Biodiversity and the Lotka–Volterra theory of species interactions: open systems and the distribution of logarithmic densities

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Theoretical interest in the distributions of species abundances observed in ecological communities has focused recently on the results of models that assume all species are identical in their interactions with one another, and rely upon immigration and speciation to promote coexistence. Here we examine a one-trophic level system with generalized species interactions, including species-specific intraspecific and interspecific interaction strengths, and density-independent immigration from a regional species pool. Comparisons between results from numerical integrations and an approximate analytic calculation for random communities demonstrate good agreement, and both approaches yield abundance distributions of nearly arbitrary shape, including bimodality for intermediate immigration rates.

Keywords: open systems; ecological communities; Lotka–Volterra model; abundance distributions

1. INTRODUCTION

Communities are structured by many different processes that are important at various ecological scales. For example, the intermediate disturbance hypothesis relates species richness of communities to the disturbance frequency experienced locally (Connell 1978). Maximal species richness is often observed at intermediate disturbance frequencies because few species can tolerate high disturbances and another set of relatively few species are present in climax states. Species-specific physiological limits and tolerances also dictate local and regional community members, yielding latitudinal and altitudinal species richness gradients (Currie 1991). Character displacement is another process structuring communities in terms of the traits of its members (e.g. Slatkin 1980). All of these well-known processes stress the differences between species in their use of habitat and resources, and the role natural selection plays in reducing interspecific competition.

In this paper we expand the Wilson *et al.* (2003) analysis for one of the most enduring empirical measures of communities, the relative species abundance distribution (e.g. Preston 1948), using the Lotka–Volterra (LV) community theory (Lotka 1925; Volterra 1926; May 1974) that stresses species differences. Here we introduce two critical generalizations. Most importantly, we derive the mean-field approach for open systems by allowing species immigration in the calculation. As expected, immigration has drastic consequences for the resulting species abundance distributions, with the 'skewness' of the abundance distributions depending sensitively on the immigration rate. We also include species-specific intraspecific interaction strengths, which previously had been considered identical, and demonstrate that variation in these terms can be neglected.

Presently, there remains disagreement concerning the general form of the species abundance distribution. For many years, the empirical pattern was strongly believed to follow a lognormal distribution of abundances (Preston 1948, 1962*a,b*), as seen, for example, through an analysis of Patrick's diatom data (MacArthur & Wilson 1967). However, recent evidence indicates a left-skew to the abundance distributions (e.g. Nee *et al.* 1991). Repeatability of some patterns seems questionable, considering that multiple examination of the same dataset can reveal differing distributions. For example, preliminary data for a British bird survey analysed by Nee *et al.* (1991, fig. 4) demonstrated left-skew, but the improved, published data analysed by Gregory (1994, fig. 3) demonstrated no significant skewness. Reanalysis of the final data by Hubbell (2001, fig. 2.6) once again demonstrated strong left-skewness. Recent evidence for tropical trees seems quite compelling that abundance distributions are often not lognormal (Hubbell 2001). Finally, empirical distributions from long time-series for single-species populations, an occasional proxy for across-species abundance distributions, also are often not lognormal, possessing a left-skew (Halley & Inchausti 2002).

On the theoretical side, a variety of models have been developed to understand community processes, with the result that essentially any pattern of species abundance distributions can be 'explained'. These models include the broken-stick (and related) models (MacArthur 1957; Sugihara 1980; Harte *et al.* 1999), stochastic birth–death models for single species populations (Dennis & Patil 1984; Diserud & Engen 2000), and the neutral theory models which are essentially multispecies stochastic birth–death models (Caswell 1976; Bell 2000; Hubbell 2001). The connection between stochastic single- and multi-species models was demonstrated and analysed in detail by McKane *et al.* (2000) using a particular mean-field approximation. They showed that under a random

assembly of species, abundance distributions of various forms, in part dependent on the rate of immigration, could be derived. Their model did not, however, consider explicit species interaction. A different mean-field approximation, introduced by Wilson *et al.* (2003), of an LV species interaction model yielded species abundance distributions and local biodiversity as a function of species-specific interaction parameters.

The LV community model embraces the previous theoretical formulations with the assumption of pairwise competitive species interactions,

$$\frac{\mathrm{d}n_i}{n_i\,\mathrm{d}t} = \left(K_i - \alpha_{ii}n_i - \sum_{j\neq i} \alpha_{ij}n_j \right). \tag{1.1}$$

Here $\alpha_{ij} > 0$ is the intraspecific ($j = i$) and interspecific ($j \neq i$) per capita interaction strength between species i and j, K_i is the maximum per capita growth rate for species i, and K_i/α_{ii} is the overall carrying capacity of species i in the absence of other species. In what follows below we will assume that there are P species in the regional pool. Note that there are no species-specific growth parameters, as justified in the derivation of the LV community model by Wilson *et al.* (2003) from a slightly more mechanistic model of births and deaths. Under this formulation K serves as both the maximum per capita growth rate and a factor in the carrying capacity for species i.

Each of the different species abundance models can be viewed from the LV model framework. The neutral model assumes $\alpha_{ij} = 1$ for all interactions and $K_i = K$ for all species. Under these assumptions, the zero growth condition for each species equilibrium density, n_i^*, yields the identical expression, specifically a constraint specifying $K = \Sigma_i n_i^*$. In other words, neutrality assumes that individuals of all species are competitively identical and can exclusively occupy one of the K locations in the local habitat. The deterministic equilibrium of such a system is that the average species has a density given by K/P; however, when stochasticity is added to a closed system (i.e. no immigration or speciation) under these conditions, it is inevitable that one species eventually dominates the system and excludes all others. Only immigration or speciation can permit the coexistence of multiple species, precisely equivalent to the dynamics of alleles in genetics models with drift (Caswell 1976): without mutation one allele is fixed at each locus.

Similarly, the broken-stick model begins with a stick of length K, the total density of all species according to the constraint $K = \Sigma_i n_i^*$. Given a pool of P species, $P - 1$ random values are chosen between 0 and K. The lengths of the P pieces can be interpreted as equilibrium species densities because all such choices yield a valid community equilibrium satisfying the constraint. Indeed, any method for choosing the random values that determine the breaks yields a valid equilibrium; however, the connection between the LV model and underpinnings for biased-breaking rules is difficult to interpret.

Finally, single-species stochastic birth–death models make an implicit assumption regarding the equality of species by replacing a single-species' temporal density distribution with a multispecies instantaneous density distribution. These models often include a carrying capacity for the single species (e.g. Leslie 1958; Leslie & Gower 1958). Neutral models represent an extension by

linking many species together into a stochastic birth–death framework (Caswell 1976; Bell 2000; Hubbell 2001), and one could consider the space unoccupied by other species as the incorporation of a dynamic, single-species carrying capacity (e.g. McKane *et al.* 2000). In most neutral models there is an explicit equality of species through the one-for-one replacement of individuals independent of their species identity, but this equivalence is not necessary; species-specific interaction strengths can be incorporated into the stochastic birth–death model framework (Leslie & Gower 1958). Finally, note that immigration (or speciation) is necessary for species coexistence in the neutral model, but is not necessary in the LV formulation, as long as intraspecific interactions exceed interspecific ones.

2. SPECIES DISTRIBUTIONS FOR CLOSED SYSTEMS

The term that presents the most mathematical difficulties (as well as most of the ecological realism) involves the interactions between species densities, and represents the term that we will focus upon. Before making any approximations, we can first rewrite a species' summed interspecific interactions as, $\Sigma_{j\neq i} \alpha_{ij}n_j = \psi_i\bar{n}(t) + \mathrm{Cov}(\alpha_{ix}, n_x)$, where $\psi_i = \Sigma_{j\neq i} \alpha_{ij}$ is a species' overall susceptibility to heterospecifics, $\bar{n}(t)$ is the average species density at time t, and $\mathrm{Cov}(\alpha_{ix}, n_x)$ is the covariance between heterospecific density and the focal species' interaction strengths (x represents the summed-over index). In this expression we have ignored the difference between the average species density and the average heterospecific density (excluding the focal species). This difference is of order P^{-1} and is therefore presumably negligible for large species pools. The mean field approximation takes the covariance term to be negligible (Wilson *et al.* 2003), or in other words, if a community contains many mutually interacting species, then the mean field assumption is that any particular interaction between two species has little influence on the density of either. Under this approximation, the mean-field LV community model, equation (1.1), becomes

$$\frac{\mathrm{d}n_i}{n_i\,\mathrm{d}t} = K_i - \alpha_{ii}n_i - \psi_i\bar{\boldsymbol{n}}, \tag{2.1}$$

which is dependent only on species-specific parameters and the average species density. Thus, we have replaced the complicated interactions with an approximate mean-field interaction between each species and the average species density. Clearly, approximate results are not exact ones, but mean-field results often provide a qualitatively useful insight (e.g. Huang 1987; Wilson 2000). Several more-refined approximations are available to test the accuracy of our mean-field results, but which approach is most appropriate is unclear: hence, we will compare our mean-field results to 'exact' results from numerical integrations. The mean field approach is useful because of its tractability, yielding solutions for community properties that depend on the means and variances of the model parameters (see also Jansen & Kokkoris 2003).

According to equation (2.1), the per capita growth rate of a particular species is a decreasing function of its own density, with zero growth at the value $[K_i - \psi_i\bar{n}]/\alpha_{ii}$. We

call these values the 'target densities',

$$\tilde{n}_i = \frac{K_i - \psi_i \bar{\bar{n}}}{\alpha_{ii}}, \tag{2.2}$$

where the average target density can be defined,

$$\bar{\bar{n}} = \frac{\bar{K}}{\bar{\alpha}_{\mathrm{I}} + (P-1)\bar{\alpha}_{\mathrm{H}}}. \tag{2.3}$$

In the above expressions, $\bar{K}$, $\bar{\alpha}_{\mathrm{I}}$, and $\bar{\alpha}_{\mathrm{H}}$ are the averages for the carrying capacity and intraspecific and interspecific interaction parameters, respectively. The average target density is the value consistent with allowing all species to take on their zero growth target densities. Our approximation assumes that all parameters are independently distributed. Under these definitions, some target densities take on negative values, clearly meaning they are unattainable as equilibrium densities.

There are several 'equilibria' discussed here that should be clarified as much as possible. Wilson *et al.* (2003) revisited how the LV equations arise from a more general model of births and deaths by Taylor series expansion about some set of species densities, which may or may not be an equilibrium of this general model. Given these LV equations with linearized per capita rates, there is one or more equilibria with densities $n_i^* \geqslant 0$, that may or may not differ from one or more of the equilibria of the general model. Only if the Taylor series is performed about one of the general model's equilibria will two of these equilibria, one from the general model and one from the LV model, be identical. By contrast, the target densities simultaneously satisfy the condition that all species' per capita growth rates, $\mathrm{d}n_i/n_i\,\mathrm{d}t$, are zero. The set of target densities for the full community does not represent the LV equilibrium because it contains negative values. Hence, there are three sets of densities: the equilibrium of a general nonlinear community model, the equilibrium densities $(n_i^* \geqslant 0)$ of the LV model, and the target densities from the LV model (which can take on positive and negative values).

3. TARGET DISTRIBUTIONS

Our primary goal is to derive the most fundamental measure of community structure: the relative species abundance distribution. According to equation (2.2), each species' target density depends on the species-specific parameters that determine its carrying capacity, its intraspecific interactions, and its susceptibility to heterospecifics. In turn, the susceptibility is composed of interaction strengths between each of the heterospecific species. It is not unreasonable to assume that each of these values are specific instances of values chosen from a probability distribution unique to each set of parameters. With no *a priori* expectation of the distribution from which these values are chosen, we assume standard deviations σ_{K}, $\sigma_{\alpha_{\mathrm{I}}}$, and $\sigma_{\alpha_{\mathrm{H}}}$, respectively, for the carrying capacity and intraspecific and interspecific interaction parameters. Using simple error propagation under the assumption of independent, normally distributed uncertainties, we obtain the distribution of target densities

$$\rho(\tilde{n}) = \frac{1}{\sqrt{2\pi}\sigma_{\tilde{n}}} \exp\left[-\frac{(\tilde{n} - \bar{\bar{n}})^2}{2\sigma_{\tilde{n}}^2}\right], \tag{3.1}$$

where

$$\bar{\bar{n}} = \frac{\bar{K}}{\bar{\alpha}_{\mathrm{I}} + (P-1)\bar{\alpha}_{\mathrm{H}}}, \tag{3.2a}$$

$$\sigma_{\tilde{n}}^2 = \left(\frac{\partial\bar{\bar{n}}}{\partial K}\right)^2\sigma_K^2 + \left(\frac{\partial\bar{\bar{n}}}{\partial\alpha_{\mathrm{I}}}\right)^2\sigma_{\alpha_{\mathrm{I}}}^2 + \left(\frac{\partial\bar{\bar{n}}}{\partial\psi}\right)^2\sigma_{\psi}^2$$
$$= \frac{1}{\bar{\alpha}_{\mathrm{I}}^2}\left(\sigma_K^2 + \bar{\bar{n}}^2\sigma_{\alpha_{\mathrm{I}}}^2 + (P-1)\bar{\bar{n}}^2\sigma_{\alpha_{\mathrm{H}}}^2\right). \tag{3.2b}$$

It was shown previously that the distribution of target densities for closed systems well represents the distribution of equilibrium densities that result from the numerical integrations of LV communities (Wilson *et al.* 2003). This more general expression—including variation in intraspecific interactions—establishes the relationship between the distributions of α and K and the abundance distribution of all species.

Figure 1*a* compares results from the analytic target distributions with results from numerical integrations for the base parameters used by Wilson *et al.* (2003) with and without variation in intraspecific interaction strengths. Minimal differences are observed, implying that the effect of intraspecific interaction strengths can be taken into account by appropriately rescaling the expected value for the carrying capacity and interspecific interaction strengths. Thus, for the remainder of this paper we will not consider variation in intraspecific interactions.

Accuracy of the target densities as predictors of the equilibrium distribution is displayed in figure 1*b,c*. Figure 1*b* compares target densities against equilibrium densities for a single, randomly selected set of carrying capacities and interaction strengths. Target densities are spread over a large range of positive and negative values, and these values are compared against species densities at $T = 2000$, determined from a numerical integration beginning with random initial densities. The dashed line compares the average target density with the average equilibrium species density (including the extinct species). We observe that all species with negative target densities become extinct in the numerical integration, but many species with positive densities are also eliminated. It was previously demonstrated that the average target density is preserved during the temporal evolution of the LV community (Wilson *et al.* 2003), and having these species with positive target densities eliminated helps preserve that average value. The concurrent elimination of these positive target density species is demonstrated in figure 1*c*, where we illustrate a pruning process that successively removes species with negative target densities. Pruning takes place as follows. For the run shown in figure 1*b*, all species with negative target densities are removed from the system, and we then recalculate the average carrying capacity, susceptibilities, and average target density of the remaining species. This recalculation yields the target densities showing for the second iteration, after which we repeat the pruning process. By the fourth iteration in this case, all species have positive target densities, which are then compared with the final densities from the numerical integration. Except for one species in this set, this iterative process accurately removes all of the species with positive target densities that are doomed to extinction in the numerical integration of this randomly selected community. Repeating this pruning process for
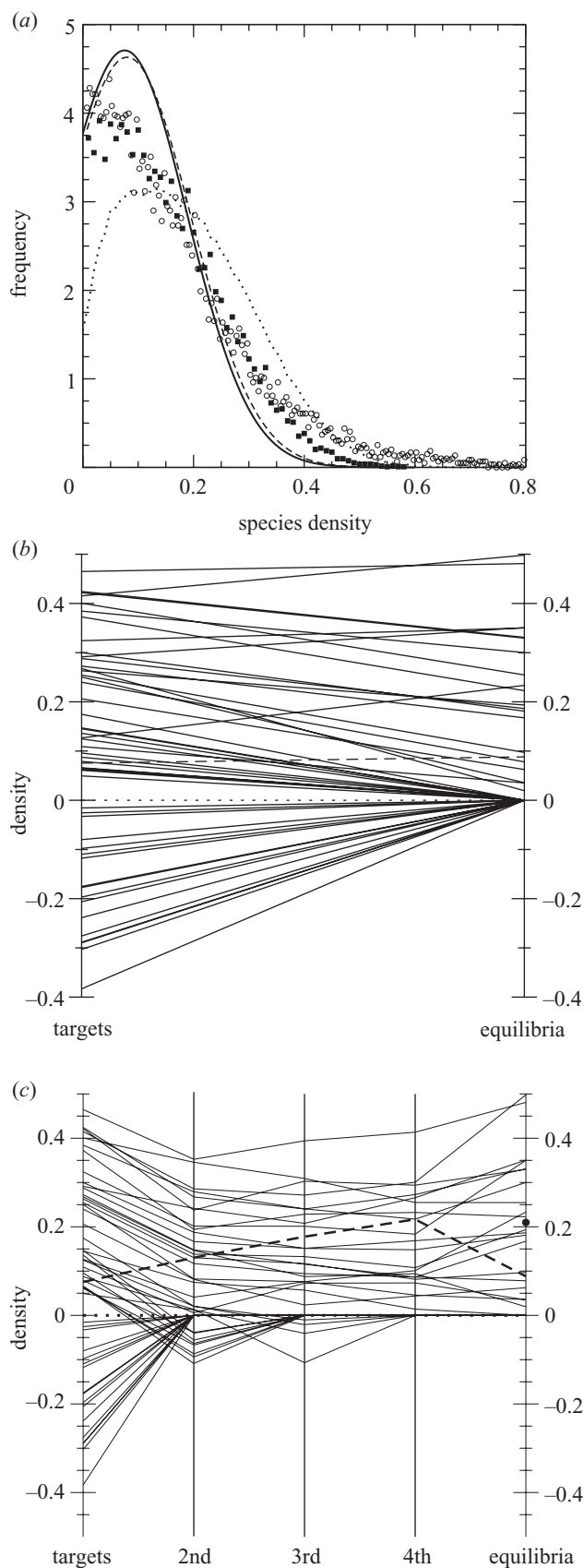
Figure 1. Comparisons of analytic and numerical abundance distributions. (*a*) Analytic distributions are determined by the target densities normalized by the species number with positive target densities. Numerical distributions arise from Runge–Kutta numerical integration of random LV communities. In both cases we compare situations with and without variation in intraspecific strengths, and find that results are insensitive to this variation. Squares, intraspecific fixed; circles, intraspecific variation; dashed line, targets with variation; solid line, target distribution; dotted line, iterated target distribution. (*b*) A comparison between the predicted target densities and of the final equilibrium abundances for a single run indicates that all negative target density species go extinct, but many species with positive target densities also perish. (*c*) Successive pruning of species with negative target densities and recalculation of the remaining target densities quite accurately predicts most species that go extinct in the numerical integration, but does not quite capture the remaining distribution, as observed from the pruned distribution in (*a*) calculated over 1000 randomly chosen LV communities.

resultant distribution from that of the initial target distribution, as observed in the numerical integration results. The discrepancy is probably due to both long-term transients in the numerical iterations and inaccuracies in the approximations leading to the target distribution, however, the details will only be determined from a more exact analysis.

4. EFFECTS OF SPECIES IMMIGRATION

Any immigration from a regional pool ensures that a species will have a presence in the local pool, independent of whether the species has a positive or negative target density. To calculate the distribution of the target densities for an open system, we again concentrate on a focal species i which alone has immigration I,

$$\frac{\mathrm{d}n_i}{\mathrm{d}t} = I + n_i(K_i - \alpha_{ii}n_i - \bar{n}\psi_i), \tag{4.1}$$

and calculate its altered target density, $\tilde{n}_i'$, from the zero growth condition,

$$0 = I - \alpha_{ii}\tilde{n}_i'(\tilde{n}_i' - \tilde{n}_i), \tag{4.2a}$$

$$\tilde{n}_i' = \frac{1}{2}\left(\tilde{n}_i + \sqrt{\sqrt{\tilde{n}_i^2 + 4I/\alpha_{ii}}}\right). \tag{4.2b}$$

This calculation assumes that the average target density is unchanged by this focal species immigration. When the immigration rate is extremely small, the altered target density is approximately equal to $I/\alpha_{ii}|\tilde{n}_i|$ for species with negative target densities, demonstrating that any amount of immigration produces a positive target density, as expected for an open system.

Figure 2*a* shows the construction for determining altered target densities by setting the altered target density $\tilde{n}_i' = \tilde{n}_i + a$, where a is to be determined. The construction arises from substituting into equation (4.2*a*), giving

$$I'/a = \tilde{n}_i + a, \tag{4.3}$$

where $I' = I/\alpha_{ii}$ is a relativized immigration rate. Immigration thus maps species with target densities between $\tilde{n}$

1000 random communities yields the species abundance distribution shown in figure 1*a*, which, when compared with the numerical integration results, underpredicts the frequency of low species abundances. One feature that is recovered, however, is an increase in the width of the
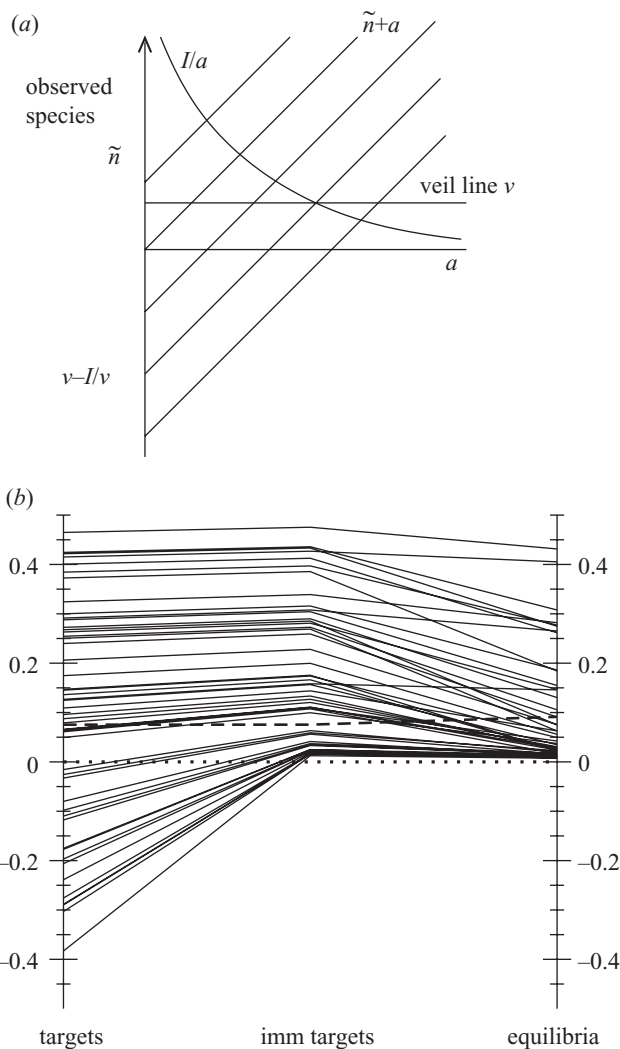
Figure 2. (*a*) A caricature of the construction for determining the effects of immigration on target densities as calculated from equation (4.3). With immigration, all species have a positive target density, although with the inclusion of a veil line, some species densities are unobserved. (*b*) For the same run shown in figure 1*b*, we compare the pre-immigration target densities with the target densities, given immigration and the final equilibrium densities resulting from the numerical integration.

and $\tilde{n} + \mathrm{d}\tilde{n}$ to altered target densities between $\tilde{n}'$ and $\tilde{n}' + \mathrm{d}\tilde{n}'$. From this mapping to equation (3.1), we can calculate the distribution of target densities with immigration from the expression,

$$\rho(\tilde{n})\,\mathrm{d}\tilde{n} = \rho(\tilde{n}')\,\mathrm{d}\tilde{n}' \Rightarrow \rho(\tilde{n}') = \rho(\tilde{n})\frac{\mathrm{d}\tilde{n}}{\mathrm{d}\tilde{n}'}, \quad (4.4)$$

where the change of variable can be determined from equation (4.2*a*),

$$(2\tilde{n}'_i - \tilde{n}_i)\,\mathrm{d}\tilde{n}'_i = \tilde{n}'_i\,\mathrm{d}\tilde{n}'_i \Rightarrow \frac{\mathrm{d}\tilde{n}_i}{\mathrm{d}\tilde{n}'_i} = \frac{2\tilde{n}'_i - \tilde{n}_i}{\tilde{n}'_i}. \quad (4.5)$$

Below, we will assume that this construction holds for all species having simultaneous immigration. This connection is demonstrated in figure 2*b*, where we compare the pre-immigration target densities against the target densities with immigration and the equilibrium densities resulting

from the numerical integration. Extinct species are clearly 'rescued' by immigration.

Figure 2*a* also characterizes the influence of a veil line, v, above which species abundances, $\tilde{n}'_i > v$ are observed. In the absence of immigration, the minimum observed target density is just the veil line. Immigration reveals species with target densities between $(v^2 - I)/v$ and v because their densities are pushed above the observable limit. Thus, one expression for the size of the community is the integral from $(v^2 - I)/v$ up through all positive target densities,

$$\frac{S}{P} = \int_{v-1/v}^{\infty} \rho(\tilde{n})\,\mathrm{d}\tilde{n} = \int_{v}^{\infty} \rho(\tilde{n}')\,\mathrm{d}\tilde{n}'. \quad (4.6)$$

When all species can immigrate into the local community from the regional pool and the veil line is set to zero density, then all species in the regional pool are also members of the observed local community.

5. OPEN SYSTEM ABUNDANCE DISTRIBUTIONS

We now consider how immigration alters the expected distributions of species abundances. Figure 3 shows the results for the species abundances distributions for a variety of immigration rates. All distributions are unnormalized, which is equivalent to being normalized to the fraction S/P.

Figure 3*a* shows the results for numerical integrations of randomly assembled LV communities. Figure 3*b* shows the results for the calculations of the target density distributions using the standard deviations implemented in the numerical integrations. Agreement is good for low immigration rates, but for the highest rate of immigration the target density distribution's peak height is much too low compared with the results observed in the numerical simulations. In figure 3*c* we plot the results of the target density distributions using standard deviations that are twice that used in the numerical integrations, an increase motivated by the observation of a wider distribution resulting from the pruning of target densities (figure 1*c*). Agreement between the target density results and the numerical integrations is improved with the wider distributions.

Figure 4*a* plots the numerical integration results according to logarithmic bins. Here we clearly observe left-skewed species abundance distributions which appear much like the empirical distributions presented by Hubbell (2001) and by Nee *et al.* (1991). Increasing the immigration rate brings many of the extinct species into the positive density realm, yielding a significant peak at low densities. Again, figure 4*b* shows the results for the target densities with the given standard deviation, and figure 4*c* shows the results for the target densities using standard deviations that are twice that used in the numerical integrations. With this larger variability we can see more significantly the bimodality that occurs with increasing immigration rate and is clearly present in the numerical simulations. Bell (2000) also observed bimodality when making a distinction between persistent and occasional species.

6. DISCUSSION AND CONCLUSIONS

We have demonstrated several new and interesting aspects of predicting species abundance distributions using the target density distributions that arise from the mean-field approximation to the LV community model (Wilson *et al.* 2003). First, the inclusion of species-specific intraspecific
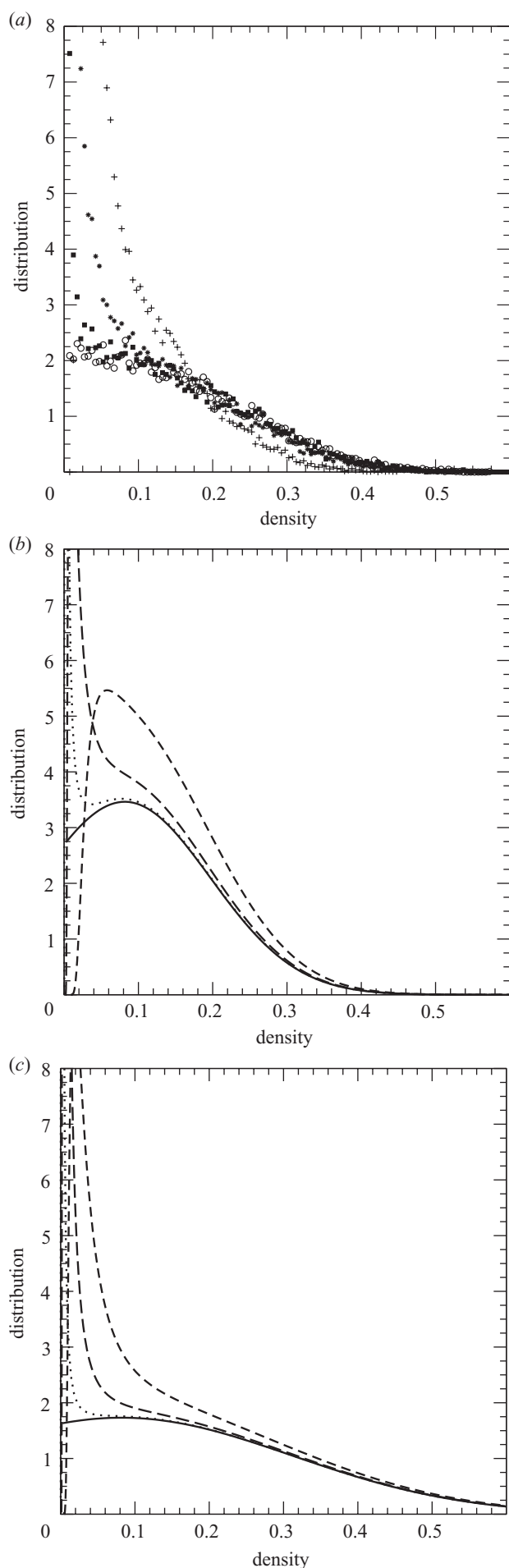
(a)

(b)

(c)

Figure 3. (*a*) Results from numerical integrations with varying degrees of immigration. Species having negative target densities bunch up at the very low equilibrium densities. Open circles, $I = 0$; filled squares, $I = 0.0001$; filled circles, $I = 0.001$; plus symbols, $I = 0.005$. (*b*) Target densities calculated from equation (4.4), that includes the influence of immigration, with the mean and standard deviations calculated from the zero-immigration case. Solid line, $I = 0$; dotted line, $I = 0.0001$; long dashes, $I = 0.001$; short dashes, $I = 0.005$. (*c*) An increased standard deviation provides better agreement with the numerical results, indicating that correlations developed between species densities is an important influence. Solid line, $I = 0$; dotted line, $I = 0.0001$; long dashes, $I = 0.001$; short dashes, $I = 0.005$.

interactions strengths appears to have no important consequences on the resultant abundance distributions from either the perspective of target densities or numerical integrations. This conclusion, however, must be limited to the case in which intraspecific interaction strengths exceed interspecific interaction strengths. If a species' intraspecific interaction strength is chosen such that its interspecific interactions are greater, then that species' population density may grow to dominate the community (results not shown). Second, previous results indicated that the target distribution provides a good approximation of the equilibrium community when properly normalized. This approximation relied upon the removal of species having negative target densities, but keeping all others in the community. Here we have shown that an iterative process that successively removes species with negative target densities partially accounts for differences between the initial target density and numerical integration results. This pruning process also accounts for the preservation of the average target density as a measure of the overall equilibrium density in the equilibrium community. It also predicts a widened distribution of species abundances, observed in the numerical results; however, an in-depth mathematical analysis will be necessary to understand this prediction fully. These aspects represent competing influences on the temporal evolution of the community. On the one hand, Wilson *et al*. (2003) demonstrated that the community tends to develop while preserving the target distribution, but on the other hand, as species with negative target densities are removed from the system, the target distribution changes because of the selective removal of species with specific properties for their parameters.

In summary, we examined communities subject to immigration from a global species pool and demonstrated that target density distributions of mean-field LV communities capture the general form of equilibrium density distributions. Immigration strongly affects these important community patterns. On a linear abundance scale, weak immigration crowds the species with negative target densities (under zero immigration) very close to zero density, resulting in a peak in the species distribution. On a logarithmic scale the distributions show a strong left-skew, even for cases without immigration. We have thus shown that the LV theory of biodiversity serves as a theoretically parsimonious and operational template for most, if not all, community properties. Instead of being regarded as a historical pedagogue inferior to biocomplex models, it should be expanded and extended, with its full potential carefully
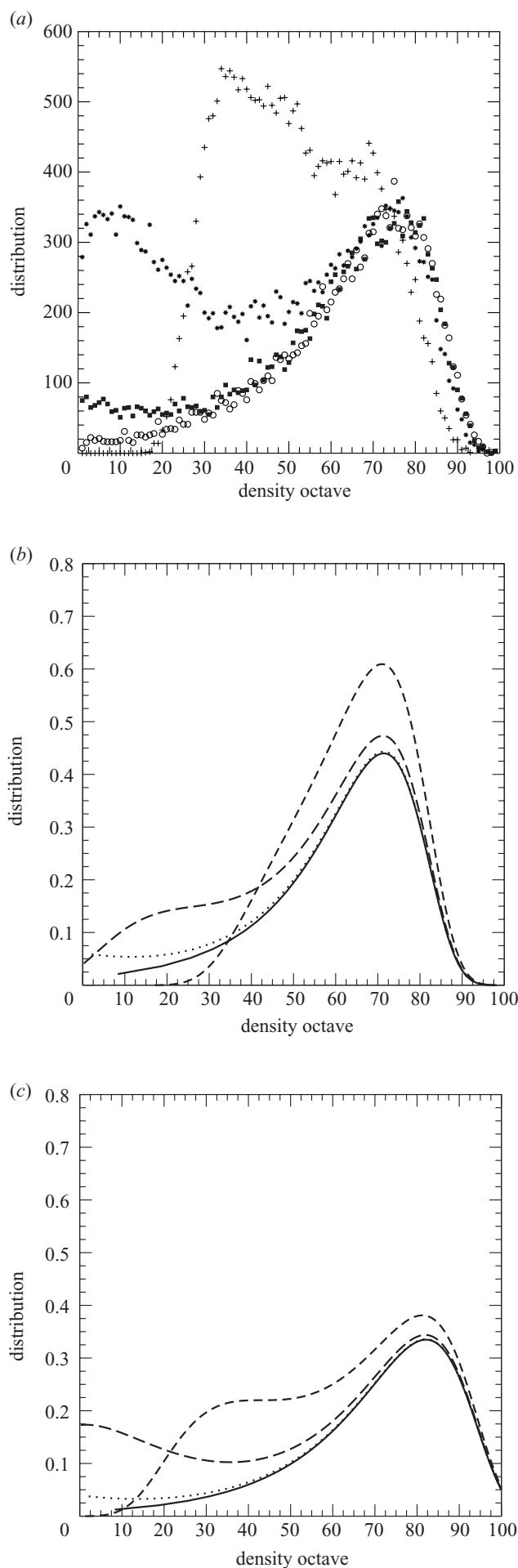
(a)

(b)

(c)

Figure 4. Results from figure 3 plotted on a logarithmic axis. (a) Results from the numerical integration collected in logarithmic bins of equal size. Open circles, $I = 0$; filled squares, $I = 0.0001$; filled circles, $I = 0.001$; plus symbols, $I = 0.005$. (b) Logarithmic distribution of the target densities for the different levels of immigration using the zero immigration standard deviation. Solid line, $I = 0$; dotted line, $I = 0.0001$; long dashes, $I = 0.001$; short dashes, $I = 0.005$. (c) Doubling the standard deviation yields distributions that closer approximate the bimodality observed in the numerical results. Solid line, $I = 0$; dotted line, $I = 0.0001$; long dashes, $I = 0.001$; short dashes, $I = 0.005$.

studied, and considered as a viable alternative to more sophisticated models of community structure and assembly. Future work will concentrate on extending the LV community model to multiple trophic levels.

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