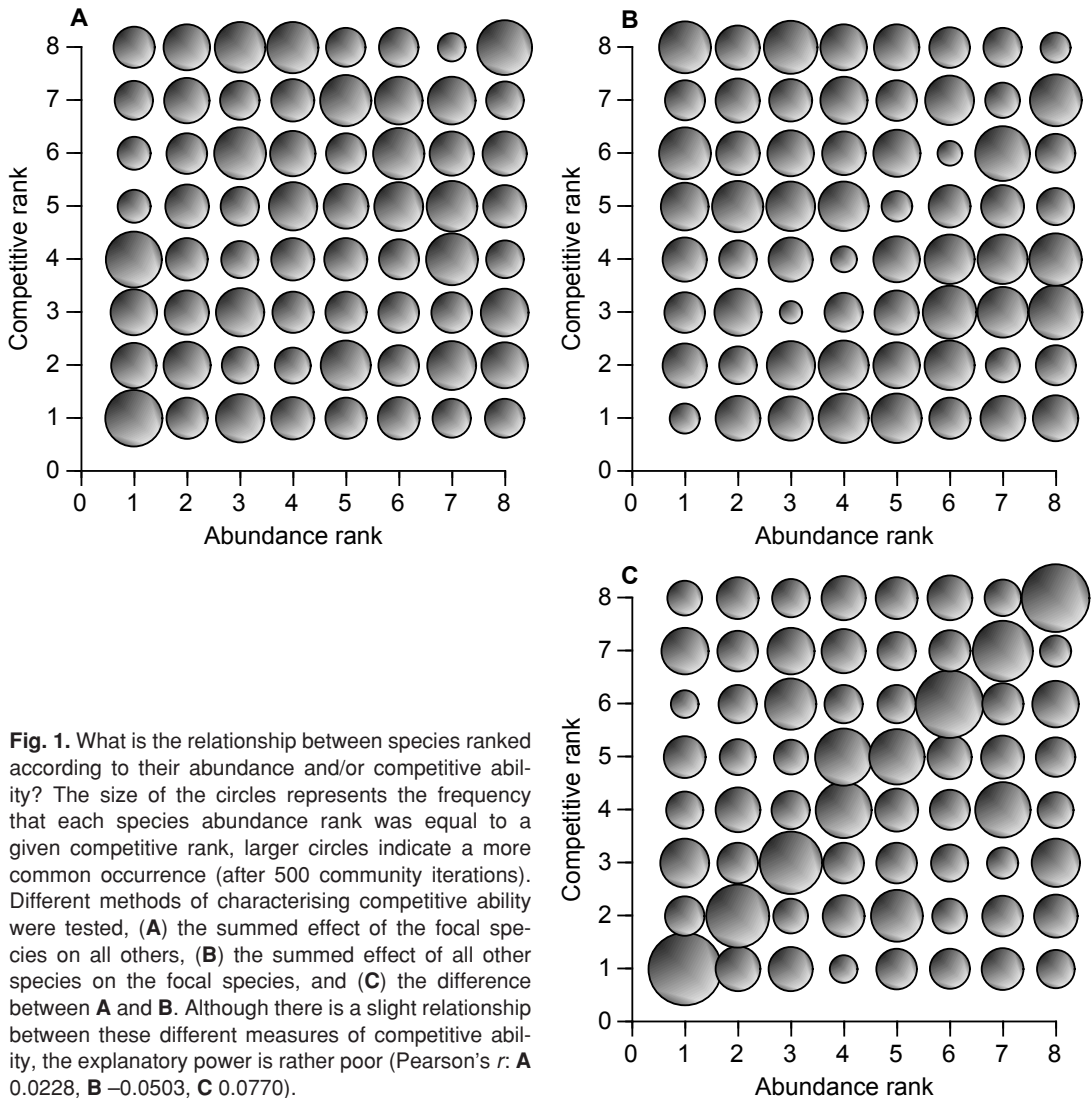
Fig. 1. What is the relationship between species ranked according to their abundance and/or competitive ability? The size of the circles represents the frequency that each species abundance rank was equal to a given competitive rank, larger circles indicate a more common occurrence (after 500 community iterations). Different methods of characterising competitive ability were tested, (**A**) the summed effect of the focal species on all others, (**B**) the summed effect of all other species on the focal species, and (**C**) the difference between **A** and **B**. Although there is a slight relationship between these different measures of competitive ability, the explanatory power is rather poor (Pearson's *r*: **A** 0.0228, **B** –0.0503, **C** 0.0770).

different methods of competitive ranking in an eight species community (Fig. 1). Here, there was only a relatively weak relationship between the abundance rank of a species and the different types of competitive ranks (Pearson's *r* = 0.0228, –0.0503, 0.0770, same comparison order as above). The third method of competitive ranking is used for illustrative purposes in the remainder of the results, although there are no qualitative differences between these different methods of competitive ranking in the following analyses.

Different patterns arise in the probability of cascading extinction events when species of different abundance ranks were removed, compared to when those of different competitive ranks were removed (Fig. 2 and Table 1). Removing species of relatively low abundance leads to considerably fewer cascading extinction events than removing those with a higher abundance (Fig. 2A). The same general pattern arises when ranking species by competitive ability (Fig. 2B), although the difference in effect between low and high ranked species is much smaller. These results suggest that assessing species importance in a community can be done in a more refined way through consideration of each species' abundance rather than their competitive ability within the community. Comparing these
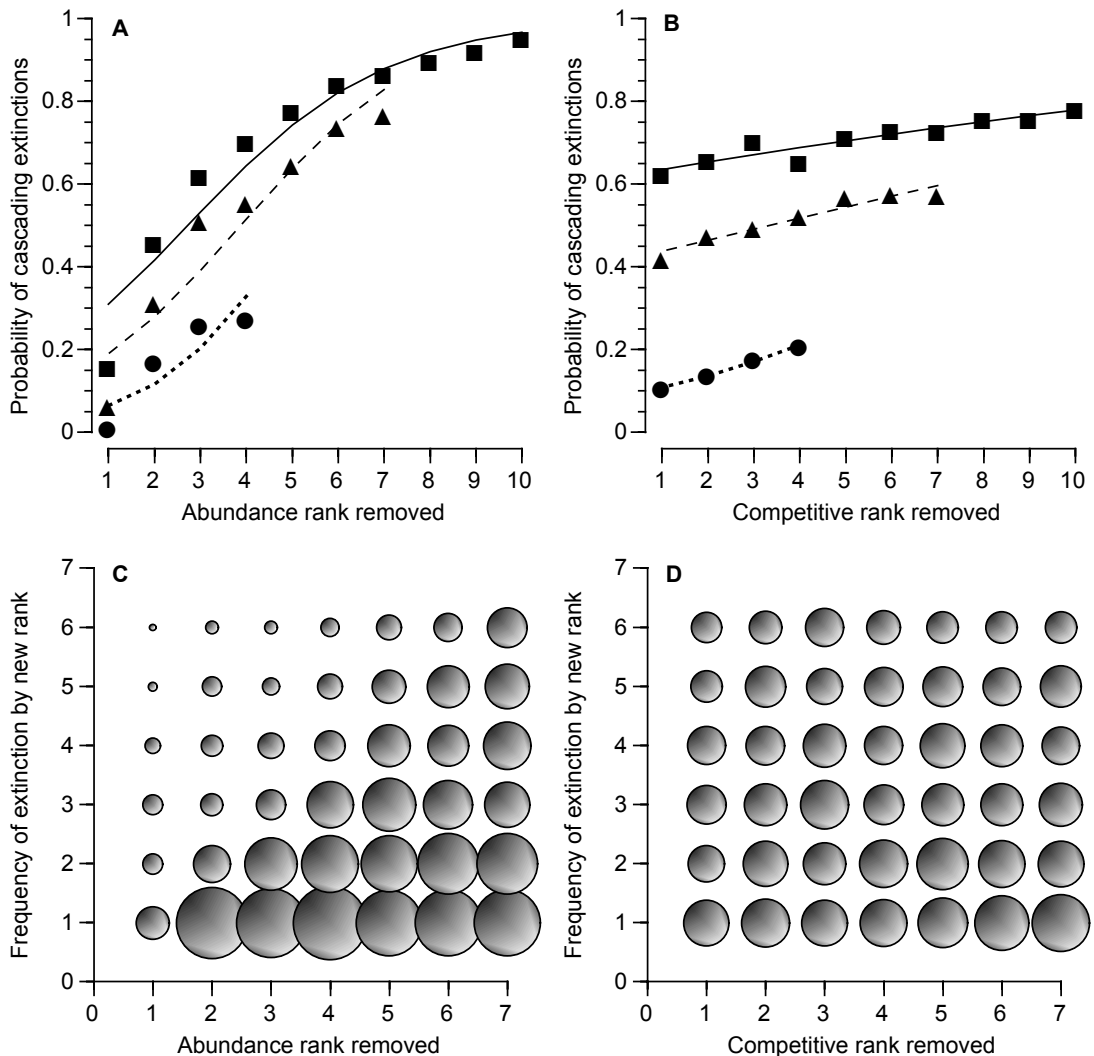
Fig. 2. Removing species of different rank from a community leads to different probabilities of further extinction events after the disturbance. Species were ranked according to their (**A**) relative abundance, or (**B**) their competitive ability. Species with low ranks (1 being the lowest) had relatively little influence on the community and higher ranks had a greater influence on community dynamics, a result that holds over different sized communities (4 [circles, dotted line], 7 [triangles, dashed line] or 10 [squares, solid line] species). In all cases there was a trend towards increasing probability of further extinctions as the rank of the species removed is increased. However, logistic regressions (statistics shown in Table 1) indicated that ranking species according to abundance gives a more refined measure of community extinction processes than ranking species according to competitive ability. Which species are likely to be lost if cascading extinctions do occur? It is shown in **C** and **D** that the same pattern arose in all community sizes tested. Less abundant species are more likely to be involved in an extinction event following the removal of a species from the community (rank was recalculated following the removal event). This pattern is consistent regardless of the relative abundance (**C**) of the removed species. However, there were a number of cases when the least abundant species was not involved in a cascading extinction, particularly so when species were ranked by competitive ability (**D**). This may be due to cascading extinction events involving more than one species at a time, or species changing their relative density or competitive ability following the removal of a specific competitor. Probabilities and the size of the circles are based on frequencies of a given outcome following 500 community iterations.

results with those of Lundberg *et al.* (2000, fig. 1b), it is clear that when species are removed at random from the community (*sensu* Lundberg *et al.* 2000), the probability of cascading extinction events will be of the same magnitude as the mean probability from the results here, averaged across all species whether ranked by abundance or competitive ability (4 species, $p = 0.168$; 7 species $p = 0.515$; 10 species, $p = 0.708$).

It is also possible to assess exactly which species are likely to be lost from the community when extinction events do occur. If species are ranked according to their relative abundance in the community, it can be shown that the least abundant species in the community is the most likely to be involved in extinction events, regardless of which species is removed from the community (Fig. 2C–D). However, there were a large number of cases where other species were lost from the community, especially when species with a relatively high abundance were removed. This pattern is even more apparent when species are ranked by competitive ability. Comparing the frequency of different ranks involved in cascading extinctions in a seven species community with even distributions shows that all cases differ significantly (abundance rank $\chi^2 = 1631.308$, d.f. = 41, $p \ll 0.0001$; competitive rank $\chi^2 = 165.546$, d.f. = 41, $p \ll 0.0001$).

A further interesting result was the relative movement of species along a rank following removal of a community member of known rank. It may be expected that species will simply move up a rank position if a species with a lower rank (abundance or competitive) is removed. Alternatively, if the highest ranked species is removed, no change in the relative ranks of the remaining

species would be expected. In many cases, this was shown not to be the case (Fig. 3), due to a more complex interspecific interaction system (asymmetric) in operation than such a simple linear ranking system, as well as the effect of indirect between species interactions. For example, after removing the lowest abundance ranked species (in a 7 species community), there is a very strong trend for the remaining species to simply rise one rank position (Fig. 3A). There are a few cases where species rise more than one position, or even fall down the rank, but these are relatively rare. A similar result occurs when the species with competitive rank 1 is removed (Fig. 3B), although there seems to be greater variability in the final ranking position.

Removing the highest ranking species from the community shows a different pattern, particularly in the case of the most abundant species (Fig. 3C–D). In many cases it was actually less likely that the new abundance rank would follow the expected trend than arriving at another rank. It is likely that cascading extinction events explain this result. If further cascading extinctions do occur following a removal event, remaining species would then be expected to shift even further along the abundance ranking. In many cases, the opposite is also true, however. After removing the most abundant species, the remaining community members often rose and fell in the abundance rank. In other words, removing the most abundant species often had a disproportionately beneficial or harmful effect on remaining community members. This result is again likely to be due to the non-linear (asymmetric) competitive effects found in the **A** matrices, and holds true for all cases of removing differently ranked

Table 1. Logistic regression statistics for removing species by competitive or abundance rank. In all cases, the variation is explained better by ranking species according to their relative abundance (density) in the community.

Original community size	R^2	p	β	Dev.	d.f.	S.E.
Abundance ranking						
4 species	0.159	< 0.001	−3.7322, 0.7244	0.0420	2	4.7066, 1.4563
7 species	0.252	< 0.001	−1.9607, 0.5058	0.2307	5	2.0119, 0.4620
10 species	0.346	< 0.001	−1.4165, 0.4871	0.2237	8	1.6550, 0.3509
Competitive ranking						
4 species	0.019	< 0.001	−2.3703, 0.2639	0.0003	2	3.6948, 1.2580
7 species	0.015	< 0.001	−0.3568, 0.1068	0.0070	5	1.7017, 0.3820
10 species	0.015	< 0.001	0.4786, 0.0782	0.0126	8	1.4636, 0.2457
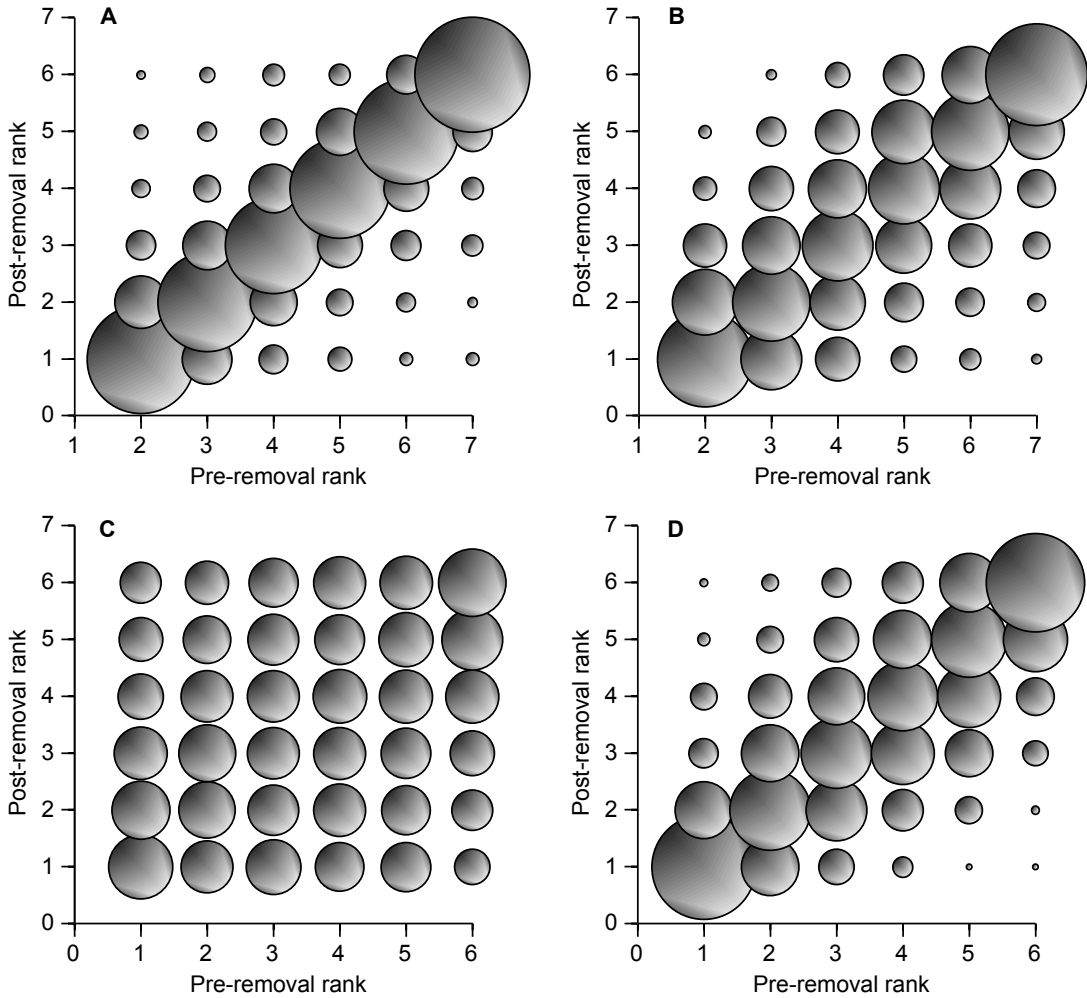
Fig. 3. Change in relative ranking following forced removal of differently ranked species. Removal of the species originally ranked 1 either by (**A**) abundance (the species with lowest abundance) or (**B**) by competitive ranking showed a strong trend for species to simply move up one place in the relevant rank. In some cases, this was not the case, however, with the possibility for unexpected changes in rank, particularly competitive rank. The same process was repeated by removing the highest ranked species from the community (**C** and **D**). There is definite deviation from an expected linear movement along the abundance ranking (**C**), after removing the most abundant species. All results taken from 500 community iterations.

species both in terms of competitive ability and abundance, across different community sizes. This result is of considerable interest, as it points to a significant restructuring of a community following the removal of one member.

Discussion

Results from the model studied here show that different ways of characterising the members

of a community are likely to lead to different predictions for the fate of communities following a disturbance event. It seems that there is little relationship between abundance and competitive ability (when competitiveness is determined by values that represent direct pairwise competition). Characterising species by relative abundance in a community provides a higher predictive power for community fate following a major disturbance, namely the extinction of another community member. These results

provide an insight into the mechanisms behind cascading extinction events in community interactions. Previous work by Lundberg *et al.* (2000) and Fowler and Lindström (2002) addressed the impact of species removals on a community using the same model framework, but did not attempt to characterise the community members as has been done here. The results presented here suggest that when studying competitive communities, species abundance is often a more appropriate measure for defining different community members' status, for two important reasons. Firstly, characterising species by abundance provides a clearer estimate of the fate of a community following disturbance (Figs. 2–3, Table 1); and secondly, species abundance is likely to be far easier to estimate than pairwise competition values. These results hold when assessing effects that may have some bearing on community level processes, e.g. the probability of extinction events occurring following different types of disturbance. However, it has also been shown here that the complex nature of interspecific interactions can lead to somewhat surprising effects arising when communities are disturbed. Some species have a disproportionately large suppressant effect on others, so when such a species is removed, the victim can actually become a better competitor in the remaining community than its original rank suggested. This analogy can apply to all members of the community and their effect on other members, regardless of their relative rank (competitive or abundance). These subtle but important processes are not obvious when a community is not viewed in the correct context, and provide a clearer insight to changes in community dynamics that can have important consequences to species persistence that may not be clear due to averaging of species performance (e.g. Lundberg *et al.* 2000, Fowler & Lindström 2002). This appears to be an encouraging finding in terms of conservation practises, as it is almost certainly easier to establish relative abundance of community members than it would be to try and establish overall community interaction between all members. The indirect consequences of disturbing communities must still be kept in mind in conservation management schemes. The results here (those presented in Fig. 3 in particular) clearly indicate that competitive communities can dramatically alter their structure following a disturbance event, in this case species removal.

The keystone species concept has been debated repeatedly in the ecological literature (Gaston 1996, Power *et al.* 1996, Coleman & Williams 2002). In addition to being part of a more general understanding of community dynamics, it has also been used in conservation biology as a means of understanding the consequences of loss of biodiversity. Should it be possible to predict the relative importance of species in ecological communities, then limited conservation effort could in principle be largely targeted towards those species with such important effects. Here, I explored the effects of a possible candidate for the definition of a keystone species in simple competitive communities. These results unambiguously indicate that density is a good predictor of the direct and indirect effects a species will have on the rest of the community. Perhaps surprisingly, removing those species with the highest density leads to a higher probability of further (cascading) extinction events. While it may be expected that removing a competitor with a high density from a system would reduce competition between the remaining community members, the above results show that in fact, such a removal is much more likely to lead directly to the loss of other competitors from the community. Power *et al.* (1996) stress that a keystone species has a disproportionately large effect on community traits relative to its abundance. This suggests that the species from these simulated communities that have the greatest impact on the species diversity of the community may not be classified as keystones. Preliminary investigations of these simulated competitive communities, and those that include both positive and negative interactions, show that the keystone definition provided by Power *et al.* (1996) is highly sensitive to the specific community trait of interest (M. S. Fowler, unpubl. data). For example, if species richness is the trait being studied, all community members may be thought of as keystone candidates, each species having a community importance "much greater than one" (Power *et al.* 1996). If biomass is the trait of choice, none of the species qualify as keystones, with community importance an

order of magnitude smaller than one. This within community test highlights some major problems that still exist with defining and assigning keystone species status.

It would be interesting to test the generality of these results by introducing a different community structure such as a multi-trophic system, e.g. the food web structure (Goldwasser & Roughgarden 1993). It remains to be seen, however, exactly how and why differently structured communities respond differently to extinction events. Also, it is possible that less rigid and deterministically structured communities than the model presented here may respond differently because of changes in the species properties as deletions occur (Abrams 1996). Williams *et al.* (2002) have recently emphasised that species dynamics within ecosystems may be more highly coupled than previously suggested, and underline the potentially catastrophic effects of biodiversity loss.

I have shown here that equilibrium density is a useful guideline for assessing species importance in competitive communities such as those studied here. Although community closure and re-introduction cascades were not specifically addressed here, they have been shown to potentially have far reaching consequences for conservation and community and ecosystem restoration (Lundberg *et al.* 2000). More detailed knowledge about species-specific effects on those processes is therefore required for successful management and protection of natural systems. Rigorous definitions of keystone species and similar concepts are therefore critical for management strategies.

Another potentially important aspect of community ecology that has not been addressed here is the effect that space has on systems such as this. The metacommunity concept has been studied elsewhere (e.g. Abrams & Wilson 2004), generally with a low number of interacting species. Abrams and Wilson (2004) suggested that spatial heterogeneity must be coupled with a competition-colonization trade-off for two species co-existence when competing over a shared resource. It has also been shown that linking discrete community patches in the environment through dispersal may either have little effect on the probability of further extinctions after some form of disturbance (Fowler 2002), but

this test was carried out under a spatially homogeneous framework. Furthermore, harvesting in one patch has been shown to have detrimental effects on species in other patches in the environment (Jonzén *et al.* 2001). However, as has been shown here, knowledge gained from removing species from the community on the basis of their abundance can help to predict population or community level processes to a higher degree than basing predictions about differences on the competitive structure of such communities. Future studies could assess whether differently ranked species react differently in a spatially explicit model. It is possible to ask whether some species suffer increased or decreased extinction risks due to the effects of dispersal between different habitat patches. If this is the case, it may be necessary to have detailed knowledge of individual species reactions to help manage and protect these species effectively.

Acknowledgements

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