

Scale-dependence of resource-biodiversity relationships

to appear in *J. Theor. Biol.*

Joshua S. Weitz^{1,2,*} and Daniel H. Rothman^{2,†}

¹ *Department of Physics, Massachusetts Institute of Technology, Cambridge, MA 02139.*

² *Department of Earth, Atmospheric, and Planetary Sciences,
Massachusetts Institute of Technology, Cambridge, MA 02139.*

(Dated: June 4, 2003)

The functional relationship between resource availability and species-richness is addressed at different spatial scales. We analyze the smaller, community, scale by using a multi-species contact process coupled to a heterogeneous landscape, i.e. a stochastic spatial model of individual behavior in a system with limited resources. Using percolation theory, the theory of competitive exclusion processes, and the results of Monte Carlo simulations we show that a unimodal resource-species relationship may be understood as a tradeoff between the availability and connectivity of resource patches. We then pose the question of how resource-species relationships may be scaled up to the larger, regional, level and discuss the theoretical basis for differences in behavior at different scales. Regional ecosystems are modeled as statistical aggregates of dynamically driven small-scale ecosystems. Observing a transition from a unimodal relationship at small scales to a monotonically increasing relationship at large scales is shown to be contingent on the presence of a resource-dependent species pool. Finally, we confirm our theoretical prediction of a transition via Monte Carlo simulations of regional landscapes and discuss the potential complicating effects of spatial correlations in the distribution of both resources and species.

I. INTRODUCTION

The organization of ecosystems depends, in part, upon the utilization and availability of resources. Given conditions necessary for life, what types of arrangements will result and in what manner will they persist? The study of ecosystem function attempts to formalize the analysis of disparate communities by considering relationships between macroscopic ecosystem indicators [1, 2]. For example, do changes in total species richness tend to stabilize or destabilize ecosystems [3–5]? Likewise, how does species richness relate to various proxies for ecosystem productivity [6] such as resource levels [7], net energy input [8–10], or biomass [11].

The study of ecosystem function is also concerned with the effect of biodiversity loss on ecosystem processes [12], the influence of landscape scale [13], and the relevance of functional relationships amongst ecosystem indicators to historical patterns [14]. Of these added complexities, we are most concerned here with the analysis of ecosystems at a variety of scales. The importance of landscape scale in shaping system dynamics, the scope of ecological interactions, and the relevance of fluctuations has been known for quite some time [15]. As measurement continues to afford more detailed views of ecosystem behavior, theory must provide a means to reconcile observations at the smaller, community level with those at the larger, regional and global scales. One interesting method involves scaling up individual based simulators of vegeta-

tion dynamics that rely on empirical fits of physiological and ecological parameters [16]. An alternative approach, presented here, is to develop a methodology to analyze how basic theoretical descriptions of community behavior may be “scaled up.” At the larger, regional, level, we may then ask if and how the fundamental relationships between ecosystem indicators change.

The relationship between productivity and diversity is one example where landscape scale possibly modifies the qualitative relationship between ecosystem indicators [17–20]. A recent literature review by Waide et al. [17] suggests that at local and community scales ($\lesssim 20$ km), plant biodiversity is often a unimodal function of productivity, in agreement with a wide range of studies [7, 21], however see Abrams [22] for an alternative perspective. The same study by Waide et al. [17] shows that at regional and global scales ($\gtrsim 4000$ km), plant biodiversity is predominantly a monotonically increasing function of resources, in accord with previous empirical findings [9]. A pictorial summary of such observations is presented in Figure 1 and forms the basis of our line of enquiry.

An independent study by Chase and Leibold [20] tests the productivity-diversity relationship in the context of pond ecosystems. There they find a unimodal relationship when comparing individual ponds and a linearly increasing relationship when those ponds are grouped within a watershed. The transition, in this case, is explained as a result of an observed correlation between species dissimilarity and ecosystem productivity.

In this paper we explore the possibility that resource heterogeneity and community history provides a stochastic, spatial mechanism to explain the scale-dependent transitions summarized in Figure 1. Of the many possible indicators of productivity and diversity, we choose

*Electronic address: jsweitz@segovia.mit.edu; Author to whom correspondence should be addressed

†Electronic address: dan@segovia.mit.edu

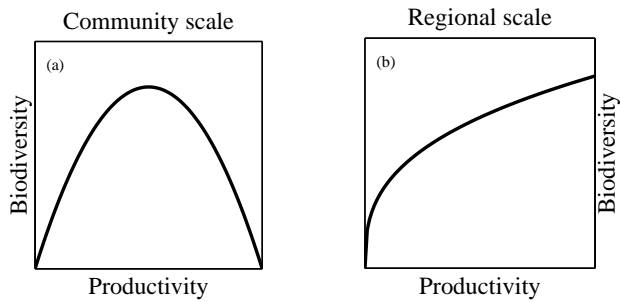


FIG. 1: Schematic of commonly observed relationships between productivity and biodiversity at the (a) smaller, community scale and at the (b) larger, regional or global scale.

to consider the relationship between resource availability and species richness. We begin with the assumption that the monotonically increasing relationship is to be expected at larger scales, an assumption well borne out by empirical data [8–10], and do not attempt to derive this from first principles. Our objective, therefore, is to present a testable quantitative mechanism that applies to both small and large scale communities. A secondary aim is to test whether such a transition is possible even in the absence of niche-differentiation amongst species [23].

We begin by introducing an artificial ecology, the multi-species contact process [24–27], which we use to analyze the dynamics and composition of local ecosystems. We then apply this stochastic spatial model to a community limited by heterogeneously distributed resources. We find that a unimodal relationship between resource availability and species richness at the community scale arises as a trade-off between the availability and connectivity of resource patches. We further test our stochastic representation of community behavior by analyzing rank-abundance relations and find that they are in good agreement with generic curves typically observed in forest communities. We then construct regional level ecosystems as dynamical statistical aggregates of local ecosystems. The behavior of these aggregates are used to calculate the change in the peak of the resource-species relationship with increasing scale. At larger scales, the transition to a linearly increasing relationship depends on the species pool of the regional landscape. Once the basic mechanism for a scale-dependent transition is established, we consider how correlations in species and resource distributions modify the transition.

II. THE MODEL

The dynamics of any choice of artificial ecology depends on the mathematical description of individual behavior, the distribution of resources, as well as initial conditions and boundary effects [28–30]. We choose

to consider a class of models called contact processes [24, 26, 27, 31]. Contact processes are characterized by local death and dispersal and are often used to mimic the behavior of sessile organisms such as plants and trees [25]. The multi-species contact process is of interest in ecology because of its generalizations to systems with hierarchical [25] or neutral [32] community structure. In this paper we will focus primarily on neutral models, i.e. stochastic models where all species behave in a statistically identical fashion and are distinguished by a unique marker. Such systems have proven to be surprisingly instructive as a means to understand aspects of community structure such as rank abundance distributions and species-area laws [32, 33].

The particular variant of contact processes we use is, following the terminology of Dickman and Moreira [34], a neutral multi-species contact process with dilution. It is essentially a model which couples the interaction of sessile organisms to a patchy landscape and restricts dispersal to certain sites [35]. The dynamics of the model are as follows: individuals are distributed on a $L \times L$ lattice, of which only a fraction $\bar{\eta}$ of the lattice sites are available for colonization. Individuals disperse seeds locally (nearest neighbors only) at a rate c and die at a rate m . The system is also subject to a global “seed rain” at a rate h . These basic mechanisms are sketched in Figure 2, keeping in mind that seeds only survive on unoccupied sites. Because this is a neutral model, individuals of all species disperse and die at the same rates. The dynamics of this system may therefore be expressed in terms of two dimensionless ratios, $\lambda \equiv c/m$ and $\theta \equiv h/m$.

In this paper, we typically consider cases of fast dispersal, $\lambda \gg 1$, and slow immigration, $\theta \ll \lambda$, to ensure long-term survival of patches in the large-system limit. Our use of slow immigration rates, $\theta \ll \lambda$, may also be viewed as a consequence of the spatially heterogeneous resource landscape across which long distance dispersal is unlikely. Given a choice of λ and θ , the distribution of species on the landscape is defined by $s(\mathbf{x})$, a scalar field whose value is a unique marker distinguishing different species. The absence of an individual at a particular site \mathbf{x} is defined by $s(\mathbf{x}) = 0$. The total number of species, $S(t)$, is equal to the total number of unique, non-zero markers on the lattice.

Much of the qualitative differences in community dynamics depends on the resource landscape, $\eta(\mathbf{x}) = \{0, 1\}$, a Boolean field whose spatial average is the mean resource availability,

$$\bar{\eta} = \frac{1}{L^2} \sum \eta(\mathbf{x}). \quad (1)$$

Note that when $\bar{\eta} = 0$ all sites are unsuitable for colonization and the system is bound in a permanently empty state. When $\bar{\eta} = 1$ every site is available for colonization. At intermediate values of $\bar{\eta}$ the species compete over what is essentially a set of percolation clusters, i.e. connected sites on a lattice [36]. Examples of typical lattices for a range of $\bar{\eta}$ can be found in Figure 3. The connection

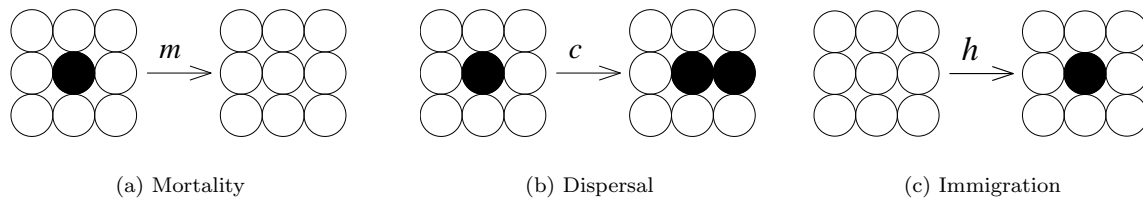


FIG. 2: Fundamental dynamics of the contact process, (a) individuals die at a rate m , (b) seeds are dispersed locally at a rate c , and (c) immigration takes place at a rate h .

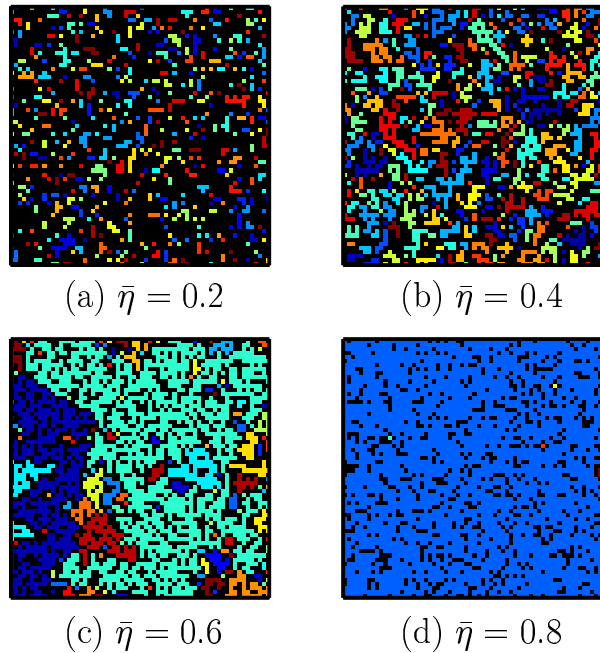


FIG. 3: Examples of percolation clusters on lattices in (a)–(d) where $\bar{\eta} = 0.2, 0.4, 0.6$ and 0.8 respectively. Every separate cluster (a connected set of sites where $\eta(\mathbf{x}) = 1$) is marked by a randomly chosen color. All inaccessible sites, $\eta(\mathbf{x}) = 0$, are marked in black.

to percolation theory will be useful in developing insight into the results from stochastic simulations of a neutral contact process implemented on a spatial grid.

Finally, it is worth noting that when we calculate the relationship between resource availability and species richness at the community level, we are comparing $\bar{\eta}$ to $S(t)$ during an equilibrium state. The mean resource availability, $\bar{\eta}$, is presumed to be a characteristic of the local community whereas the species richness $S(t)$ is a consequence of it.

III. RESOURCE AVAILABILITY AND SPECIES RICHNESS AT THE COMMUNITY SCALE

In this section we propose a series of small-scale, community level models for which a well-defined notion of “resources” and “biodiversity” may be used to classify and compare landscapes. Our primary aim is to quantify the relationship between species richness, $S(t)$, and mean resource availability, $\bar{\eta}$, in the context of a neutral model of ecological dynamics. The notion that heterogeneity might explain why resources and biodiversity are unimodally related has already been proposed [37]. As such, a secondary aim of this section is to formally extend the heterogeneity theory of biodiversity to a system amenable to analysis at multiple scales. We begin with a discussion of the contact process where $\lambda = \infty$, for which long-term dynamics are nearly equivalent to the statistics of percolation clusters. We then discuss the contact process with finite λ . Finally, we briefly examine how changes in θ affect patterns of diversity at the community scale, and in so doing propose conditions for which a scale-dependent transition may be observed.

A. Contact processes with $\lambda = \infty$

In a contact process where $\lambda = \infty$ every individual who dies is immediately replaced by a randomly chosen neighbor. This leads to a maximally occupied ecosystem, where individuals occupy every allowed lattice site; a situation especially relevant to dense forest ecosystems [32]. Due to this effectively infinite re-colonization rate, Monte Carlo simulations of such systems persist indefinitely, even in the absence of immigration, $\theta = 0$. For the present, resource levels $\eta(\mathbf{x})$ are modeled as Boolean landscapes generated by a Poisson process such that their spatial covariance (two-point correlation function) has the following structure:

$$\langle \eta(\mathbf{x})\eta(\mathbf{y}) \rangle = \begin{cases} \bar{\eta} & \text{if } \mathbf{x} = \mathbf{y}, \\ \bar{\eta}^2 & \text{otherwise.} \end{cases} \quad (2)$$

Such a lattice is composed of a number of independent clusters on which species may live, spread and die out as already described in Figure 3.

A contact process with $\lambda = \infty$ is equivalent to the voter model with exponentially distributed waiting times between votes at any location [29]. As is well understood for the voter model, each cluster functions as an isolated island and eventually becomes a monoculture. Since islands are disconnected the total number of species is equal to the total number of islands greater than unit size; islands of unit size will eventually be vacant because once an isolated individual dies there are no neighbors to replace it. Determining the total number of islands as a function of the resource level may be framed in the language of percolation theory. Such a calculation is equivalent to computing the integral of the cluster distribution $c_n(p)$ [36, 38], where $c_n(p)$ is the normalized number of clusters of size n in a lattice with occupation density p . Given a lattice of size $L \times L$ and a site occupancy probability p , the total number of clusters per lattice site, $\hat{c}_L(p) = L^{-2} \sum_n c_n(p)$, has a well defined thermodynamic limit. In fact, $\hat{c}_L(p)$ is a *unimodal* curve whose maximum p_{max} lies below the critical point p_c [38].

The unimodal relationship between total number of clusters and occupation density could have been qualitatively anticipated from the simple calculation of the variance σ^2 present in a lattice with occupation density p , $\sigma^2 = p(1 - p)$. When resources are low the lattice is nearly uniformly barren, while when resources are high the situation is symmetric, except the lattice is now nearly uniformly occupied. The maximum number of clusters is at an intermediate occupation level (Figure 3 serves as a useful visual reference). This implies that the maximum number of patches on which species may exist is at an intermediate value of $\bar{\eta}$. In other words, $S(t)$ is unimodally related to $\bar{\eta}$ when $\lambda = \infty$ and $\theta \simeq 0$. Although a unimodal relationship arises naturally from percolation theory, we proceed to investigate how this result changes when local dynamics are included via the use of a finite λ .

B. Contact processes with finite λ

When considering simulations of contact processes with finite $\lambda \gg 1$ and $\theta \simeq 0$, the death of an individual is not immediately replaced by an individual of a neighboring site. But the essence of the results of the previous section still hold, as we are about to show. The Monte Carlo simulations in this section are initialized with a maximally diverse initial condition. For every occupied site in the lattice we assign an individual with a unique species marker. If $S_{\bar{\eta}}(t)$ denotes the number of species alive at time t for a system with resource availability $\bar{\eta}$, then $S_{\bar{\eta}}(0) \approx \bar{\eta}L^2$. The presence of an absorbing state implies that $S_{\bar{\eta}}(t \rightarrow \infty) \rightarrow 0$ for any finite size lattice. When θ is small, but finite, this absorbing boundary condition vanishes. The steady flux of individuals, which can be seen as a way to couple local communities to regional species pools, leads to a fluctuating steady state in $S_{\bar{\eta}}(t)$. Both asynchronous and synchronous updates are used for

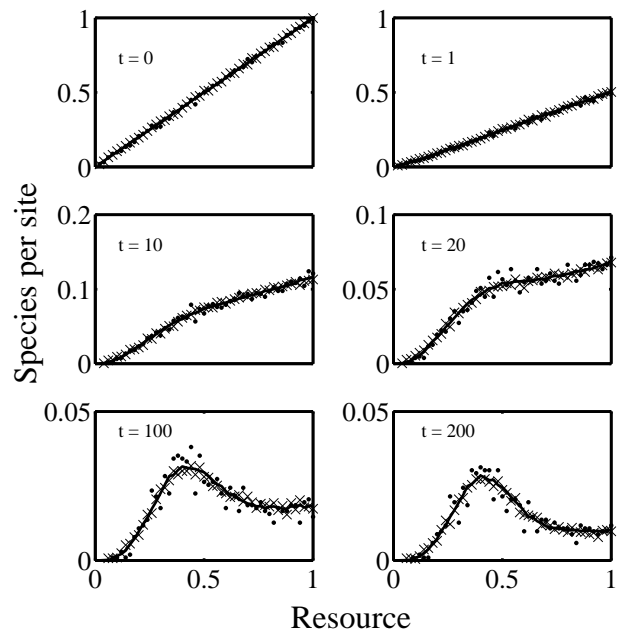


FIG. 4: Species–resource relations, $S_{\bar{\eta}}(t)/L^2$ vs. $\bar{\eta}$, for simulations of contact processes with $\lambda = 50$ and $\theta = 0$. Lines, \times -marks, and dots are from simulations where $L = 256, 64$ and 32 respectively. All times are in dimensionless units, $t \rightarrow mt$.

Monte Carlo simulations; neither approach changes the results in a substantive fashion.

Given initial conditions, the species richness $S_{\bar{\eta}}(t)$ depends on the local extinction of small patches as well as on the assimilation of patches of all scales into monocultures. The time scale of local extinction increases exponentially with the size of the patches [26]. At longer time scales monocultures will begin to emerge on larger patches leading to a decline of $S_{\bar{\eta}}(t)$. Typical numerical results are summarized in Figure 4 where simulations on lattices where $L = 32, 64$ and 256 are reported for the parameters $\lambda = 50, \theta = 0$. All plots in Figure 4 depict the normalized number of species per site, $S_{\bar{\eta}}(t)/L^2$, vs. the mean resource availability, $\bar{\eta}$. Notice that $S_{\bar{\eta}}(t=0)/L^2 \approx \bar{\eta}$ because of the initial conditions, but that slowly the species richness declines at all levels. $S_{\bar{\eta}}(t)$ eventually develops a peak at intermediate t which then stabilizes for $t \gg 1$. Even for $t \gg 1$, $S_{\bar{\eta}}(t) > 1$ because of the slow time scales over which a contact process without displacement may replace a species.

The behavior for $\bar{\eta} \approx 1$ is that of many species interacting on a well-connected landscape. Some aspects of the steady state behavior of interacting particle systems with low relative mortality rates often approaches that of a non-spatial model. The dynamics of $\rho_i(t)$, the density of sites occupied by species i , may be approximated by ignoring spatial structure, i.e. correlations. Such an approximation is referred to as mean field theory. For a contact process with $\theta = 0$, the mean field description of

the system is [26, 39]

$$\frac{d\rho_i(t)}{dt} = \lambda\rho_i \left(\bar{\eta} - \sum_{j=1}^{\hat{D}} \rho_j(t) \right) - \rho_i(t), \quad (3)$$

where \hat{D} is the maximal number of species. The term in parentheses limits the total density of species to be less than or equal to $\bar{\eta}$, the density of sites available for colonization. One possible steady state of this system is that $\rho_i(t) = 0$ for each of the \hat{D} species. There is also a hypersurface of non-trivial fixed points that satisfy the condition

$$\sum_{i=1}^{\hat{D}} \rho_i(t) = \bar{\eta} - \frac{1}{\lambda}. \quad (4)$$

Because the logarithmic rate of change of species density, $d \log \rho_i(t)/dt$, is identical, the ratios between species densities $\rho_i(t)/\rho_j(t)$ remain fixed for the entire dynamics. Trajectories move in phase space to the hypersurface of fixed points, and multiple-species coexistence is possible. However, any competitive advantage (for example if rates of dispersal differ, even infinitesimally) will eliminate the possibility of coexistence. Instead, a single stable fixed point emerges where one species dominates the others, a process analogous to competitive exclusion [40–42].

In a spatial implementation of a neutral model, effective differences in dispersal ability arise because of the distribution of species inside percolation clusters. Those differences in dispersal effectiveness, in addition to the inevitable effects of demographic stochasticity, lead to a diversity collapse. For low resources, $\bar{\eta} \approx 0$, the long-term species level $S_{\bar{\eta}}(t)$ is small because it is unlikely for many species to persist on a set of disconnected patches. When resources are high, $\bar{\eta} \approx 1$, isolated patches die off, leading to homogeneous systems whose largest patch is dominated by a small subset of species. At an intermediate value of $\bar{\eta}$ the trade-off between opportunity and connectivity leads to a maximal number of species. The unimodal curve remains a feature of systems for finite λ just as it is for systems where $\lambda = \infty$.

C. Implications and extensions of the community model

Thus far we have shown that when the dimensionless immigration rate $\theta \simeq 0$, then a contact process for which $\lambda \gg 1$ coupled to a heterogeneous landscape yields a unimodal relationship between species richness and resource availability. We now assess the robustness of the conditions under which such a community-level relationship should be expected to hold.

Consider first what happens when we implement the model with finite colonization rate λ and finite immigration rate θ . In this case patches that become vacant are not bound to be permanently extinct. In essence, the

inclusion of immigration permits a regional species pool to re-stock local communities. If the number of species in such a pool, \hat{D} , is finite, then the mean field equations for the dynamics of species densities becomes [26, 39]

$$\frac{d\rho_i(t)}{dt} = (\lambda\rho_i + \theta/\hat{D}) \left(\bar{\eta} - \sum_{j=1}^{\hat{D}} \rho_j(t) \right) - \rho_i(t), \quad (5)$$

where we assume all species from the pool \hat{D} have an equal chance of immigrating. Mean field theory once again spuriously implies that either all species co-exist or none do.

However, the equilibrium value of $S_{\bar{\eta}}(t)$ from numerical simulations increases monotonically with θ . The relevant point here is that so long as $\theta \ll \lambda$, the presence of immigration merely stabilizes the diversity, leading to a true, fluctuating equilibrium state for $S_{\bar{\eta}}(t)$. Furthermore, the equilibrium species richness $S_{\bar{\eta}}(t)$ remains unimodally related to $\bar{\eta}$. When $\theta \gg \lambda$, then immigration events dominate the dynamics, and simulations exhibit a monotonic relationship between resource availability and species richness.

In light of these observations, it appears that the multi-species contact process with $\lambda \gg 1$ and $\theta \ll \lambda$ is a suitable candidate of a “model” community, collections of which may then be aggregated to represent behavior at the regional scale. As a further test of the community level model, we calculate a generic feature of ecosystems, namely the rank abundance relationship, the details of which are included in Appendix A. The results are consistent with an S-shaped curve observed in similar models [30] and from empirical observations on plant and tree communities [32].

We now turn to explain how statistical aggregates of community level ecosystems may be constructed, and in so doing analyze the relationship between resource availability and species richness at larger length scales.

IV. SCALING UP ECOSYSTEM RELATIONSHIPS

In this section we outline and test a framework to scale-up a known resource-diversity relationship at the community scale to the regional level. In principle, we may imagine constructing a network of community sites, each of which have a resource level $\bar{\eta}(\mathbf{x})$ and a collection of species which exist at that site. If these sites are grouped together spatially, what can we say about the relationship between resources and species richness at each higher level of grouping? The resulting relationship depends primarily on the available species pool, and to a lesser extent on the spatial distribution of both resources and species. We concentrate our efforts on the situation where ecosystems are grouped spatially on the condition that they have similar resource levels. We then briefly address how spatial correlations in both resource

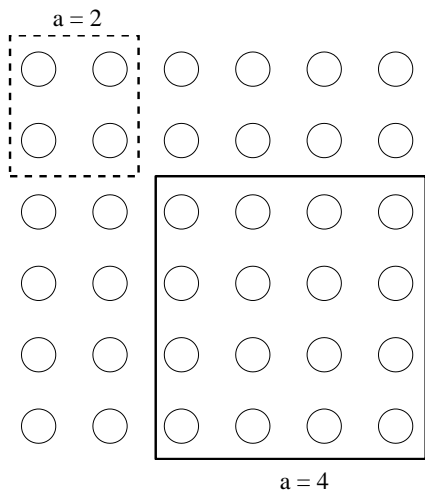


FIG. 5: Depiction of a regional landscape comprised of a collection of 36 local ecosystems distributed on a 6×6 lattice. Each local ecosystem is modeled via a multi-species contact process as described in Section III. Possible regional level “sites” are considered as dynamical statistical aggregates of $a \times a$ blocks of local communities. Examples of such rescalings are denoted by the dashed box ($a = 2$) and by the solid box ($a = 4$).

and species distributions influence aspects of the scale-dependent transition.

In our conception of a regional landscape, we consider a collection of equally sized ecosystems fixed on a lattice of size $L_r \times L_r$, as outlined in Figure 5. The dynamics of each ecosystem is presumed to be controlled by a stochastic spatial process similar to that presented in Section III.

We begin with a few definitions. Let $\bar{\eta}(\mathbf{x})$ be the mean resource availability of the community ecosystem at position \mathbf{x} in the regional aggregate. The expected number of species in a community is $D_1(\bar{\eta}(\mathbf{x}))$ where $D_a(\bar{\eta})$ denotes the average diversity in a collection of $a \times a$ community habitats each with mean resource availability $\bar{\eta}$. As per the results of Section III, $D_1(\bar{\eta})$ is a unimodal function of $\bar{\eta}$. However, the identity of these species will be critical in determining changes of species richness with increasing scale. We assume that the available species pool, $\hat{D}(\bar{\eta})$, from which species may colonize individual ecosystems, is a monotonic function of $\bar{\eta}$. In a sense, many more species are present in a high resource region than in a low resource region, even if the local dynamics are the same in each.

For the purpose of numerical simulations, consider a rescaling length a , such that the $L_r \times L_r$ sized landscape is regrouped into blocks of size $a \times a$, as in Figure 5. The resulting regional landscape is now of size $L_r/a \times L_r/a$ and the average resource level and total species richness at each “regional site” may be calculated. The numerical procedure is as follows: simulate an ensemble of $L_r \times L_r$ community level models with identical values of $\bar{\eta}$, λ , θ

and $\hat{D}(\bar{\eta})$. Once these simulations reach steady state, determine the species composition for each system. For a given re-scaling size a , calculate $D_a(\bar{\eta})$. By re-doing this procedure for regional level ecosystems with different values of $\bar{\eta}$ we may probe the relationship between resource availability and species richness at a range of scales.

Because of the nature of local dispersal and species immigration in this model, every community in the regional landscape is linked to the regional species pool, but not to its neighbors in any special way. This should be considered as a first approximation to the more complex spatial structure of assembled communities. The benefit of such a model is that it is possible to analytically predict the functional relationship, $D_a(\bar{\eta})$, between species richness and average resource availability at a scale a , as follows. The random immigration of species (5) means that every available species has a probability $p = D_1(\bar{\eta})/\hat{D}(\bar{\eta})$ of being present in any ecosystem. Every species then has a probability of $1 - (1 - p)^m$ of existing in at least one of m ecosystems. Therefore, the functional relationship between species richness and average resource availability is

$$D_a(\bar{\eta}) = \hat{D}(\bar{\eta}) \left(1 - \left(1 - \frac{D_1(\bar{\eta})}{\hat{D}(\bar{\eta})} \right)^{a^2} \right), \quad (6)$$

where the exponent a^2 denotes the number of community ecosystems in each rescaled regional site of size $a \times a$.

We verify this result (6) on a 12×12 regional landscape with varying $\bar{\eta}$, the results of which are in Figure 6. Each community in the regional landscape is modeled as a 50×50 lattice with $\lambda = 20$, $\theta = 0.1$, and a resource dependent species pool,

$$\hat{D}(\bar{\eta}) = 256 + 400\sqrt{\bar{\eta}}. \quad (7)$$

When $a = 6$, the regional landscapes begin to display a monotonically increasing relationship between resource availability and species richness as seen in Figure 6. We also confirm the theoretical prediction of (6), for which $D_1(\bar{\eta})$ is averaged from Monte Carlo simulations of the $a = 1$, i.e. small-scale, ecosystems.

Distinguishing between a unimodal or monotonically increasing curve depends on how the maximum of $D_a(\bar{\eta})$ changes as a function of the rescaling length a . We undertake a resampling of the community level data in Figure 6 in order to generate landscapes with arbitrary re-scaling lengths. For each re-scaling length a , we randomly select $a \times a$ local communities from the original data in Figure 6 for a range of resources, $0 \leq \eta \leq 1$. We then calculate total species richness $D_a(\bar{\eta})$ as a function of resources using (6). Using 1000 resamplings for each value of $\bar{\eta}$ we show in Figure 7 how the peak of $D_a(\bar{\eta})$ denoted by $\bar{\eta}_{max}$ moves closer to $\bar{\eta} = 1$ as $a \gg 1$. The shaded region in the plot represents 95% error bars on this result. We therefore conclude that any independent-sampling of regional level ecosystems will lead to a monotonic curve given a sufficiently large rescaling length.

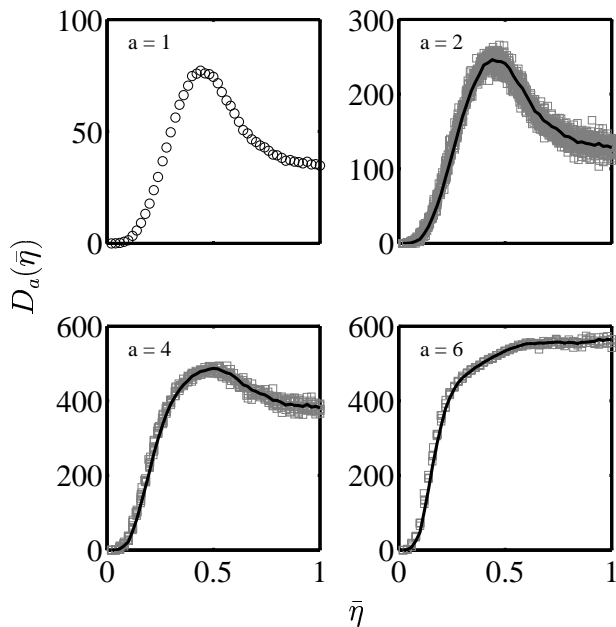


FIG. 6: Resource-species relationships, $D_a(\bar{\eta})$ from a Monte Carlo simulation of a 12×12 regional-level aggregate of community level models. Each community is modeled as a 50×50 square lattice, with $\lambda = 20$, $\theta = 0.1$, and $\hat{D}(\bar{\eta})$ a monotonically increasing function of resources. The unimodal community relationship, $D_1(\bar{\eta})$, from simulation is in the upper left subplot denoted by $a = 1$. For $a = 2, 4$ and 6 , the re-scaled value (gray squares) is compared to theory (6) (black lines).

The transition from unimodal to monotonically increasing is predicated on the assumption that nearby communities have similar overall resource levels. If not, then spatial averages of resource availability would all converge to similar values. This is the approach we have taken in the Monte Carlo simulations of this section, as it seems reasonable to consider regional landscapes in which local communities reside in similar habitats. A potential complicating factor of the transition arises when the distribution of species is spatially correlated. Given the presence of correlations, the theoretical prediction of Eq. (6) is only a first approximation. In qualitative terms, the spatial correlation of species increases similarity of nearby communities, thus slowing down the rate at which species richness increases with increasing scale. Therefore $D_a(\bar{\eta})$ is smaller than what one expects in an uncorrelated system. Spatial clustering of species slows down the process by which the unimodal curve converges to a monotonically increasing curve.

V. DISCUSSION

The relationship between productivity and diversity is most commonly observed to be either unimodal or monotonically increasing [7, 9, 17, 22]. In this paper

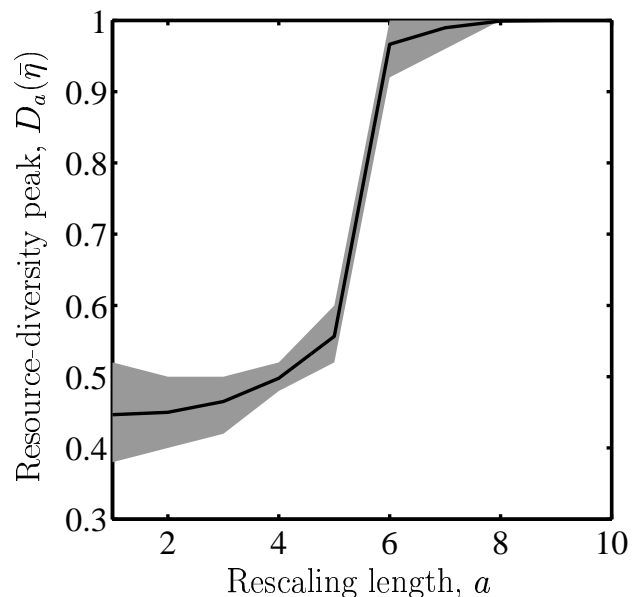


FIG. 7: Peak of the resource-species relationship, $D_a(\bar{\eta})$, for varying rescaling lengths a . For any given a , the value $\bar{\eta}_{max}$ (solid black line) denotes the average resource availability level at which the $D_a(\bar{\eta})$ curve is maximized. Shaded regions indicate 95% confidence intervals based on a resampling technique to scale-up the $a = 1$ results of Figure 6 to regional landscapes of arbitrary size. Note that as rescaling length increases, the peak, $\bar{\eta}_{max}$, of the $D_a(\bar{\eta})$ curve approaches 1.

we demonstrate that quantitative results concerning the relationship between resource availability and species richness at different scales are possible in the context of a neutral model of ecological interactions. When resources are poor there are few species that are likely to survive in a given ecosystem. As conditions improve so too does the likelihood of increasing not only the available species pool but the patchiness of local landscapes. However when resources become abundant the local landscape becomes effectively homogeneous. Species are then free to disperse throughout the entire ecosystem, leading to domination by a limited number of species. The presence of the unimodal curve is also supported by corresponding results in percolation theory.

The proposed model of ecosystem dynamics presumes that resources can be classified as either sufficient or insufficient to support an organism at any given site. Such a model is an oversimplification of how resource levels affect the survival and dispersal of organisms. Nevertheless, the use of percolation clusters permits analytical and computational progress to be made in understanding how barriers to dispersal and colonization impact community assembly, particularly in neutral models. Alternatively one might imagine modeling the heterogeneous resource landscape as a continuously varying scalar field akin to water or nutrient levels. This would lead to an approach that seems best suited to investigate how bar-

riers that slow, but not necessarily stop, the dispersal of populations affect the relationship between ecosystem indicators.

Scaling up a collection of ecosystems or habitats can lead to a qualitative shift in the relationship between underlying resource availability and species richness at different scales. If the unimodal curve is generic at the local scale then the regional scale behavior depends on the characteristics of the regional species pool. A scale-dependent transition occurs, in our model, when the regional species pool increases with increasing resources. We have used a model of a regional landscape in which resource availability is similar within nearby communities. The presence of spatial correlations in community level productivity is a condition satisfied implicitly in one example of a system which exhibits a scale-dependent transition [20]. In a related vein, extensions of the current model to include the spatial clustering of species will not alter the basis of the observed phenomena. The presence of spatial correlations in the distribution of species merely delays the onset of the transition to longer length scales.

The model of ecosystem dynamics presented in this paper provides a framework to quantitatively test predictions concerning the relationship between ecosystem indicators at different scales. Our choice of the multi-species contact process on a heterogeneous landscape facilitates analysis of the scale-dependency of a pair of indicators, i.e. the relationship between species richness and resource availability. However there are many other ecosystem relationships that could, in principle, change with scale. In analyzing such relationships, this work demonstrates that whatever scale-dependency may be present depends on the community model as well as the spatial correlations between ecosystem indicators at regional scales.

Acknowledgements

We thank Hyman Hartman for useful discussions and an anonymous reviewer for critical and helpful comments. JSW also thanks the members of the Theoretical Ecology Lab at Princeton University for useful suggestions. This work was supported in part by National Science Foundation Grant DEB-0083983.

APPENDIX A: SPECIES ABUNDANCE RELATIONS FOR CONTACT PROCESSES

Consider a group of S species in an ecosystem whose relative abundances are ordered from 1 (the most abundance species) to S (the least abundant species). If we denote f_i as the relative abundance of species with rank i then the convention for plotting rank abundance distributions is to compare $\log f_i$ vs. i [43]. Typical results are shown in Figure 8 for the relevant cases $\lambda \gg 1$, $\theta \ll \lambda$. These display the expected S-shaped curve observed in similar models [30] and in empirical observations of plant and tree communities [32, 44]. Finding such curves is not wholly surprising. Any community model that has (i) a mechanism by which a limited number of species become dominant, and (ii) demographic stochasticity that sets a threshold for the extinction of small populations, will tend to exhibit generic S-shaped curves. We are nonetheless re-assured that the multi-species contact process with dilution retains such features, as do other models [30].

-
- [1] E. D. Schulze and H. A. Mooney, eds., *Biodiversity and Ecosystem Function* (Springer-Verlag, Berlin; New York, 1993).
- [2] M. Loreau, S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, et al., *Science* **294**, 804 (2001).
- [3] R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton University Press, Princeton, NJ, 1974).
- [4] J. E. Cohen and C. M. Newman, *J. Theor. Biol.* **113**, 153 (1985).
- [5] D. Tilman, *Ecology* **77**, 350 (1996).
- [6] J. P. Grime, *Science* **277**, 1260 (1997).
- [7] M. L. Rosenzweig and Z. Abramsky, in *Diversity in Ecological Communities*, edited by R. E. Ricklefs and D. Schluter (University of Chicago Press, Chicago, 1993), pp. 52–65.
- [8] D. H. Wright, *OIKOS* **41**, 496 (1983).
- [9] D. J. Currie, *American Naturalist* **137**, 27 (1991).
- [10] D. H. Wright, D. J. Currie, and B. A. Maurer, in *Diversity in Ecological Communities*, edited by R. Ricklefs and D. Schluter (University of Chicago Press, Chicago, IL, 1993), pp. 66–74.
- [11] P. B. Reich, J. Knops, D. Tilman, J. Craine, D. Ellsworth, M. Tjoelker, T. Lee, D. Wedin, S. Naeem, D. Bahauddin, et al., *Nature* **410**, 809 (2001).
- [12] S. Naeem, L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin, *Nature* **368** (1994).
- [13] K. J. Gaston, *Nature* **405**, 220 (2000).
- [14] D. H. Rothman, *Proc. Natl. Acad. Sci. USA* **98**, 4305 (2001).
- [15] S. A. Levin, *Ecology* **73**, 1943 (1992).
- [16] P. R. Moorcroft, G. C. Hurtt, and S. W. Pacala, *Ecological monographs* **71**, 557 (2001).
- [17] R. B. Waide, M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter, *Annu. Rev. Ecol. Syst.* **30**, 257 (1999).
- [18] R. J. Whittaker, K. J. Willis, and R. Field, *Journal of Biogeography* **28**, 453 (2001).
- [19] G. G. Mittelbach, C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough, *Ecology* **82**, 2381 (2001).
- [20] J. M. Chase and M. A. Leibold, *Nature* **416**, 427 (2002).

- [21] R. Kassen, A. Buckling, G. Bell, and P. B. Rainey, *Nature* **406**, 508 (2000).
- [22] P. Abrams, *Ecology* **76**, 2019 (1995).
- [23] E. M. Bond and J. M. Chase, *Ecology Letters* **5**, 467 (2002).
- [24] T. Harris, *Ann. Probability* **2**, 969 (1974).
- [25] D. Tilman, *Ecology* **75**, 2 (1994).
- [26] J. Marro and R. Dickman, *Nonequilibrium Phase Transitions in Lattice Models* (Cambridge University Press, Cambridge, UK, 1999).
- [27] H. Hinrichsen, *Adv. in Phys.* **49**, 815 (2000).
- [28] D. Tilman, *Resource Competition and Community Structure*, Monographs in Population Biology (Princeton University Press, Princeton, NJ, 1982).
- [29] R. Durrett, *SIAM Review* **41**, 677 (1994).
- [30] J. Chave, H. C. Muller-Landau, and S. A. Levin, *Am. Nat.* **159**, 1 (2002).
- [31] T. M. Liggett, *Interacting Particle Systems* (Springer-Verlag, New York, 1985).
- [32] S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography*, no. 32 in Monographs in population biology (Princeton University Press, Princeton, NJ, 2001).
- [33] G. Bell, *Science* **293**, 2413 (2001).
- [34] R. Dickman and A. G. Moreira, *Phys. Rev. E* **57**, 1263 (1998).
- [35] C. Neuhauser, *J. Theor. Biol.* **193**, 445 (1998).
- [36] D. Stauffer and A. Aharony, *Introduction to Percolation Theory* (Taylor and Francis, London, U. K., 1992), 2nd ed.
- [37] Z. Abramsky and M. L. Rosenzweig, *Nature* **309**, 150 (1984).
- [38] D. Stauffer, *Phys. Rev. Lett.* **35**, 394 (1975).
- [39] M. Loreau and N. Mouquet, *Am. Nat.* **154**, 427 (1999).
- [40] G. F. Gause, *The Struggle for Existence* (Wilkins and Wilkins, Baltimore, MD, 1934).
- [41] R. A. Armstrong and R. McGehee, *American Naturalist* **115**, 151 (1980).
- [42] P. Chesson and N. Huntly, *Am. Nat.* **150**, 519 (1997).
- [43] G. E. Hutchinson, in *Population studies: animal ecology and demography* (1957), vol. 22 of *Cold Spring Harbor Symposia on Quantitative Biology*, pp. 415–27.
- [44] B. McGill, *Nature* **422**, 881 (2003).

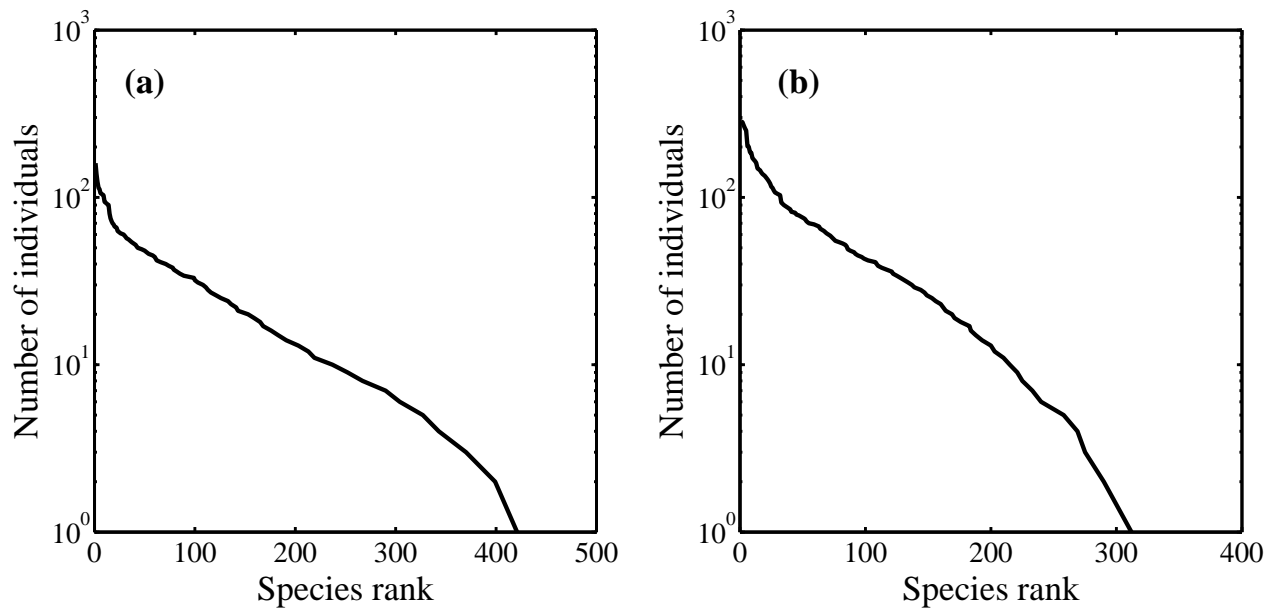


FIG. 8: Steady state rank abundance of a 128×128 simulation with $\lambda = 25$, $\theta = 0.25$, and $\hat{D} = 1024$. In (a) $\bar{\eta} = 0.6$, $S \approx 430$ while in (b) $\bar{\eta} = 0.8$, $S \approx 350$.