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REPORT

Biodiversity and species interactions: extending Lotka–Volterra community theory

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Abstract

A new analysis of the nearly century-old Lotka–Volterra theory allows us to link species interactions to biodiversity patterns, including: species abundance distributions, estimates of total community size, patterns of community invasibility, and predicted responses to disturbance. Based on a few restrictive assumptions about species interactions, our calculations require only that the community is sufficiently large to allow a mean-field approximation. We develop this analysis to show how an initial assemblage of species with varying interaction strengths is predicted to sort out into the final community based on the species' predicted target densities. The sorting process yields predictions of covarying patterns of species abundance, community size, and species interaction strengths. These predictions can be tested using enrichment experiments, examination of latitudinal and productivity gradients, and features of community assembly.

Keywords

Community structure, interaction strength, invasive species, Lotka–Volterra theory, productivity, species abundance.

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INTRODUCTION

Understanding patterns in species richness and species abundance is one of the fundamental goals in ecology (May 1973; Berlow 1999; McCann 2000; Abrams 2001; Hubbell 2001). Classical theory asserts that each species is unique in its environmental demands and the resulting variation in pairwise species interactions determines biodiversity and relative abundance in a community (e.g. Chesson 2000). Recently, this assertion has been challenged by the neutral theory of community structure (Bell 2000; Hubbell 2001), which posits that species differences play a minor role relative to speciation, extinction, and immigration in determining community patterns. Here we reconsider the importance of species interactions by presenting a novel extension of the century-old Lotka–Volterra (LV) theory of population dynamics. Although many previous analyses have used LV theory to study community dynamics (e.g. May 1973; Pimm 1982; Ginzburg *et al.* 1988; Taylor 1988a,b; Drake 1990; McCann *et al.* 1998), none of the previous analyses have used this framework to unify species interactions and community patterns for competitive systems. As we demonstrate here, this unification leads to predictions regarding how changes in pairwise species interactions alter the total number of species in a local community, the distribution of their relative abundances, and the community–specific properties of invasive species.

The LV theory rests on the assumption that species interactions play a major role in structuring the community. Taking a mean-field approximation of those interactions across the community enables us to calculate a distribution of 'target' species densities that determines, to a large degree, the temporal development of the ecological community. Results of this mean-field approximation are compared with a brute force numerical integration of many random LV communities, and we show good agreement between the two approaches. We then demonstrate how community-level properties, such as species abundance distributions and the size of the local community, depend on the species-level statistical properties of the LV

parameters. Given an established ecological community, we then use this approach to predict the interaction properties necessary for a species to successfully invade.

THE LOTKA–VOLTERRA MODEL

We develop the LV model of community structure for interacting species under the simple assumption that every species in a local community has the potential to interact with any other. Dynamics of closed systems result from species-specific per capita births, $B(\{n\})$, and deaths, $D(\{n\})$, dependent on the set of species densities, $\{n\}$. The traditional formulation of a LV model can be viewed as a linear approximation (by Taylor series expansion) of these arbitrary birth and death functions. The resulting set of equations,

$$\begin{aligned}\frac{\mathrm{d}n_i}{\mathrm{d}t} &= n_i[B_i(\{n_j\}) - D_i(\{n_j\})] \\ &\approx n_i\left[\left(b_i - \sum_{j=1}^{P}\beta_{ij}n_j\right) - \left(d_i + \sum_{j=1}^{P}\delta_{ij}n_j\right)\right] \\ &= r_i n_i\left(K_i - \alpha_{ii}n_i - \sum_{j\neq i}^{P}\alpha_{ij}n_j\right),\end{aligned} \tag{1}$$

is the classic Lotka–Volterra community model (Lotka 1925; Volterra 1926). Here we have chosen the expansion point to be zero density, but the choice is not critical for our argument below. This set of equations, defined for a closed regional pool of P-species, specifies the rate of change for population density (either number or biomass), n_i, where $r_iK_i = b_i - d_i$ is the maximum per capita growth rate, $K_i/\alpha_{ii} = (b_i - d_i)/(\beta_{ii} + \delta_{ii})$ is the carrying capacity, and $r_i\alpha_{ij} = \beta_{ij} + \delta_{ij}$ are the elements of the 'interaction matrix', representing the direct intraspecific ($j = i$) and interspecific ($j \neq i$) interaction strengths between species i and j. There are several choices for the parameter definitions of the LV community model in terms of more fundamental birth and death parameters because the three LV parameters, r_i, K_i, and α_{ii}, are determined by only two birth–death parameter combinations, $b_i - d_i$ and $\beta_{ii} + \delta_{ii}$. Each choice entails different expected values and correlations between parameters because of their more fundamental basis in terms of the birth and death functions. In the following analysis, we assume that the growth parameters, $r_i = 1$, $\alpha_{ii} = 1$, and the parameters K_i and α_{ij} take on randomly chosen independent values from specified probability distributions. Our least-justified assumption is to set all of the intraspecific interaction coefficients to 1, which we do for simplicity, but we provide a discussion of this assumption's implications later. Independent of the debate concerning the loss of mechanism or gain of generality in the derivation of the LV community model, the linearized model represents a simplified ecological community, and our results provide insight into how community properties vary with the nature of interactions between species.

SPECIES–ABUNDANCE RELATIONSHIPS

Our first goal is to calculate the species–abundance relationship. It is not possible to derive an exact analytical solution for the equilibrium distribution of densities, but we can estimate this distribution using a mean-field approximation. First rewrite a species' summed interspecific interactions as,

$$\sum\nolimits_{j\neq i}\alpha_{ij}n_j = \bar{n}\psi_i + (P-1)\mathrm{cov}(n_\bullet, \alpha_{i\bullet}), \tag{2}$$

where $\psi_i = \sum_{j\neq i}\alpha_{ij}$ is a species' overall susceptibility to heterospecifics, $\bar{n}$ is the average species density, $\mathrm{cov}(n_\bullet,\alpha_{i\bullet})$ is the covariance measured over the distribution of heterospecific densities and the focal species' interaction strengths (the dot represents the summed-over index). In eqn 2, we have ignored the difference between the average species density and the average heterospecific density, which is of order P^{-1} and therefore presumably negligible for large species pools. The mean field approximation takes the covariance term to be negligible, which is equivalent to assuming that if a community contains many species, then the interaction with any particular species has little influence on the density of another. Under this approximation, the LV community model becomes

$$\frac{\mathrm{d}n_i}{n_i\mathrm{d}t} = r_i[K_i - n_i - \psi_i\bar{n}(t)], \tag{3}$$

for which a species' density increases or decreases dependent on the sign of the term in parentheses. We call the values at which these densities change sign 'target densities', $\tilde{n}_i$, determined by the set of equations,

$$\tilde{n}_i = K_i - \bar{\tilde{n}}\psi_i, \tag{4}$$

where $\bar{\tilde{n}}$ is the average target density. Target densities are values towards which population densities would move if they were allowed to take on any value. By substituting $n_i(t) = \tilde{n}_i + \tilde{\eta}_i(t)$ and $\bar{n}(t) = \bar{\tilde{n}} + \bar{\tilde{\eta}}(t)$ into eqn 3, we show in the Appendix that the deviations $\tilde{\eta}_i(t)$ and $\bar{\tilde{\eta}}(t)$ tend to decrease as the system evolves temporally. The behaviour of these target density deviations is analogous to the behaviour of deviations in normal species densities near a stable equilibrium. Thus, target densities, like equilibrium densities, have an important influence on the temporal development of the community. However, target densities are not equilibrium densities – a negative target density can occur when a species' carrying capacity is too small, and/or its susceptibility to heterospecifics is too large.

Our demonstration of the stability of target densities means that to obtain the species–abundance distribution we

simply appeal to a species sorting process for which there exists a critical minimum threshold for population densities (Gilpin & Case 1976), rather than successively removing species with negative equilibrium densities and recalculating the remaining ones (e.g. Tregonning & Roberts 1979). Species having negative target densities fall below this threshold and are purged from the community. Although this species sorting process alters the resultant distribution of carrying capacities and susceptibilities, the product of the average species density and susceptibility is expected to be nearly constant for large communities (see Appendix), meaning that the effect of the species sorting process on individual species' target densities should be weak. Thus, the distribution of initial target densities ought to reflect the distribution of equilibrium species densities, save for the existence of negative species densities.

The species–abundance distribution, estimated by the distribution of target densities, arises from folding together the distributions of susceptibilities and carrying capacities. The exact target density distribution's moments can be calculated using the moment generating functions (Karlin & Taylor 1975) for the carrying capacities and the susceptibilities, yielding the moment generating function for the target densities, $\phi_{\tilde{n}}(k) = \int \exp[k(K - \bar{\tilde{n}}\psi)]\rho_K(K)\rho_\psi(\psi)\,dK\,d\psi = \phi_K(k)\phi_\psi(-\bar{\tilde{n}}k)$. These moments arise from the mth derivatives of the generating function, $\overline{\tilde{n}^m} = \phi_{\tilde{n}}^{(m)}(0)$, and will only correspond to a normal distribution if the distributions for the carrying capacities and the susceptibilities are both normal. As the result of the central limit theorem, the susceptibilities, constituting the sum of $P - 1$ random values, will be normally distributed with mean $(P - 1)\bar{\alpha}$ and variance $(P - 1)\sigma_\alpha^2$, where $\bar{\alpha}$ and σ_α, are the mean and standard deviation of the individual interaction strengths. It is not clear what an empirically realistic distribution of carrying capacities might be for a given community, however, the distribution of target densities will be normal only when the carrying capacity distribution is normal. Independent of the specific forms of the input distributions, the underlying distribution for the species target densities, $\rho_{\tilde{n}}(\tilde{n})$, has a mean and variance given by

$$\bar{\tilde{n}} = \frac{\bar{K}}{1 + (P-1)\bar{\alpha}} \tag{5a}$$

$$\sigma_{\tilde{n}}^2 = \frac{(P-1)\bar{K}^2\sigma_\alpha^2}{[1 + (P-1)\bar{\alpha}]^2} + \sigma_K^2, \tag{5b}$$

where $\bar{K}$ and σ_K^2 are the mean and variance of the carrying capacity distribution.

How well does the distribution of target densities predict the equilibrium density distribution? To answer this question, we examined the outcomes of numerical integrations of random LV communities (e.g. Gilpin & Case 1976; see Appendix) that have no approximations and compared them with the results for target densities assuming a normal distribution with the above mean and variance for several parameter combinations. Given our choice of a non-normal input distribution of carrying capacities for the numerical integrations, the exact target density distribution is also not normal. Although these comparisons thus represent 'worst-case scenarios', the target species distributions truncated at zero density provide reasonable estimates of the equilibrium species distributions (Fig. 1), thereby supporting the approximations made in the analytical derivations and encouraging further analysis. We have not made the comparison quantitative because, as we will show, other concomitant properties show only qualitative agreement, thereby making overall quantitative agreement meaningless.

Target density distributions, and their corresponding rank–abundance curves, are sensitive to changes in key LV model interaction parameters. For example, a decrease in the average interaction strength widens the density distribution and increases the mode, resulting in a more even distribution of species abundances and a greater number of species persisting in the community (Fig. 1a,b). In contrast, a change in the SD in species interactions has a relatively weaker effect on the density distribution because $\sigma_{\tilde{n}}^2 \propto P^{-1}\sigma_\alpha^2$ (data not shown). Increasing the mean and SD of the carrying capacity distribution leads to similar changes in the species density distributions, however, the resultant rank–abundance distributions differ considerably (Fig. 1c,d). An increase in mean carrying capacity leads to species abundances that are more evenly distributed over a larger community, whereas an increase in the SD results in a steeper rank–abundance curve and fewer species in the community. It is also important to note that our results extend beyond purely competitive interactions: correspondence is observed at the lowest average interaction strength examined for which 20% of the interaction terms are negative (implying predation and mutualisms).

The species sorting process greatly modifies the underlying frequency distributions of the LV parameters. The carrying capacity distribution is highly sensitive to species sorting and, not surprisingly given eqn 4, becomes skewed towards high carrying capacities (Fig. 2a). In contrast, the distribution of individual interaction strengths becomes skewed towards lower values (Fig. 2b), but to a much lesser degree because interaction strengths are primarily affected through a species' overall susceptibility which, as the sum of many random individual interaction strengths, averages out much of the sortable variability. The net result of this influence is seen after species sorting takes place through the observation that species density is negatively correlated with both susceptibility and competitiveness, $\chi_j = \sum_i \alpha_{ij}$, with respect to the remaining community (Fig. 2c). However,

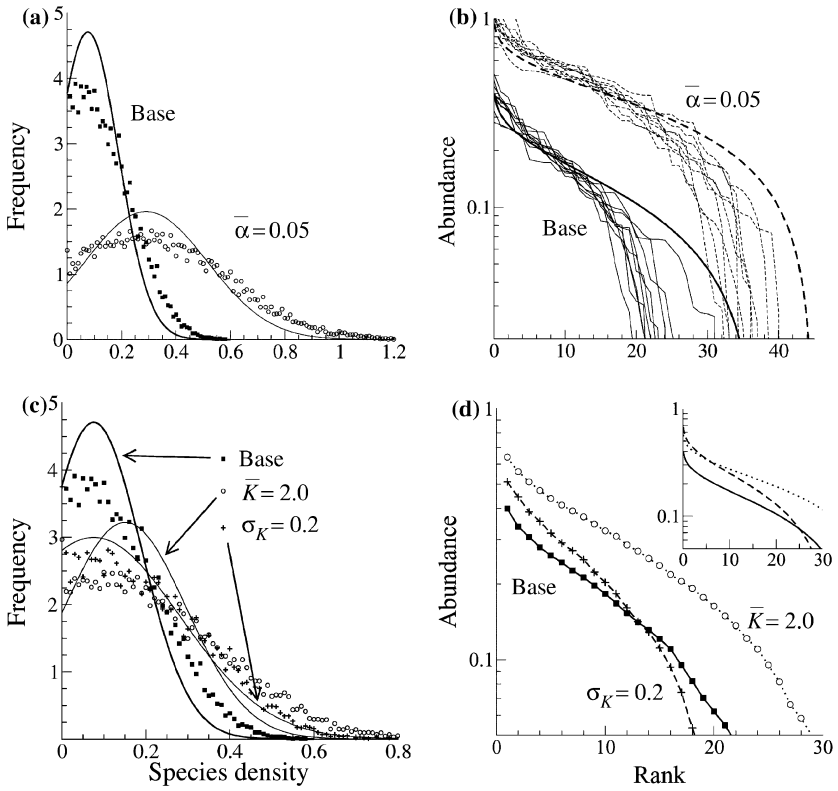

Figure 1 Distributions of target and equilibrium densities. In (a), target density distributions (lines) are contrasted with equilibrium distributions (data points) obtained from numerical integrations for two sets of model parameters, the base parameter set and a second set with $\bar{\alpha} = 0.05$. Target density distributions compare well with the equilibrium distributions, although the target variances tend to underestimate the equilibrium variances. In (b) the corresponding rank–abundance curves to (a) are shown for the target distributions and the curves resulting from 10 replicate numerical integrations. Panel (c) shows target and equilibrium distributions for the base parameter set, and two treatment sets, $\bar{K} = 2$ and $\sigma_K = 0.2$. (d) Despite similar equilibrium distributions for the two treatments, their rank–abundance curves (symbols; averaged over 50 replicates of the numerical integrations) are greatly separated and reproduced well by the results of the target rank–abundance curves (inset lines). Increases in the mean carrying capacity produce flatter rank–abundance curves, whereas increases in the carrying capacity's variance steepens the rank–abundance curve.

species density is most strongly determined by susceptibility, and the relationship with competitiveness arises when species with high susceptibility are eliminated from the system, thereby necessarily reducing the competitiveness of the remaining species.

COMMUNITY SIZE

Our analysis of the LV model also provides insight into the dependence of community size on the underlying model parameters. One estimate of eventual community size is based on the supposition that species with negative target densities eventually will be excluded from the system. Thus, given a species pool of size P and assuming a normal distribution of target densities with mean and variance given by eqn 5, the size of the remaining community, S, is

$$1-\frac{S}{P}=\int_{-\infty}^{0}\rho(\tilde{n})\mathrm{d}\tilde{n}\approx\frac{\sigma_{\tilde{n}}}{\sqrt{2\pi}\tilde{\bar{n}}}e^{-\tilde{\bar{n}}^2/2\sigma_{\tilde{n}}^2}\Rightarrow\frac{S}{P}=1-\frac{\sigma_{\tilde{n}}}{\sqrt{2\pi}\tilde{\bar{n}}}e^{-\tilde{\bar{n}}^2/2\sigma_{\tilde{n}}^2}. \quad (6)$$

The approximation arises from an integration by parts of the species density distribution (Mathews & Walker 1970), which we use here to provide an explicit expression indicating that the local community size increases monotonically with decreasing $\sigma_n^2/\bar{n}^2 \approx P\sigma_\alpha^2 + (P\bar{\alpha}\sigma_K/\bar{K})^2$ for large species pools. (Note that our later numerical comparisons implement the exact expression.) Thus, the number of species in a community should decrease with increasing $\bar{\alpha}$ and variability in interaction strengths or carrying capacities, and increase with increasing $\bar{K}$ (Fig. 3). The theory also predicts that the ratio of the local community size to the regional species pool

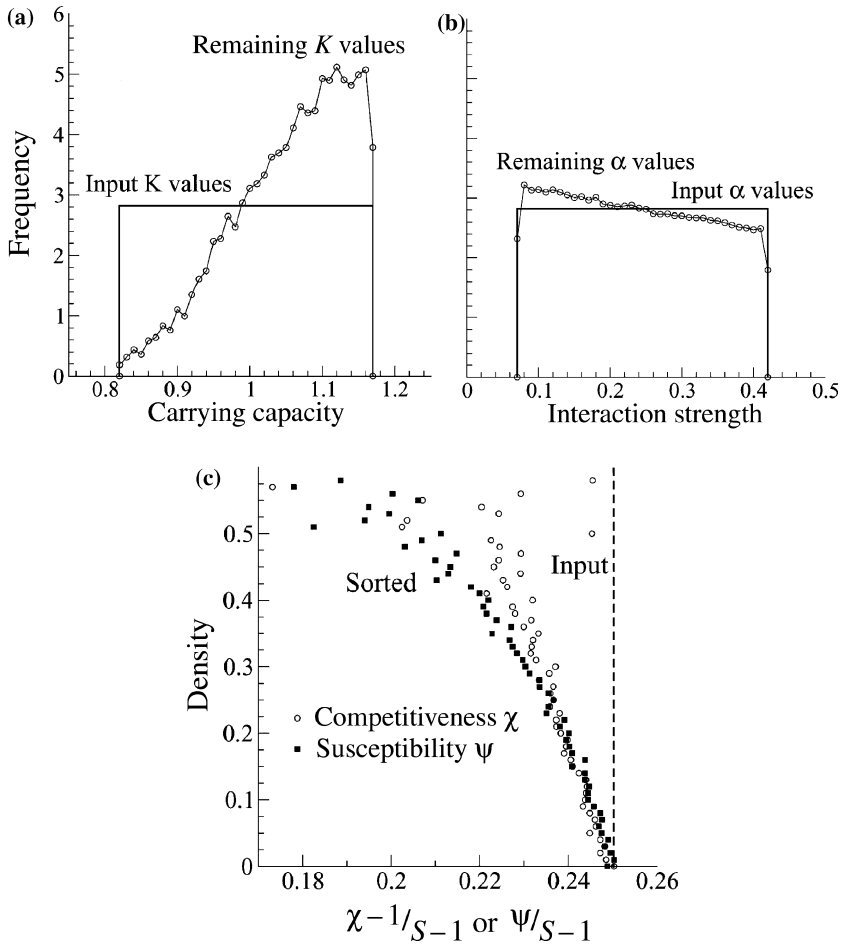

Figure 2 Equilibrium distributions for (a) carrying capacities and (b) interaction strengths for the base parameter set (see Fig. 1) become skewed by the species sorting process, with greatest impact observed on *K*. (c) Initially, all susceptibility and competitiveness values are tightly grouped around the average interaction strength (vertical dashed line). As the species sorting process takes place and species with negative target densities drop out, the susceptibilities of the remaining species are reduced differentially. At equilibrium, species having low susceptibility also have high density, as expected by the expression determining target species densities. In addition, as species with high susceptibility are removed, the competitiveness of the remaining species is thereby reduced, producing a similar, but less marked, effect in competitiveness.

decreases with increasing pool size (data not shown), in agreement with previous predictions and observations (Ricklefs 1987; Cornell 1999; Srivastava 1999).

With this understanding of the dependence of community size on the distributional properties of species interactions, we can use the LV framework to explore how natural variation in productivity or anthropogenic enrichments may affect local diversity. Although we examined this dependence using the aggregate LV model parameters, a more mechanistic analysis could examine this dependence given how the fundamental birth and death functions are themselves affected by enrichment experiments. For example, a burning treatment may release nutrients and make them available for some species, while causing additional mortality for other species. Our present consideration assumes that changes in environmental productivity can be modelled directly as changes in species' carrying capacities. We find that increasing $\bar{K}$ leads to larger communities and lower dominance (shallower rank–abundance curves) because of a decrease in the relative abundance of rare species (Fig. 1c,d; Fig. 3). Such positive relationships between productivity and community size are often observed across broad climatic gradients where we might expect large and consistent increases in carrying capacity for all species (Mittelbach *et al.* 2001). However, increasing σ_K decreases community size because of increased dominance by common species (Fig. 1c,d). Such declines in community size and changes in rank–abundance are often observed in enrichment studies (Gough *et al.* 2000), where we might expect the addition of a single (or few) limiting resource(s) to strongly increase σ_K because of variation among species in resource limitation (Rajaniemi 2003). Finally, when changing productivity is reflected by different nonlinear responses in $\bar{K}$ and σ_K, the relationship between productivity and community size can be hump-shaped or U-shaped. Thus, all the observed forms of the productivity–diversity relationship (increasing, decreasing, or unimodal; Waide *et al.* 1999; Mittelbach *et al.* 2001) can be predicted by the LV community theory, depending on how the mean and variance in species' carrying capacities change along environmental gradients or in response to perturbations or manipulations.

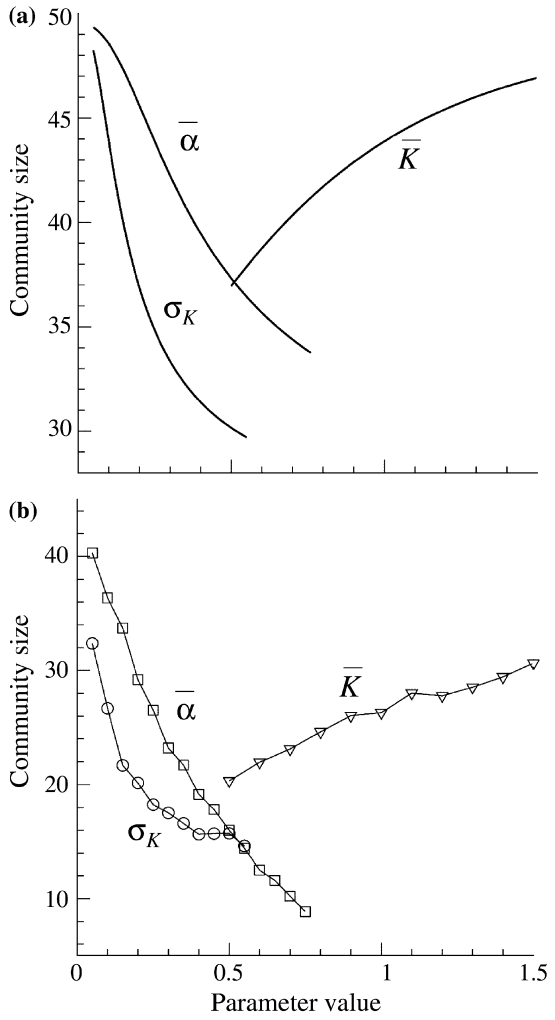

Figure 3 Consequences of species interactions on community size. (a) Community size is estimated from the target density distribution as the fraction of the species pool having positive target densities using the exact expression in eqn 6. Using the base parameter set (see Fig. 1), an increase in the variances of interaction strength or carrying capacity leads to a decrease in community size, but an increase in the average carrying capacity increases community size. (b) Similar trends in community size are observed in the equilibrium results of the numerical approach, although quantitative predictions are inaccurate.

INVASIBILITY

The LV theory coupled with the mean-field approximation also yields predictions concerning the properties of a species invading an established community of S species or, similarly, the processes of community assembly within a natural regional species pool. Such predictions have an obvious relevance, particularly given the increasing attention that biological invasions are receiving (Drake *et al.* 1989; Williamson 1996; Mooney & Hobbs 2000). Within the LV model, successful invasion requires that a species' growth rate be greater than zero,

$$\frac{\mathrm{d}n_\mathrm{I}}{n_\mathrm{I}\,\mathrm{d}t} = r_\mathrm{I}\left(K_\mathrm{I} - n_\mathrm{I} - \sum_j^S \alpha_{\mathrm{I}j} n_j\right) > 0, \qquad (7)$$

where the subscript I refers to the invader species. If the invading species invades at low density, then the establishment condition is $S\,\overline{n\alpha_\mathrm{I}} \equiv \sum_{j=1}^{S} \alpha_{\mathrm{I}j} n_j < K_\mathrm{I}$. Simply stated, for a species to invade the overall effect of the resident species on the potential invader has to be small. As above, the average population-level effect of residents on the invader can be written as the product of the average abundances and interaction strengths plus their covariance, $\overline{n\alpha_\mathrm{I}} = \bar{n}\bar{\alpha}_\mathrm{I} + \mathrm{cov}(n_\bullet, \alpha_{\mathrm{I}\bullet}) = \bar{n}\bar{\alpha}_\mathrm{I} + \sigma_{\alpha_\mathrm{I}}\sigma_n\rho_{\alpha_{\mathrm{I}\bullet},n_\bullet}$, where $\rho_{\alpha_{\mathrm{I}\bullet},n_\bullet}$ is the correlation coefficient between interaction strength and heterospecific density. A positive coefficient means that a species has stronger interactions with dominant heterospecifics, and likewise, a negative coefficient implies stronger interactions with heterospecifics of low density. Substituting the covariance expression into the invasion condition yields, for large communities,

$$\frac{K_\mathrm{I}}{S}\left(1 - \frac{\bar{\alpha}_\mathrm{I}}{\bar{\alpha}}\frac{\bar{K}}{K_\mathrm{I}}\right) > \sigma_{\alpha_\mathrm{I}}\sigma_n\rho_{\alpha_{\mathrm{I}\bullet},n_\bullet}. \qquad (8)$$

Invasion success is partly determined by the ratio $\bar{\alpha}_\mathrm{I}\bar{K}/\bar{\alpha}K_\mathrm{I}$; the smaller this ratio the more likely is successful invasion. If the invader interacts like the average species in the community ($\bar{\alpha}_\mathrm{I}/K_\mathrm{I} = \bar{\alpha}/\bar{K}$), then there must be a negative covariance between interaction strengths and heterospecific densities. However, if the invader interacts less strongly with other species or has a higher carrying capacity than the average species ($\bar{\alpha}_\mathrm{I}/K_\mathrm{I} < \bar{\alpha}/\bar{K}$), then it can invade even if there is some positive covariance. Species richness complicates the situation by bringing the left-hand side of eqn 8, whether positive or negative, towards zero: thus, species richness hampers invasion by weakly interacting invaders but facilitates invasion by strongly interacting invaders. Predictions for successful invasion are further complicated in that if σ_n is large (implying a strong abundance-dominance structure in the community) and the sign of $\rho_{\alpha_{\mathrm{I}\bullet},n_\bullet}$ is negative, then invasion may proceed despite a large community size. Thus, our model provides a potential explanation for the existing situation in which experimental and observational data provide mixed evidence for the effect of species richness on invasibility (Levine & D'Antonio 1999).

Either as a community sorts out from an initial distribution or assembles from successive invading species, we have a general expectation that average interaction strength weakens with time. Above we have also shown that communities with strong interspecific interactions should show greater dominance than those with weak interactions

(Fig. 1). A number of theories already suggest that the intensity of interspecific interactions changes predictably along successional or disturbance gradients (Grime 1973; Menge & Sutherland 1987; Tilman 1988; Huston 1994). Our modelling suggests that such changes should be accompanied by predictable differences in abundance relations.

LIMITATIONS OF PRESENT ANALYSIS

There remain many extensions to this analysis of the LV community model. We limited our development of this approach to examining a closed community in ecological time and therefore did not consider how processes such as migration or speciation, which are of fundamental importance to the neutral models, might influence these patterns. Also, while we allowed species interaction strengths and carrying capacities to vary, we assumed that all species possess the same intraspecific interaction strength and growth rate parameter *r*. As we demonstrated in the derivation of the LV model, the choice for the growth rate parameter is perfectly valid, however, our assumption that all intraspecific interaction strengths are one may have important consequences. In particular, in the calculation of the target densities, species-specific values for the intraspecific interactions would lead to correlations between a species' carrying capacity and all of its interspecific interaction strengths. In effect, each species would have a distinct average interspecific interaction strength. It remains to be seen whether these correlations would have a qualitative effect on our overall predictions.

In addition to variation in intraspecific interaction parameters, there might also exist trade-offs between the various parameters, for example, a species with high susceptibility might also have a high growth rate (Chave *et al.* 2002). The results of this trade-off would imply that species with high susceptibility, which are those that tend to have negative target densities, could more quickly expand their populations and significantly alter the distributional properties under which the community develops.

Each of the above features can be incorporated to extend the LV framework. Furthermore, an appeal could also be made to the original birth and death functions (or recasting these as growth and metabolism functions) to provide more mechanistic interpretations of the underlying pairwise species interaction parameters. It is clear that careful interpretations will be necessary to relate community properties such as standing biomass to parameters such as the carrying capacity's mean and variance.

CONCLUSIONS

We have shown that the classic LV theory of species interactions can be expanded to examine the causes and consequences of biodiversity. It can serve as a foundation for predictions concerning community structure and dynamics, including responses to environmental gradients or perturbations such as nutrient enrichment, and the susceptibility of communities to invasion. Although the exact equilibrium species abundance distribution is incalculable, we demonstrated that the easily calculated target density distribution provides an accurate estimate. Contrasting with the niche-based LV model, neutral models based on ecological drift have recently been proposed (Bell 2000; Hubbell 2001). Proponents of neutral models argue that ecological drift leads to very specific shapes for abundance distributions (Bell 2000; Hubbell 2001), although the agreement between these and empirical data has been challenged (Clark & McLachlan 2003; McGill 2003a,b). The expanded LV theory predicts a wide range of abundance distributions depending on the detailed distributions of the underlying parameters that describe the nature of species interactions. Distinguishing between models based on their ability to fit any one empirically observed pattern (e.g. the species abundance distribution) is rarely successful; numerous studies show how a variety of models may provide equally good fits to the data when the models contain unconstrained parameters (Nee *et al.* 1991; Harte *et al.* 1999; Abrams 2001; Chave *et al.* 2002; McGill 2003a). Such flexibility makes the empirical comparison of abundance patterns alone essentially useless to invalidate one or more models. However, our analysis of the LV model yields additional predictions of how several community properties depend on and covary with interaction strengths, carrying capacity, and the size of the regional species pool. This more constraining set of predictions enables empirical refutation using enrichment experiments, examinations of latitudinal and productivity gradients, and features of community assembly.

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APPENDIX

(1) Given the mean-field approximation leading to eqn 3, $\mathrm{d}n_i/r_i n_i \mathrm{d}t = K_i - n_i - \bar{n}(t)\psi_i$, where $\bar{n}(t)$ is the average species density, we can instead consider the dynamics of deviations about the target densities by substituting, $n_i(t) = \tilde{n}_i + \tilde{\eta}_i(t)$ and $\bar{n}(t) = \bar{\tilde{n}} + \bar{\tilde{\eta}}(t)$. For each species, $\mathrm{d}\tilde{\eta}_i(t)/\mathrm{dt} = -r_i n_i[\tilde{\eta}_i(t) + \psi_i\bar{\tilde{\eta}}(t)]$, demonstrating a general reduction in deviations from target densities except when the average deviation is significant. We obtain after summing over all species $\sum_i \mathrm{d}\tilde{\eta}_i/r_i n_i \,\mathrm{d}t = -P\big(1 + \bar{\psi}\big)\bar{\tilde{\eta}}$. Considering the summation we see $[P/(rn)_{\mathrm{MAX}}]\,\mathrm{d}\bar{\tilde{\eta}}/\mathrm{dt} < \sum_i \mathrm{d}\tilde{\eta}_i/r_i n_i \mathrm{d}t < [P/(rn)_{\mathrm{MIN}}]\mathrm{d}\bar{\tilde{\eta}}/\mathrm{dt}$, where the terms in the brackets are positive [the terms $(rn)_{\mathrm{MIN}}$ and $(rn)_{\mathrm{MAX}}$ represent the minimum and maximum values of the product of growth rate and species density, respectively]. Thus, deviations from the mean target density tend to decrease, at least over the short term, and we might expect that the system evolves temporally while preserving the average target density.

(2) Given a community of S species at equilibrium, the average equilibrium species density is $\bar{n}^*_S = \bar{K}_S/[1 + (S - 1)\bar{\alpha}_S]$, and the average susceptibility is

$\bar{\psi}_S = (S-1)\bar{\alpha}_S$. The derivative of the product with respect to S, $d(\bar{n}_S^*\bar{\psi}_S)/dS \approx \bar{K}_S/S^2\bar{\alpha}_S$, demonstrates only a weak dependence on community size as long as the parameter averages are relatively constant. Thus, the pool's average target density multiplied by the pool's average susceptibility, which is a measure of community susceptibility, provides a good estimate of the equilibrium product.

(3) Each replicate in the numerical integration involves a random species pool of size P generated by choosing the K_i uniformly over $\bar{K} \pm \sqrt{3}\sigma_K$ and interaction strengths α_{ij} over $\bar{\alpha} \pm \sqrt{3}\sigma_\alpha$ (except $\alpha_{ii} = 1$). Initial densities are chosen randomly between zero and $\bar{K}/\bar{\alpha}P$. A fourth-order Runge–Kutta numerical integration algorithm with adaptive time steps integrates the differential equations. When a species density falls below a critical threshold density, 10^{-5}, it is dropped from the community. The system is integrated for $T = 2000$ time units and the density distributions are averaged over 500 replicates. We use a base parameter set $\bar{K} = 1$, $\sigma_K = 0.1$, $\bar{\alpha} = 0.25$, $\sigma_\alpha = 0.1$, $r_i = 1$ and $P = 50$.

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