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Variability in interaction strength and implications for biodiversity

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Summary

1. We examined the species richness of theoretical communities in relation to interaction strength between species.

2. To do so, we used randomly constructed interaction matrices for competitive systems. To determine co-existence, we tested for local stability and equilibrium feasibility of these theoretical assemblages.

3. As expected, we found that a low mean species interaction strength could allow for many species to co-exist. However, variance in the interaction strengths may alter previous results; two systems with the same mean interaction strength show markedly different diversity depending critically on the magnitude of the variance. If species are similar enough then many can co-exist, even if they compete strongly.

4. In addition we found that the species richness of a competitive community can greatly depend on the correlation between interaction strengths, an issue that so far has gone unreported. This correlation, a result of trade-offs between species' characteristics, may profoundly increase the potential for stable co-existence of a highly species-rich community.

5. Competition may not be an anathema to diversity. Statistical properties of species' interactions may be critical factors that contribute to the explanation of species diversity in natural communities.

Key-words: biodiversity, co-variation, hierarchies, interaction matrices, interaction strength, stability probability, variance.

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Introduction

The relationships between species interaction strength, species diversity and ecosystem stability are of great importance to conservation biology in the face of the increased anthropogenic pressure on natural ecosystems through species extinctions and additions (McCann 2000). Early, mainly verbal, theories on the diversity–stability relationship supported the view that complex and more diverse communities are more stable than simple and less diverse ones (MacArthur 1955; Elton 1958). These ideas were later challenged by May (1972, 1974), who used random Jacobian matrices to investigate the question of stability of ecological communities. He used an elementary result from theoretical physics to show that the stability of ecosystems tends to decrease with the number of species, thus refuting that 'complexity begets stability'. This result, however, apparently contrasts with the high species richness found in nature.

The question of how diversity and stability are related in natural systems remains unanswered, mainly because empirical studies are still uncommon. Recent empirical studies (Paine 1992; Fagan & Hurd 1994; Raffaelli & Hall 1992; Berlow 1999) have shown that weak interactions are prevalent in natural communities. Hardly any of these studies measure interaction strength (*sensu* May 1974), which results in a quite difficult interpretation of the empirical data. Theoretical investigations have pointed to mechanisms that can explain the stabilization effect of weak interactions on community dynamics (Ives & Jansen 1998; McCann, Hastings & Huxel 1998; McCann 2000). Notably,

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McCann *et al.* (1998), working with simple food web models, found that weak interactions tend to stabilize a community by suppressing the destabilizing effect of strong interactions. This takes place through the limitation of energy flow in a possibly strong predator–prey interaction. To our knowledge nobody has ever demonstrated experimentally community stabilization via any of the mechanisms proposed by McCann *et al.* (1998).

In an intelligent and industrious attempt to examine the relationship between diversity and stability in natural and agricultural soils, de Ruiter, Neutel & Moore (1995) found that the strengths of the interactions among species were patterned in a way that promoted stability. Roxburgh & Wilson (2000) arrived at similar conclusions studying competition in a lawn community. Both of these studies examined interaction strength, *sensu* May (1974), the elements of the Jacobian matrix.

Studying a single trophic level and attempting to explain the high diversity of natural communities, the importance of competition strength on species diversity may broadly be categorized as follows (modified from Tokeshi 1999).

1. Competition does not occur at all, and thus it is unimportant.

2. Competition occurs, but is intrinsically not sufficiently strong to influence the state of co-existence, or previously strong competition has left communities characterized by niche partitioning and therefore weak interspecific interactions: 'the ghost of competition past'.

3. Competition occurs and can potentially influence the state of co-existence. However, there may be factors or patterns of interaction strength that prevent it from exerting a significant influence upon co-existence. That is, competition may be intense at the level of two individuals but may be unimportant on net population growth (*sensu* Welden & Slauson 1986).

In this work we set out to re-examine and assess the effect of interaction strength and species richness on the stability probability of randomly constructed interaction matrices for competitive systems.

We did this by creating random interaction matrices (sometimes referred to as community matrices) for communities and studied the feasibility of a positive and stable equilibrium. This methodology is similar to the one used by May (1972, 1974) to show that the stability of an ecological community depends on the variance of the interaction strength. There are, however, some subtle but important differences between May's approach and ours. We constructed interaction matrices, used these to assess equilibrium feasibility and hence realize species richness, and then proceeded to examine the Jacobian matrix for stability. May (1972, 1974) studied random Jacobian matrices (confusingly, these are also referred to as community matrices; Case 2000) from which the stability of the equilibrium could be inferred.

The use of a Jacobian matrix assumes that a positive equilibrium exists. Therefore May's model provides an important result about the stability of ecological interactions, but gives no information about the relation between interaction strength and feasibility of the equilibrium. This limits the use of the model to study species richness. The use of random Jacobian matrices is convenient from a mathematical point of view, as results are available that link the distribution of the matrix entries to the probability of the equilibrium being stable. It can be justified by assuming there exists some model that could be parameterized to give the right Jacobian matrix. However, the disadvantage of this approach is that without knowing the appropriate model, it not possible to compare the model to ecological data.

Another limitation of May's work is the assumption that the elements of the Jacobian have zero mean. This condition might be appropriate for food web models, but not for competitive systems, for instance. It has been shown that relaxation of this assumption may have important consequences for the stability of ecosystems (Hogg, Huberman & McGlade 1989; Haydon 1994).

We constructed communities by creating random interaction matrices instead of Jacobian matrices. In ecology information is often presented in the form of interaction coefficients and these coefficients can be measured (Bender, Case & Gilpin 1984). The advantage of this approach is that our results can be related much more directly to measurable quantities. We also relaxed the assumption for the mean of the interactions to be zero. We asked whether ecologically plausible structures of the interaction matrix have significant effects on the stability probability of the resulting competitive system.

Model presentation

Species' interactions are governed by the following generalized Lotka–Volterra competition equations:

$$\frac{dN_i}{dt} = N_i\left(1 - \sum_{j=1}^{m}\alpha_{ij}N_j\right) \quad i = 1, \dots, m. \qquad \text{eqn 1}$$

where m is the species number, N_i is the density of species i scaled by its carrying capacity, and α_{ij} represents the effect of interspecific (if $i \neq j$) or intraspecific (if $i = j$) competition. This scaling does not imply that diagonal elements of the Jacobian matrix all take value one. In fact, generally they do not. The term α_{ij} may be read as the effect of an individual of species j on the per capita growth rate of species i. The intrinsic rates of natural increase of all species are assumed to be equal, and accordingly do not appear in equation 1, to facilitate the interpretation of results. The elements α_{ij} form the m by m interaction matrix **A**. In what follows we test the consequences of different ecological assumptions by assigning the value of the elements of **A** randomly, using several different distribution functions.

In our model the existence of a feasible equilibrium is not guaranteed. One of the questions we try to answer is how likely it is that an equilibrium is feasible, i.e. that all species' equilibrium densities are positive. The second question we address is the stability of the equilibrium. Stability of an equilibrium can be determined by studying the linearization of equation 1 around the equilibrium. The linearized model is of the form:

$$\frac{\mathbf{dn}}{\mathbf{dt}} = \mathbf{Jn} \qquad \text{eqn 2}$$

(boldface type to signify matrices and vectors). The matrix **J** is known as the Jacobian matrix and its elements are:

$$J_{ij} = n_i^* \alpha_{ij}, \qquad \text{eqn 3}$$

where n_i^* is the equilibrium value of species *i*. An equilibrium is stable if the real part of the dominant eigenvalue, and hence of all the eigenvalues of the Jacobian matrix **J**, is negative. It is important to note that in order to find the Jacobian matrix the equilibrium values need to be known. Therefore there is an important difference between our approach, in which we construct an interaction matrix, and approaches in which the Jacobian is constructed; the latter approach implicitly assumes the existence of a feasible equilibrium. The drawback of our approach is the need to assume a specific model, with consequently some loss of generality. We are not aware of analytical methods in which the distribution of the elements of the Jacobian matrix can be derived by analytic means from the distribution of elements of the interaction matrix, and therefore used a Monte Carlo approach to answer questions of feasibility and stability.

A sufficient, but not necessary, condition for stability is diagonal dominance of the interaction matrix (and the Jacobian) (Hofbauer & Sigmund 1988; Logofet 1993). An interaction matrix has a dominant diagonal if the equilibrium is feasible and intraspecific competition exceeds the total interspecific competitive impact from all other species:

$$|\alpha_{ii}| > \sum_{j \neq i}^{n} |\alpha_{ij}| \text{ for all} \qquad \text{eqn 4}$$

Communities are stable when intraspecific competition exceeds the total interspecific competitive impact from all other species.

General results

To guide the intuition, we first consider the limiting case in which the interspecific interaction coefficients are positive but in which there is no variation in the off-diagonal elements, i.e. all $\alpha_{ij} = \alpha > 0$ for $i \neq j$ and $\alpha_{ii} = 1$. In this case all species are identical and their equilibrium density B_i is given by:

$$B_i = \frac{1}{1 + (m-1)\alpha}. \qquad \text{eqn 5}$$

The total biomass B_t equals:

$$B_t = \frac{m}{1 + (m-1)\alpha}; \qquad \text{eqn 6}$$

If $\alpha > 1$ (i.e. if interspecific competition is greater than intraspecific competition) the total biomass decreases with the number of species, whereas it increases if $\alpha < 1$ (i.e. if intraspecific competition is greater than interspecific competition). However, if there is no variation in the interaction coefficients there is no upper bound to the number of species that can co-exist provided that $\alpha < 1$. The dominant eigenvalue of the Jacobian matrix, whose sign determines the stability of the interaction, is:

$$\lambda_{\max} = \frac{\alpha - 1}{1 + (m-1)\alpha} \qquad \text{eqn 7}$$

Note that stability declines with *m*.

Next, we consider the case in which the interaction coefficients have a positive mean and in which there is variation in the interaction coefficients. Simulations show that the larger the number of species, the smaller the probability of finding a feasible and stable equilibrium. In Fig. 1 we have chosen the off-diagonal elements from uniform distributions with different intervals: I = (0, 0·1), II = (0, 0·25), III = (0, 0·5), IV = (0, 1·0) and V = (0, 1·5), with respective means 0·05, 0·125, 0·25, 0·5 and 0·75. (For the uniform distribution over the interval(a,b), $Mean = \frac{a+b}{2}$ and $Variance = \frac{(b-a)^2}{12}$.) The model was simulated for 3, 5, 7, 10, 13, 16, 20, 25, 30, 40, 60, 80, 100 and 150 species present. Each simulation was repeated 10 000 times. The stability probability for each value of species richness was calculated as the frequency of locally stable and feasible systems. Results show that systems may be of four types: (a) stable and feasible; (b) neither stable nor feasible; (c) feasible but not stable; and (d) stable but not feasible. Increasing species richness generally results in a decreasing probability of finding systems of type (a), as shown in Fig. 1. For very few species all systems are almost always stable; very large systems are almost always unstable. In between there is a range in which the probability of finding a stable system decreases rapidly with the number of species. By increasing the interval from which the interaction coefficients are drawn, this range tends to become less wide and its midpoint tends to shift to smaller values.

As mean interaction strength increases, systems are encountered that belong to two 'irregular' types (c and d, results not shown). These irregular systems can make up to 25% of all simulations in some cases. This is a fact that it is not usually taken into consideration in community assembly simulations or in the evaluation of local stability in randomly constructed food webs (Drake 1990).

Examining data from empirical studies (Paine 1992; de Ruiter *et al.* 1995; Roxburgh & Wilson 2000) one observes high variation in the values of interaction strengths both within a community and among different

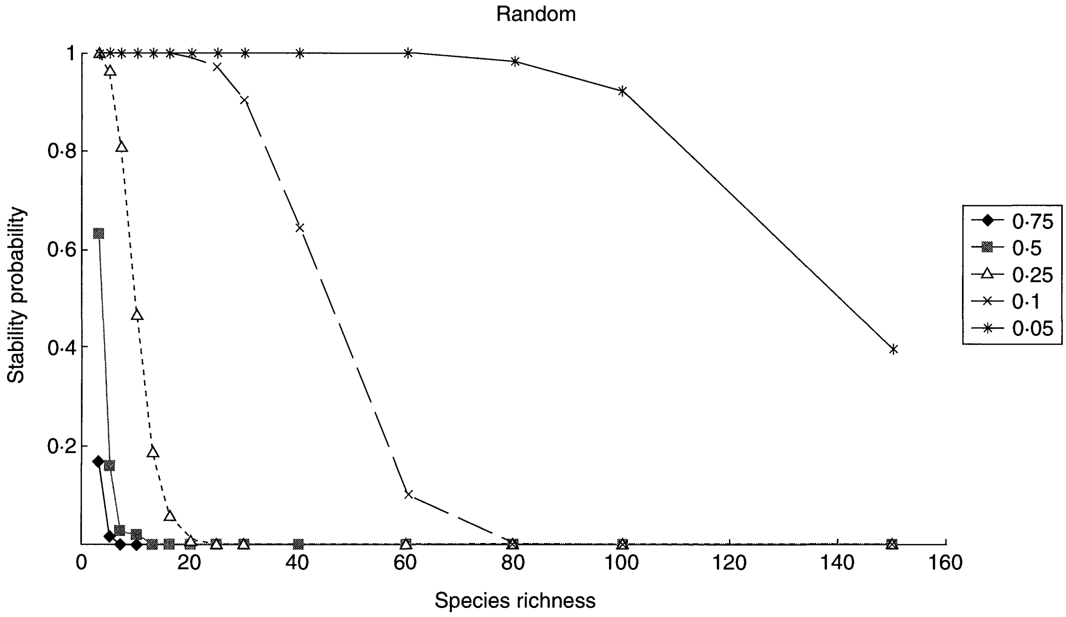

Fig. 1. Probability of a feasible and stable equilibrium for different mean interaction strengths and species richnesses for random community matrices. Intervals for the off-diagonal matrices of the simulations are (0, 1·5) (0, 1) (0, 0·5) (0, 0·2) (0, 0·1). Respective means are presented in the graph.

communities. This variation may often have the form of competitive hierarchy. This calls for a closer study of the effect this may have on stability on model communities. In the next section we will study the effects of variance on the stability of theoretical assembled communities.

Mean vs. variance of interaction strength

In the previous section our choice of distributions results in the variance and mean of the interaction coefficients being coupled so that they increase or decrease together. In this section we consider distributions for which mean and variance can be independently changed in order to illustrate the combined effects of the mean and variance of the entries in the interaction matrix on the stability probability of Lotka–Volterra competitive systems. The off-diagonal matrix entries were drawn from uniform distributions on the interval $[a, b]$. By choosing the parameters a and b appropriately, the mean and variance can be chosen. For a given mean and variance, we calculated the number of species as the number of species for which half of the matrices yielded stable and feasible equilibria. Results are presented in Fig. 2 as contour plots of identical species richness.

It is apparent that the variance plays a critical role in stable co-existence. Figure 2 shows that species richness decreases as both the variance and the mean of interaction strength increases. As a consequence, to promote species richness, it is not sufficient to decrease the mean interaction strength if this goes together with an increase in the variance. Figure 2 suggests that this trade-off is approximately linear.

To generalize these results we performed simulations in which the interaction matrices were constructed in a similar way but in which the entries were drawn from normal distributions and from distributions in which the entries were either zero or drawn from a uniform interval. In all cases these simulations yielded very similar results. The mean and variance of the distribution provided accurate predictions for the number of species that can co-exist. This suggests that our results represent a general phenomenon.

Competitive hierarchy: increasing the variance

Hitherto we examined stability probability assuming that the interaction matrix was 'stochastically symmetric' in the sense that the entries α_{ij} were drawn from the same distribution as the α_{ji}. This might not be valid when competition between different species is asymmetrical, i.e. when in pairwise competition one species suffers heavily from the presence of the other, but not the other way around. At its extreme, such an asymmetric competition leads to a perfect competitive hierarchy in which competitors of higher ranks affect species of lower ranks, but the reciprocal effect is zero. Entire interaction or Jacobian matrices are rarely published in the literature but there are exceptions. For instance, Gilpin, Carpenter & Pomerantz (1986) determined such a matrix for an experimental fly community, and Goldsmith (1978), Wilson & Keddy (1986) and Roxburgh & Wilson (2000) for plant communities. It appears that many communities have such competitive hierarchies. From a theoretical point of view, Hastings (1980) and Tilman (1994) considered a site-occupancy model in which a superior competitor would always and immediately take over a site from an inferior competitor upon arrival at that site, but in which a superior competitor is a worse colonizer and

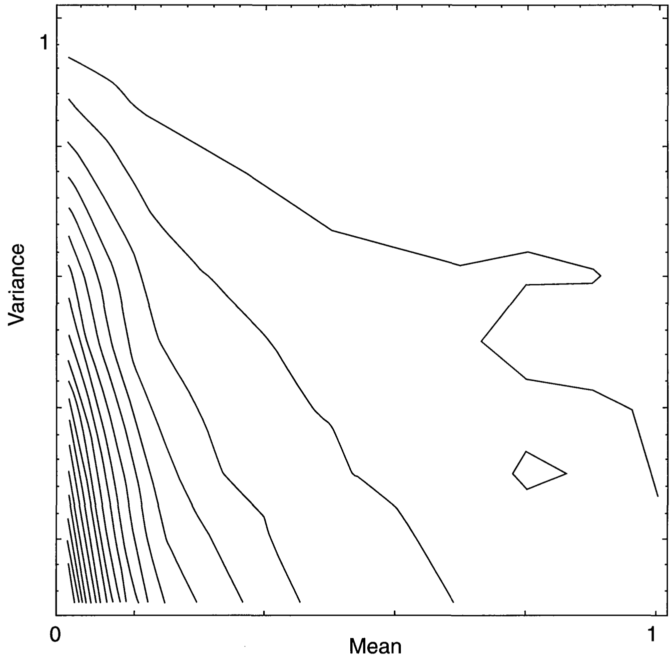

Fig. 2. Contour plots that depict communities of same species richness as a function of the mean and the variance of interaction strength that result in stable and feasible configurations with probability 1/2. The most species-rich communities can be found in the lower left corner near the axis origin, where in half the simulation over 20 species co-existed stably. In the upper right corner in half of the simulations less than two species could stably co-exist. The irregularity in the right lower of the graph is a result of the stochastic nature of the simulations.

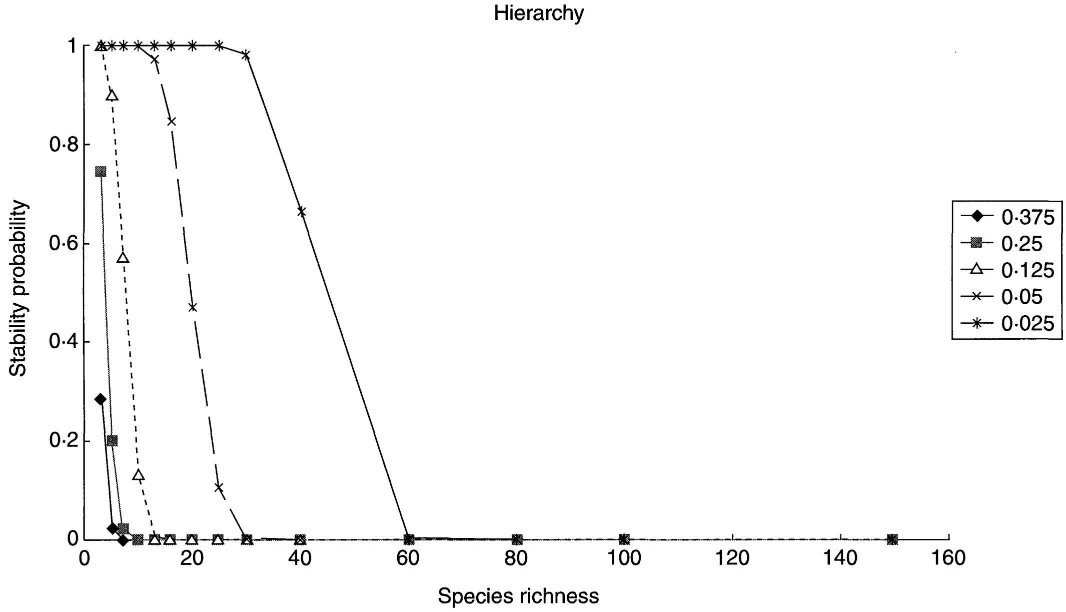

Fig. 3. Probability of a feasible and stable equilibrium for different mean interaction strengths and species richnesses for hierarchically organized (triangular) interaction matrices. Intervals for the off-diagonal matrices of the simulations are (0, 1·5) (0, 1) (0, 0·5) (0, 0·2) (0, 0·1). Respective means are presented in the graph.

therefore occupies fewer new sites. This approach can easily be transformed into a Lotka–Volterra competition system similar to the one used above. The interaction matrix in this case is a lower triangular matrix; its upper triangle consists of zeros. We constructed random matrices, as specified in the previous section, but kept the values in the upper triangle zero. We chose the same intervals as before for off-diagonal elements, but note that the means are lower (0·025, 0·05, 0·125, 0·25, 0·375, respectively) and the variances are higher. For the calculation of the variance, see the Appendix. The same method was followed for the evaluation of stability probability and the results are presented in Fig. 3.

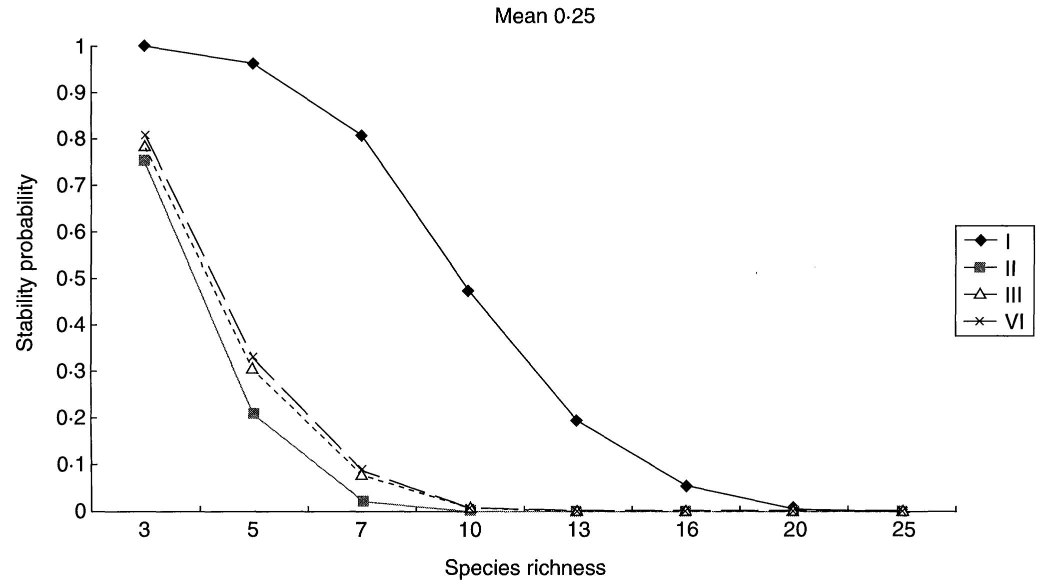

Fig. 4. Probability of a feasible and stable equilibrium for randomly and hierarchically organized interaction matrices with the same mean interaction strength (0·25) and different variance: I, random assembly, interval (0·5), variance 1/48; II, hierarchical assembly (triangular matrix), interval (0, 1), variance 5/48; III, random assembly, interval $(0.25 - \frac{\sqrt{5}}{2}, 0.25 + \frac{\sqrt{5}}{2})$, variance 5/48; IV, same data as in II but now the coefficients are randomly placed on the off-diagonal entries.

Despite the fact that the means are lower, the stability probability in the competitive hierarchy is lower, not higher as would be expected if the only factor that influenced stability probability was mean interaction strength. This result is illustrated with an example in Fig. 4. For the same mean of value 0·25, we compare the stability probability of three sets of randomly and one set of hierarchically organized matrices. The probability of encountering a feasible and stable configuration is lower in the hierarchically organized communities. Clearly, the factor that creates this difference is again the variance of the entries in the interaction matrix. The values of the variance in this particular example are: for simulation I, 1/48 in the random matrices, and for simulation II, 5/48 in the hierarchically organized matrices.

The increased variance of hierarchical matrices is one factor that will contribute to the fact that the species richness is reduced, but this is not necessarily the only factor. We therefore constructed (simulation III) randomly assembled matrices according to the procedure described in the previous paragraph with a mean 0·25 and variance of 5/48. As shown in Fig. 4, hierarchically constructed matrices were even less species rich than the randomly constructed matrices with comparable mean and variance. To find out if the reduced species richness was caused by the specific way in which these matrices were constructed, i.e. with the elements of the upper triangle all equal to 0, we randomized the positions of the matrix entries (following Roxburgh & Wilson 2000). To do so we used the entries of the hierarchical matrices used for Fig. 4 but destroyed the hierarchy by randomizing the positions of the non-diagonal elements (simulation IV). The resulting probability of the equilibrium being stable was higher than in the hierarchical matrices. This is an important observation as it shows that the mean and the variance of the interaction coefficients are not the only factors that control species richness: ecological constraints on the interactions can lead to departures from the results found for random matrices. Such constraints manifest themselves in the correlation structure of the interaction coefficients.

It is interesting to note that these findings contrast with those of Roxburgh & Wilson (2000). They found that hierarchy might increase the stability probability of competitive communities. The fact that the community under study was assumed to be at equilibrium, or the possible lack of feasibility of that equilibrium, may contribute to that discrepancy.

Hierarchy with trade-off: correlation structure in the community matrix

To illustrate the point that ecological constraints can lead to departures from the results found for random matrices we will consider a community defined by the model:

$$\frac{dM_i}{dt} = M_i\left(1 - \sum_{j=1}^{n} \frac{h_{ij}M_j}{K_i}\right)$$

where the interaction coefficient $h_{ij} = 0$ if $j > i$ and $h_{ij} = 1$ if $j \leq i$. The parameters K_i represent the carrying capacities. Note that this model differs from the ones previously described in this paper in that the carrying capacities are not scaled to unity. Instead, we assume that the carrying capacities are chosen from a uniform distribution on $[0, b]$ and ordered such that they decrease with competitive rank, i.e. $K_i > K_{i-1}$. This assumes that the better a competitor a species is, the lower its carrying capacity. (This assumption may not be generally true: in a non-spatial context, highly competitive plants are usually large-bodied, namely they have high carrying capacity K.) This model represents a strict competitive hierarchy with a trade-off between competitive rank and carrying capacity. This is also the case in the Hastings (1980) and Tilman (1994) model where the carrying capacity is determined by the ratio mortality over colonization. The equilibrium densities are given by K_1 for $i = 1$ and by $K_i - K_{i-1}$ for $i > 1$. Obviously, all equilibrium densities are positive since $K_i > K_{i-1}$. In this model, there is no limit to the number of stably co-existing species.

To enable comparison of the model with the models used in the rest of this paper, we rescale all population densities by their carrying capacities, $N_i = M_i/K_i$, and define $\alpha_{ij} = h_{ij}\frac{K_j}{K_i}$. As a result of this scaling, all diagonal elements of the community matrix take the value one, the upper triangle consists of zeros and it can be shown that the elements of the lower triangle are uniformly distributed on the unit interval (see the Appendix). The diagonal elements and the distribution of the off-diagonal elements are the same as in the model described in the previous paragraph.

The previous section shows that a competitive hierarchy *per se* tends to decrease diversity because of increased variance of community matrix entries. In the model proposed by Hastings (1980) and Tilman (1994), however, there is an additional element that contributes to increasing the potential for stable co-existence, that is the competition–colonization trade-off. More generally, trade-offs between different competitive abilities generate co-variation between community matrix entries that can greatly favour co-existence.

To illustrate this, consider the following interaction matrix:

$$A = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0.562 & 1 & 0 & 0 & 0 \\ 0.521 & 0.927 & 1 & 0 & 0 \\ 0.499 & 0.888 & 0.958 & 1 & 0 \\ 0.495 & 0.880 & 0.949 & 0.990 & 1 \end{bmatrix}$$

The matrix elements in the lower triangle are between 0 and 1, and this matrix describes a system with positive and stable equilibrium. This matrix was constructed as set out above and it can be made arbitrarily large and always have a positive and stable equilibrium, this in contrast with the results in the previous paragraph. The reason for this difference is that this matrix has an internal structure which ensures that a feasible and stable equilibrium always exists. The matrix elements were drawn at random but were correlated. This structure is reflected by the fact that the values of the matrix elements decrease within a column. A proof that this structure renders the equilibrium feasible and stable is given in the Appendix. The reason that strictly hierarchical systems can support arbitrarily large numbers of species is that the strongest competitors do not perceive the presence of the weaker competitors at all. If these systems are constrained such that weaker competitors have a higher carrying capacity, weaker competitors can survive through the extra resources that are thus granted and that are not used by the stronger competitors (Jansen & Mulder 1999).

Although the mean and variance of the matrix elements are identical to those in the model in the previous section, this model differs in that there is no limit to the number of co-existing species. The main reason for this is that the community matrix was constructed by choosing m parameters from a distribution, and not $m(m-1)/2$, as was done in the previous section. Therefore the elements of the community matrix are correlated, generating a structure in the matrix (here, its elements decrease gradually along each column in the lower triangle).

Correlations between interaction strengths have so far not been studied in ecological communities. This example demonstrates that such correlations whose biological basis resides on the presence of trade-offs, can be a major factor determining the species richness of ecological communities.

Discussion

Our results can be summarized as follows: the number of co-existing species statistically depends on the mean and the variance of the interaction strength. An increase in mean or variance decreases the expected number of species, and the effects of mean and variance can be traded-off approximately linearly. These results corroborate the findings of May (1972, 1974). Although the results are similar we arrived at this conclusion by considering per capita interaction strengths, not elements of the Jacobian matrix. Our findings generalize May's findings to two ecologically relevant parameters, the mean and the variance of the per capita interaction strength. In addition we found that these results can be modified by the structure of the ecological community. Competitive hierarchies, for instance, tend to be less species rich than randomly assembled communities with the same mean and variances in the interaction strength. Correlation between interaction strengths can modify species richness further.

Our results show that weak mean interaction strength in random community matrices allows the co-existence of many species. This result is equivalent to the assumption that intraspecific competition is much greater than interspecific. In one of the few published matrices in the literature, Rees, Grubb & Kelly (1996) published the matrix of a four-species annual plant guild. They demonstrated that interspecific interactions were extremely weak (mean = 0·062, variance = 0·01), relative to intraspecific ones. It is interesting to note that this represents an almost perfect transitive competitive hierarchy *sensu* Keddy (1989), as is the case with the second of our models presented in this paper (see Competitive hierarchy: increasing the variance).

We also found that other important critical factors that determine the stability probability are the variation (expressed as variance or standard deviation in our approach) and co-variation of the off-diagonal entries in the interaction matrix. If species are more similar (the off-diagonal community matrix entries are chosen from a smaller interval), then many more species can co-exist. If there are trade-offs between different competitive abilities that generate correlations between matrix entries, unlimited co-existence is even possible. The competition–colonization trade-off model (Hastings 1980; Tilman 1994) can be viewed as a special case of our simple model, with a trade-off between competitive rank and carrying capacity, the difference being that there are additional constraints on parameter values (carrying capacities, and hence matrix entries) in the competition–colonization trade-off model that limit co-existence compared with our model.

A number of theories that consider biodiversity have been formulated, based on the idea that competition is neutral or near enough neutral (Bell 2000; Hubbell 2001). In our simulations this scenario corresponds to a mean of 1 and a variance of 0 (neutral competition). Our results indeed show that an infinite number of species can stably co-exist under such conditions. However, if the assumption of zero variance is relaxed to a low variance, the probability of finding a stable and feasible system with a large number of species drops rapidly to zero, indicating that much of the reported behaviour is not robust and will change qualitatively if the assumptions are changed slightly. Our results also demonstrate that large numbers of species do not only occur for these rather specific conditions and that substantial but finite numbers of species can co-exist under conditions for which neutrality does not hold, thus limiting the generality of these theories. Alternative theories for biodiversity are based on competitive hierarchies (Tilman 1994; Jansen & Mulder 1999).

Recently, it has also been shown that when assembling theoretical competition communities from a regional species pool, the resulting systems tend to have a significantly lower mean interaction strength than would be expected by chance (Kokkoris, Troumbis & Lawton 1999). But our results also show that ecologically plausible community matrices with similar weak mean interaction strengths do not necessarily allow co-existence of the same number of species. Recently, there have been a number of attempts to generate species-rich communities through evolutionary models (Geritz *et al.* 1998; Jansen & Mulder 1999; Kisdi 1999). It would be interesting to assess how far the results from assembly models and evolutionary models overlap and when they lead to different results.

The Lotka–Volterra model captures the barest essentials of a multispecies system. As such, it is natural that the modification of various factors may potentially change the outcomes. However, criticisms of the model with reference to its 'unrealistic' nature miss an important point. This model, as with other heuristic models in community ecology, was not designed to incorporate all possible factors (e.g. autecology of the species) but to show the consequences of having a minimum set of key features in a system of interacting populations. The model is the simplest possible general representation of interacting species. If the patterns created by the model are comparable with those observed in nature, the features involved might be sufficient to explain the observed patterns, and therefore provide testable hypotheses (Tokeshi 1999). Traditional approaches to the issue of competitive co-existence point out that species that compete strongly cannot co-exist. But competition may not be anathema to co-existence. Here we find that many moderately strong competitors can co-exist if they are similar enough. The idea is not entirely new to the literature. Leibold (1998) suggested that co-existing species are more similar than expected by chance. That similarity involved traits that affected the relative response of the organisms to their environment.

In an effort to resolve the discrepancy between modelling results and empirical observations, novel interpretations and results have been added to May's (1972, 1974) and Gardner & Ashby's (1970) theoretical investigations (McMurtrie 1975; Haydon 1994; Solow, Costello & Beet 1999; Haydon 2000). Conditions have been sought to allow for more species to co-exist. Almost all results so far are based on Jacobian matrices probably partly because of mathematical tractability. This work is another attempt in that direction by using interaction matrices that from an ecological point of view carry far more information. One question that needs further investigation is whether these results can be generalized from single trophic-level competitive systems to entire food webs and ecosystems.

What we suggest here is not that natural communities necessarily follow our simple model and always have a lower mean or variance or a particular structure of interaction strengths to allow for the great biodiversity that we observe. Neither do we advocate an ecosystem management approach based on average properties of theoretical dynamic models, which might be misleading (Haydon 2000). But we maintain that the statistical properties of species' interactions have been insufficiently studied and may be critical factors that contribute to explain the diversity of species in natural communities.

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Appendix

1. Calculation of the mean and variance of a distribution that takes value 0 with probability 1/2 and is uniformly distributed on the interval (a, b) otherwise:

$$\bar{x} = 0 \quad p = \frac{1}{2}$$

$$\bar{x} = x \quad p = \frac{1}{(b-a)} \cdot \frac{1}{2} \quad x \in (a, b)$$

$$\text{Mean} = \frac{1}{4} \cdot (b + a)$$

$$\text{Variance} = \sigma^2 = E(x^2) - (E(x))^2$$

$$E(x^2) = \int_a^b x^2 \frac{1}{2(b-a)}\, dx = \left[\frac{1}{3}x^3 \frac{1}{2(b-a)}\right]_a^b \quad \text{so}$$

$$= \frac{1}{6}(b^2 + ab + a^2),$$

$$\sigma^2 = \frac{1}{6}(b^2 + ab + a^2) - \frac{1}{16}(a+b)^2 \quad \text{or}$$

$$\sigma^2 = \frac{(a-b)^2}{12} + \frac{1}{3}\left(\frac{a+b}{4}\right)^2 + \frac{1}{6}ab$$

2. Let x and y be stochastic variables with uniform probability distributions on the interval $(0, b)$ and $z = y/x$ where $x \geq y$. Because x and y take values between 0 and b, and $x \geq y$, z takes values between 1 and 0. The probability density function of z is on the unit interval is: $p(z) = \lim_{\Delta \to 0} \int_a^b \int_{zx}^{(z+\Delta)x} \frac{2}{b^2}\, dydx = 1$ and z is therefore uniformly distributed on the unit interval.

3. Lemma 1: A model given by equation 1 in which the matrix elements in the upper triangle are zero, i.e. $\alpha_{ij} = 0$ if $i < j$, $\alpha_{ii} = 1$ and $r_i = 1$, the eigenvalues of the Jacobian matrix are equal to the equilibrium densities times -1.

Proof: First consider a subsystem consisting of only the first species. This system is described by a single differential equation that only depends on density of species 1. Obviously the equilibrium density is $x_1 = 1$ and the eigenvalue of this subsystem is -1. Next consider a subsystem consisting of species 1 to i. This system is described by i differential equations that only depend on densities of species 1 to i. The first $i - 1$ differential equations describe a similar subsystem consisting of $i - 1$ species. The eigenvalues of the subsystem consisting of i species therefore are the $i - 1$ eigenvalues of the subsystem consisting of $i - 1$ species plus one other eigenvalue. The sum of the eigenvalues equals the trace of the Jacobian matrix, the extra eigenvalue can be found by subtracting the trace of Jacobian belonging to the $i - 1$ system from the trace of Jacobian belonging to the ith subsystem. The value of the extra eigenvalue is therefore the one diagonal element of the ith subsystem that is not in the $i - 1$th subsystem, which is $-x_i$. Therefore, if lemma 1 holds for a subsystem of i species, it therefore holds for a system of $i + 1$. By induction the proof holds for the complete system.

Corollary 1: For a hierarchical system all feasible equilibria are stable.

Lemma 2: A model given by equation 1 in which the matrix elements in the upper triangle are zero and in which the elements in a column decrease from the diagonal down, i.e. $\alpha_{ij} = 0$ if $i < j$, $\alpha_{ii} = 1$ and $\alpha_{i-1j} > \alpha_{ij}$ if $i > j$ and $r_i = 1$, has an equilibrium in which all densities are positive.

Proof: Obviously species 1 has a positive equilibrium and the equilibrium value is $x_1 = 1$. Next observe that if species i has a positive equilibrium it follows $1 = \sum_{j=1}^{i} x_j \alpha_{ij} > \sum_{j=1}^{i} x_j \alpha_{i+1j}$. Hence $x_{i+1} = 1 - \sum_{j=1}^{i} x_j \alpha_{i+1j} > 0$. We can thus conclude that if the species i has a positive equilibrium, so has species $i + 1$. The proof that all equilibrium densities are positive follows by induction.

Corollary 2. Systems of this form always have a feasible and stable equilibrium.