A neutral metapopulation model of biodiversity in river networks

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Abstract

In this paper, we develop a stochastic, discrete, structured metapopulation model to explore the dynamics and patterns of biodiversity of riparian vegetation. In the model, individual plants spread along a branched network via directional dispersal and undergo neutral ecological drift. Simulation results suggest that in comparison to 2-D landscapes with non-directional dispersal, river networks with directional dispersal have lower local and overall diversities, but higher between-community diversity, implying that riparian species are distributed in a more localized pattern and more vulnerable to local extinction. The relative abundance patterns also change, such that higher percentages of species are in low-abundance, or rare, classes, accompanied by concave rank-abundance curves. In contrast to existing theories, the results suggest that in river networks, increased directional dispersal reduces diversity. These altered patterns and trends result from the combined effects of directionality of dispersal and river network structure, whose relative importance is in need of continuing study. In addition, riparian communities obeying neutral dynamics seem to exhibit abrupt changes where large tributaries confluence; this pattern may provide a signature to identify types of interspecific dynamics in river networks.

Keywords: River network; Biodiversity; Metapopulation; Neutral; Directional dispersal

1. Introduction

Riparian zones play many important roles in regulating ecosystem function within streams, surrounding environments, and up-land areas (Gregory et al., 1991; Malanson, 1993; Naiman and Décamps, 1997). They are key landscape components in maintaining biological connections along extended and dynamic environmental gradients and in controlling transport of water and nutrients (Naiman and Décamps, 1997). Existing literature suggests that riparian zones typically have more biodiversity than their surrounding and up-land areas (Gregory et al., 1991; Malanson, 1993) and perhaps contribute to biodiversity at watershed scales (Goebel et al., 2003). They act as physical buffers, e.g. controlling erosion and sediment transport, shaping channel geometry, and providing shading (and thus livable temperature) for fish and benthos in streams (Horne and Goldman, 1994), as well as biological buffers, e.g. nutrient filtering (Lowrance et al., 1984; Peterjohn and Correll, 1984; Malanson, 1993), providing biogeochemical hotspots (McClain et al., 2003), and influencing food webs in its surroundings (Naiman and Décamps, 1997). Indeed, the importance of riparian zones has been recognized, as reflected by their being incorporated into large-scale resource management (Nilsson and Svedmark, 2002).

Riparian vegetation is indispensably involved in all processes described above. Thus, it is critical to understand how the composition and distribution of riparian vegetation communities develop from a dynamical ecological perspective. Ecological studies in recent years have investigated some processes and patterns in riparian plant communities (e.g. Nilsson et al., 1989, 1994; Levine, 2000a, b; Honnay et al., 2001; Goebel et al., 2003). Yet, a theory on the dynamics of riparian vegetation communities is lacking.
Pursuit of such a theory poses a serious scientific challenge for, at least, two reasons. First, riparian systems, associated with network landscapes, are geometrically and topologically very different from the much-studied two-dimensional (2-D) landscapes. Second, since streamflows are a major dispersing agent of propagules in these systems, the dispersal is directional—an issue that has not been addressed adequately in dispersal–diversity literature. The key question here is thus: how does network structure and directional dispersal influence species diversity and compositional changes in riparian systems?

Presently, dynamical models of multi-species communities in regular 2-D landscapes with symmetric dispersal have been extensively studied (e.g. Chave et al., 2002), but those in river networks have only recently received attention (Fagan, 2002; Levine, 2003). There already exists a well-established body of knowledge in geomorphology of river networks (Rodriguez-Iturbe and Rinaldo, 1997; Dodds and Rothman, 1999; Benda et al., 2004), which focuses on the relationships between topography, topology, channel geometry, and streamflow, among others; these features apparently bear strong relevance to the dynamics of riparian vegetation. We aim to address the relation between habitat structure, dispersal, and diversity, at least partially, by integrating a multi-species model and the geomorphology of river networks.

To that end, we recognize stochastic structured metapopulation models (Hanski and Gilpin, 1997; Hanski, 1999) as a viable candidate. Mean-field approaches cannot appropriately capture the effects of river network landscape, whereas individual-based approaches are overly complex for this system. With the metapopulation approach employed here, in which the dispersal in river network landscape is explicitly spatial and within-streamlink dynamics is implicitly spatial (see details in Section 2), we can tackle the problem while balancing different types of model complexity. Metapopulation models have been applied to many problems (Hanski and Thomas, 1994; Moilanen, 1999; Levine, 2003), but not yet to river networks, which is precisely what we attempt to achieve in this paper.

Of the many ecological models of plant competition and dynamics, this paper focuses on the neutral model, in which biodiversity patterns arise from ecological drift (Hubbell, 2001). We recognize that many mechanisms have been proposed to explain the maintenance of biodiversity (Chave et al., 2002), e.g. control by environmental factors and competition among species. However, the neutral model is taken here as a starting point in order to see what biodiversity patterns emerge in river networks without trade-offs. This model also contributes to a more general question of how “fragmented” landscapes alter biological outcome (Hanski and Gilpin, 1997; Gilbert et al., 1998; Hanski, 1999; Bolker, 2003).

This paper is organized as follows. Section 2 describes the model and how it is implemented. The model results are presented and analysed in Section 3. Section 4 provides discussion and conclusions regarding the results and future work.

2. Model

We have developed a stochastic, discrete, structured metapopulation model to study biodiversity patterns of riparian vegetation communities. By definition, a structured metapopulation model is explicitly spatial. However, in the present model, we allow for implicitly spatial dynamics within a streamlink, while maintaining the explicitly spatial characteristics between streamlinks through the dispersal kernel. In this context, streamlinks are essentially the patches within the river network landscape and they contain sites that are occupied by individual plants (see Fig. 1). In the following sections, we describe various elements of the model.

2.1. Habitat size

We define $H_i$, habitat size, as the number of sites at a given streamlink. One site can support only one individual plant. Therefore, $H_i$ represents the maximum number of individual plants that can inhabit a given streamlink. In this paper, we focus on riparian vegetation residing on depositional bars along rivers, i.e. those that would be inundated by flows at or above the bankfull discharge, $Q_{bf}$ (Fig. 2). It is customary to characterize the drainage network through the magnitude of each of its links. Links of magnitude 1 or “sources” are those without upstream tributaries and the magnitude of a link is then defined as the number of sources upstream draining through the link. The average length and average area directly draining to a link are random variables independent of magnitude and remain approximately the same throughout the drainage network (Rodriguez-Iturbe and Rinaldo, 1997). Thus,

\[ H_i = \text{number of sites at a given streamlink}. \]
based on well-established geomorphological relations (Leopold et al., 1964; Rodriguez-Iturbe and Rinaldo, 1997), we hypothesize the following relationships between riparian habitat size, $H$, channel width, $w$, and drainage area of a streamlink, $A$:

$$H \propto w \propto Q_{bf}^{0.5} \propto (A^{0.75})^{0.5} \propto A^{0.375}. \tag{1}$$

We employ the bankfull discharge, $Q_{bf}$, because it contributes the most to forming and maintaining the channel geometry; in many rivers, $Q_{bf}$ corresponds to the flow with a return period of approximately 1.5 years (see Leopold et al., 1964). After the calculation based on Eq. (1), $H$ is rounded to the nearest integer.

Let us reemphasize that this is a hypothesis based mainly on geomorphological relationships. Depending on the nature of the posted question, riparian zones may be defined differently, based on other factors, e.g. types of vegetation, in which case Eq. (1) needs to be modified accordingly.

### 2.2. Ecological processes at a streamlink

At each time step, the relevant processes within a streamlink are modeled in the following order: propagule production, death, diversification (due to either speciation or immigration), and colonization. While some models determine the number of propagules in each time step from the surviving, i.e. after-death, population, in this model we use the before-death population to do so.

**Propagule production:** The number of propagules of species $k$ produced at link $i$ at time $t$ is $f_k N_i(t)$, where $f_k$ and $N_i(t)$ are the fecundity rate and the population size at time $t$ at link $i$ of species $k$, respectively. The newly produced propagules are dispersed to destination links (according to the dispersal kernel discussed in Section 2.3). Following the dispersal, the propagules may colonize sites and establish themselves as individual adult plants. Upon their arrival at a link, propagules are uniformly distributed and engage in an implicitly spatial dynamic within the link (see Colonization and establishment below).

**Death and survival:** The surviving population is modeled as a binomial random variable with parameters $N_i(t)$ and $s_0$, that is $N_i(t)$ trials, each with a surviving probability of $s_0$.

**Diversification:** A fixed number of new species, $\theta$, are introduced into the system at each time step. In this paper, the term diversification includes both speciation and immigration of new species. Each of these new species is introduced as one individual and is located in a randomly chosen streamlink, whose empty sites are freed up by the death process. We assume that every site has an equal probability of acquiring the individual of a new species. Therefore, the probability of choosing a streamlink for diversification is weighted by its habitat size. Thus, this diversification scheme is density-independent—$\theta$ is fixed; other schemes, which may be dependent on population density or other factors, could also be implemented in the present model context.

**Colonization and establishment:** As mentioned, we only consider the neutral model, i.e. every species has the same fecundity rate, survival probability, and dispersal kernel. Propagules can occupy empty sites, but cannot replace established plants. Assuming that propagules are uniformly distributed within streamlinks, the number of occupied sites is a random variable following the occupancy distribution (Johnson and Kotz, 1969). This distribution implies that more than one propagule may arrive at the same site and only one will survive to reproduce in the next time step. To accelerate the computation, we approximated the occupancy distribution by a beta distribution with identical mean and variance; the approximation is generally very good. Note that the occupancy distribution is discrete, whereas the beta distribution is continuous; therefore, the integers nearest to the values drawn from the corresponding beta distributions are used in the model. The details of the estimation are provided in Appendix A.

### 2.3. Dispersal kernel

Before the propagule recruitment is finalized, the propagules are redistributed throughout the system by dispersal. The dispersal process depends on distance along the network between streamlinks. Here, we assume that the dispersal kernel takes the form of a back-to-back exponential. Thus, it can be expressed as follows:

$$K_{ij} = C d^{ND_{ij}} u^{NU_{ij}}, \tag{2}$$

where $K_{ij}$ is the fraction of propagules produced at link $i$ that end up at link $i$ after the dispersal; $C$ is the normalization constant, which is equal to $(1 - 2u)(1 - \theta)/ (1 - ud)$; $NU_{ij}$ and $ND_{ij}$ are the numbers of upstream and downstream steps comprising the shortest path from link $j$ to link $i$; and $u$ and $d$, both less than 1, are the decay fractions of the dispersed propagules in the upstream and downstream directions, respectively. This is clearly shown in Fig. 11 in Appendix B, where the derivation of $C$ is provided.

Accordingly, for any finite river network, $\sum_j K_{ij} < 1$; the summation is smaller if link $j$ is located on the periphery of the network than if it is an interior link. This is because a larger fraction of propagules produced at streamlinks on the periphery is transported out of the system by dispersal, and considered lost. Therefore,
the model explicitly includes the edge effect. Finally, as water flow biases the transport of propagules in river networks, we assume that $d \geq u$ in all simulations.

2.4. River network

In this paper, we use the network extracted from the digital elevation maps (DEMs) of Elder Creek, a 17-km² river basin located in the Heath and Marjorie Angelo Coast Range Reserve, CA (Fig. 3). The Reserve’s elevation range is approximately between 372 and 1295 m above sea level with annual precipitation of approximately 220 cm; the topography of the Reserve is characterized by mostly steep, mostly soil-mantled hillslopes, which harbors a diverse range of habitats, e.g. mixed forests, woodlands, mixed chaparral, bald hill prairie, and grassland (Herring, 1997). With this particular extraction, the river network has 97 streamlinks. It is important to note that the model employs the topological, not geometrical, representation of Elder Creek.

Although relatively small, Elder Creek fulfills general geomorphological signatures of river networks. It exhibits a power law character of the exceedance probability distribution of drainage area at a randomly selected link of the network with slope of approximately $-0.43$ (Rodriguez-Iturbe and Rinaldo, 1997); this is shown in Fig. 4. Because of the small size of Elder Creek, the power law behavior only covers close to two logarithmic scales before the finite size effect dominates.

2.5. Implementation

This section reports the specific model parameters corresponding to the simulations presented in this paper. The definitions of key variables and parameters in the model are summarized in Table 1.

![Fig. 3. The network extracted from Elder Creek’s digital elevation maps (DEMs). Most simulations in this paper are done on this network.](image)

**Habitat size:** The habitat size of source streams is denoted as $H_0$. In most simulations, we assume that $H_0 = 500$. Therefore, the habitat size of streamlink $i$ is the nearest integer to $H_0 A_i^{0.375}$, where $A_i$ is the area draining through link $i$ (Section 2.1). This results in a total habitat size of 98,490 sites for the entire network. The value 500 is selected such that the riparian habitats are large enough to accommodate a large number of species necessary for investigating the biodiversity patterns, but not too large for reasonable computational time.

For this extraction, the average length of streamlinks is 355 m. The width of the riparian zone at the outlet link of Elder Creek is in the order of 10 m (based on fieldwork inspection). The habitat size at the outlet link under this setting is 2780 sites, implying that a site corresponds to an area of approximately 1 m².

**Death and survival:** $\alpha_0$ is assumed to be 0.8 for all species (i.e. the death probability at each time step is 0.2), which corresponds to a reasonable average lifespan of 5 years.

**Diversification and demographic parameters:** At each time step, five new species are introduced to the system, i.e. $\theta = 5$. As a new species is introduced, it is assigned identical demographic parameters, i.e. $\alpha_0 = 0.8$ and $f_k = 6$. The diversification rate is observed to be high enough to result in sufficiently high species richness—necessary for any patterns to be discernible—for this particular river network. In a larger, more complex river network, a lower diversification rate may suffice.

The fecundity rate of 6 is observed to be high enough so that the single individual of a newly introduced species has at least one propagule remaining at the link of origin (i.e. the link where the propagules are produced) after being...
consequently, there is no significant difference in vegetation density to confound the resulting patterns. Higher sensitivity of propagule distribution at the origin. Therefore, the average number of species present in the drainage area of the link in question; if the link in question is the outlet link, the diversity in the river network to the dispersal rate. In all cases, we keep $u$ constant at 0.1, and vary $d$ among three values, 0.2, 0.5, and 0.8, to investigate the effects of the strength of directional dispersal.

Table 1
Summary of key variables and parameters in the model

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A$</td>
<td>The drainage area of a link</td>
</tr>
<tr>
<td>$H$</td>
<td>The habitat size of a link, i.e. the number of sites, in the riparian zone of the link</td>
</tr>
<tr>
<td>$H_i$</td>
<td>The upstream habitat size of a link, i.e. the total habitat size of the riparian zones contained in the link’s drainage area</td>
</tr>
<tr>
<td>$N_k(t)$</td>
<td>Population size of species $k$ at link $i$ at time $t$</td>
</tr>
<tr>
<td>$f_k$</td>
<td>Fecundity rate of species $k$</td>
</tr>
<tr>
<td>$z_0$</td>
<td>Survival probability, i.e. 1 – death probability</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Diversification rate, i.e. the number of new species introduced to the system at each time step</td>
</tr>
<tr>
<td>$v$</td>
<td>Per-site diversification rate, i.e. $\theta$ divided by the total habitat size of the system</td>
</tr>
<tr>
<td>$K_{ij}$</td>
<td>The fraction of propagules produced at link $j$ that ends up at link $i$ after dispersal</td>
</tr>
<tr>
<td>$C$</td>
<td>The normalization constant of the dispersal kernel; it also represents the fraction of propagules remaining at the link of origin after dispersal</td>
</tr>
<tr>
<td>$a$</td>
<td>The decay fraction of the dispersed propagules in the upstream direction</td>
</tr>
<tr>
<td>$d$</td>
<td>The decay fraction of the dispersed propagules in the downstream direction</td>
</tr>
<tr>
<td>$NU_{ij}$</td>
<td>The number of upstream steps (in unit of link) comprising the shortest path from link $j$ to link $i$</td>
</tr>
<tr>
<td>$ND_{ij}$</td>
<td>The number of downstream steps (in unit of link) comprising the shortest path from link $j$ to link $i$</td>
</tr>
<tr>
<td>$z$</td>
<td>The average number of species present in a streamlink normalized by the link’s habitat size</td>
</tr>
<tr>
<td>$\beta$</td>
<td>Between-streamlink diversity, defined as the scaling exponent of the species-cumulative habitat size relationship</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>The average total number of species present in the drainage area of the link in question; if the link in question is the outlet link, $\gamma$ is the total number of species in the river network</td>
</tr>
<tr>
<td>$\rho$</td>
<td>The fraction of sites in the entire system that are occupied by vegetation</td>
</tr>
</tbody>
</table>

Table 2
The $\alpha$, $\beta$, and $\gamma$ diversities, and the average fraction of sites occupied by vegetation, $\rho$, for different settings in the river network and the 2-D landscape with non-directional dispersal (see text)

<table>
<thead>
<tr>
<th>River network ($u = 0.1$)</th>
<th>2-D</th>
</tr>
</thead>
<tbody>
<tr>
<td>$d$</td>
<td>0.2</td>
</tr>
<tr>
<td>$1 - C$</td>
<td>0.347</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>30.4</td>
</tr>
<tr>
<td>$\beta$</td>
<td>0.818</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>159</td>
</tr>
<tr>
<td>$\rho$</td>
<td>0.999</td>
</tr>
</tbody>
</table>

In all simulations, $z_0 = 0.8$, and $f_k = 6$ for all species. Recall that $C$ is the normalization constant of the dispersal kernel in river networks; it also represents the fraction of propagules remaining at the origin. Therefore, $1 - C$ represents the fraction of propagules dispersed to other locations, and thus the dispersal rate. Note the different trends of $\alpha$ and $\beta$ diversities in the river network and 2-D landscape as the dispersal rate increases. Note also the higher sensitivity of $\gamma$ diversity in the river network to the dispersal rate. In all cases, $\rho$ is close to 1—–the system is nearly saturated with the vegetation; consequently, there is no significant difference in vegetation density to confound the resulting patterns.

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Dispersal: Propagules are redistributed by the dispersal before the recruitment is finalized. This is done by performing a matrix multiplication between the dispersal kernel and the propagule matrix. Let $N$ denote the total number of streamlinks, and $G$ the total number of species present in the river network. Then, the dispersal kernel is a $N \times N$ matrix whose elements are $K_{ij}$ (Section 2.3 and Eq. (2)). The propagule matrix is a $N \times G$ matrix whose element $jk$ represents the number of propagules of species $k$ produced at link $j$. Therefore, the product of the multiplication is a $N \times G$ matrix whose element $jk$ represents the number of propagules of species $k$ dispersed to or remaining at link $j$ after the dispersal. The elements in this resulting matrix are then rounded to their nearest integers. This particular step of the calculation is deterministic, not stochastic as in other steps; doing so reduces the computational time and is not expected to affect the resulting patterns and conclusions. In all simulations, we keep $u$ constant at 0.1, and vary $d$ among three values, 0.2, 0.5, and 0.8, to investigate the effects of the strength of directional dispersal.
3. Results and analysis

In this section, we report and analyse model results by studying basic patterns, including relative abundance distribution (rank-abundance curves and histograms of abundance), at both basin and link scales, and species-habitat size relationships. Also, we examine other patterns more specific to river networks, namely the probability of exceedance of species richness and local abundance profiles along mainstreams. Unless stated otherwise, the analyses are performed on the results taken after the simulations have been run for 30,000–40,000 time steps and the process has reached a statistical steady state.

3.1. Basin-scale relative abundance

First, we explore the basin-scale relative abundance by considering the rank-abundance curves, the histograms of abundance, and the $\alpha$, $\beta$, and $\gamma$ diversities. In this paper, $\alpha$ diversity refers to the average number of species present in a streamlink—a local community—normalized by the link’s habitat size; for the sake of presentation, we multiply this normalized local species richness by 1000, making the unit of $\alpha$ diversity “number of species per 1000 sites”. $\gamma$ diversity of link $i$ is the average total number of species present in the drainage area of link $i$—the $\gamma$ diversity of the outlet link is thus the total number of species in the entire river network.

Regarding between-community diversity or $\beta$ diversity, we recognize that many definitions exist and have been extensively used, e.g. the difference and ratio between $\gamma$ and $\alpha$ diversities. It is important to note that the notions of $\alpha$, $\beta$, and $\gamma$ diversities are conventionally applied to metacommunities whose local communities are, at least implicitly assumed, of equal size; we do not have that luxury here due to the intrinsic nature of riparian systems (see Eq. (1)). In this paper, to circumvent the issue of varying sizes of streamlinks, we define $\beta$ diversity as the scaling exponent of the species-cumulative habitat size relationship, or more specifically for river networks, the relationship between $\gamma$ diversity and upstream habitat size, $H_U$ (see Section 3.2). The rationale is that while other definitions seem appropriate on the assumption that local communities are of the same size, the slope definition does not deal with the individual sizes of the local communities. Rather, it deals with the cumulative habitat size, where adding increments of varying sizes to the cumulative does not cause problems. Nonetheless, it is important to keep in mind that the results and interpretation of $\beta$ diversity are likely definition dependent.

Before considering the results, it is important to recognize that by keeping $u$ constant and increasing $d$, we simultaneously increase both the dispersal rate and directionality. Consequently, the resulting trends and patterns arise from the combined effects of the two changes. To illustrate the effects, we compare the results to those associated with a 2-D metacommunity that has the comparable total habitat size (98,500 sites), consists of a comparable number (100, i.e. $10 \times 10$ grid) of local communities, and experience the same level of diversification ($\theta = 5$); the comparison is presented in Fig. 5. To achieve fair comparison, the back-to-back exponential dispersal is implemented in the 2-D metacommunity such that the fraction of propagules remaining at their origin is the same as its river network counterpart. As in the river network, the edge effect is explicitly recognized: fractions of propagules are constantly dispersed out of the system.

Table 2 and Fig. 6 indicate that stronger dispersal, i.e. higher values of $d$, reduces $\gamma$ diversity, which is in agreement with existing theories for typical 2-D landscapes (Hubbell, 2001). This is because the stronger dispersal facilitates the spread of highly abundant species, and thus allows them to suppress species with lower abundance. Despite the same qualitative trend, the sensitivity of $\gamma$ diversity to dispersal is much higher in the river network than in the 2-D landscape. Preliminary results of our

![Fig. 5](image-url) The comparison between relative abundance patterns associated with the river network and the 2-D landscape: the bold line and gray bars represent the river network; and the regular line and white bars the 2-D landscape. The results of the river network are associated with $u = 0.1$ and $d = 0.5$. The 2-D landscape is a 10-by-10 grid consisting of cells of equal habitat size. Its total habitat size is the same as that of the river network. To achieve fair comparison, the symmetric, back-to-back exponential dispersal implemented in the 2-D landscape is such that the fraction of propagules remaining at the cell of origin is the same as its river network counterpart. As in the river network, the edge effect is explicitly recognized: the propagules are constantly dispersed out of the system.
ongoing research suggest that this is primarily due to directionality.

Interestingly and in contrast to the existing theories (Loreau, 2000; Hubbell, 2001), in which \( z \) diversity increases and \( \beta \) diversity decreases as dispersal becomes stronger, the results suggest that in river networks, increased directional dispersal reduces \( z \) diversity and does not significantly affect \( \beta \) diversity (based on the present definition). Apart from the different trends, \( \beta \) diversity is much higher in the river network than in the 2-D landscape. This is likely due to the limited upstream dispersal, which effectively hinders between-tributary dispersal and thus differentiates species compositions in different tributaries.

Let us now consider the relative abundance patterns. A striking feature is the concavity of the rank-abundance curves (Figs. 5 and 6). This implies that in riparian vegetation communities obeying the neutral model, most species are rare. This is clearly shown by the histograms of abundance (Fig. 6), in which the percentages of the low-abundance classes are relatively high. For example, the high frequencies of low-abundance classes up to more abundant ones are greatly reduced. This results in lower numbers of species in intermediate-abundance classes and faster extinction rates for most species, except the highly abundant ones. Naturally, the faster extinction rates drive the entire system to lower biodiversity. At the other end of spectrum, the sites that would have been occupied by the rare species, whose propagules now have lower probability of success, are most likely displaced by a few species with very high abundance. We collectively call the dynamics described in this paragraph rarification.

Net propagule exporters also exist, namely the source streams. However, due to the habitat size distribution, i.e. the riparian habitats becoming larger downstream, most riparian habitats belong to the net-propagule-importer streamlinks. In addition, most new species are introduced at these locations. Therefore, the effects discussed in the previous paragraph dominate. Note that other mechanisms may also be at work here, some of which are being investigated in our ongoing research.

### 3.2. Species–habitat size relationship

To study the relationship between \( \gamma \) diversity and habitat size, we start out from the outlet link and record the number of species in its drainage area, i.e. the entire river network. Then, we progress upstream by following the upstream link with the largest drainage area, and continue the process until we reach a source stream. These streamlinks constitute what we will refer to as the mainstream.

The plots of the relationship between \( \gamma \) diversity and habitat size for different dispersal parameters are shown in Fig. 7, along with their 2-D landscape counterparts; the difference in slope—\( \beta \) diversity—between the river network and 2-D landscape is clearly depicted here. The three plots associated with the river network can be collapsed into one when \( \gamma d^{0.5} \) is used, suggesting similar dynamical mechanisms over the range of \( d \) used in the simulations. Furthermore, a power law with a slope of 0.83 is nicely fit to the collapse plot over the intermediate to large habitat size range. We do not have, as yet, a quantitative theory to
explain the slope. Over the small habitat size range, the plot deviates from the 0.83-power law. This is presumably because the effects of directional dispersal and aggregative structure are not yet fully felt, and thus the dynamics at these few upstream links differ from that at other links located downstream of them.

Although the explanation of why $\gamma d^{0.5}$ results in the collapse plot in Fig. 7 is not currently available, we discuss here an interesting implication of this result. Let us describe the dynamics of $\gamma$ diversity with the following simple model: $\gamma_{t+1} - \gamma_t = \theta - \bar{c}_t$, where $\gamma_t$ represents the $\gamma$ diversity at time $t$, and $\bar{c}_t$ represents the species-average extinction rate. At equilibrium, $\gamma = 0/\bar{c}$.

Now, the collapse plot suggests that $\gamma d^{0.5} \sim H_U^{0.83}$; thus, $\gamma \sim H_U^{0.83}/d^{0.5}$. Consequently, $\bar{c} \sim 0d^{0.5}/H_U^{0.83}$. Assuming that the relationship $\theta = vH_U$ applies at all subnetworks, we arrive at $\bar{c} \sim d^{0.5}H_U^{0.17}$. While this does not explain the origin of the exponents, it provides an alternative framework for future analysis in that the extinction rate reflects a nonlinear coupling between dispersal and upstream effects.

3.3. Exceedance probability of $\gamma$ diversity

River networks have numerous geomorphological signatures, one of which is the power law for the exceedance probability of drainage area upstream of a randomly selected streamlink (Fig. 4). This signature, coupled with the species–habitat size relationship just discussed (Fig. 7 and Section 3.2), points to the possibility of a power law for the exceedance probability of species richness in the drainage area upstream of a randomly selected streamlink, i.e., $\gamma$ diversity. Fig. 8 indicates that this may be the case. In addition, the plots can again be collapsed into one by plotting the exceedance probability of $\gamma d^{0.5}$; the resulting slope is approximately $-1.08$. This power law may have some practical implications for ecological field study in riparian systems. For example, one only needs to know the dispersal parameters and the $\gamma$ diversity at one streamlink to predict the diversity at other locations. Of course, this assumes that ecological drift dominates the dynamics taking place in the river network. In reality, other types of interaction, such as trade-offs among species, as well as other factors, such as disturbances and climate fluctuations, modify the patterns. Yet, the power law associated with the neutral model provides a null hypothesis to compare with real data.

3.4. Spatial patterns

We gain additional insights through the analysis of the spatial patterns of the riparian vegetation, namely the profiles along the mainstream of $\gamma$ diversity and local, link-scale, abundance (Fig. 9). Let us first note that for this particular network, two large tributaries confluence at 13 links away from the outlet; hereinafter, we will refer to this link as the confluence link (Fig. 3).

It is clear from the $\gamma$ diversity profiles that mainstream is divided into regions of high and low local diversity, approximately corresponding to the portions downstream and upstream of the confluence link, respectively. This pattern is a result of interplay between downstream-biased dispersal and river network structure: the downstream portion receives propagules of species residing in the two upstream tributaries, between which the dispersal is limited. Interestingly, the role of confluences in enhancing downstream diversity has been reported for fish (Fernandes et al., 2004).

Another spatial pattern of interest is the abundance profiles along the mainstream. The profiles (Fig. 9) show that the species’ spatial coverage is far from uniform. For instance, common species at the basin scale may be rare or even absent locally. The profiles suggest that the riparian species, at least the most common ones, often exhibit abrupt changes in their profiles around the confluence link (Fig. 9). In this particular setting, the influence of the network structure is quite pronounced for the three most...
common species. For the less abundant species (e.g. the fourth and fifth most abundant ones in Fig. 9), their spatial patterns are also affected by the patterns of the more common species, thereby diluting the influence of the network structure and resulting in less abrupt changes around the confluence link. Additional results (not shown here) indicate that the effects of river network structure increase with the directionality of dispersal.

Keep in mind, however, that while the abrupt changes around confluences are a typical pattern, the locations of high abundance of different species are not always as shown in Fig. 9. For instance, due to the intrinsic randomness of the dynamics, it is not necessary that the most common species is more abundant in the downstream portions; the pattern in which it is more abundant upstream is entirely possible. However, these changes do not affect such basin-scale patterns as those in Figs. 6–8.
3.5. Link-scale relative abundance

We study the link-scale relative abundance by considering the rank-abundance curves and histograms of abundance of selected streamlinks, namely the outlet link, the confluence link, and a source stream at the end of the mainstream (Fig. 10). The relative abundance patterns apparently differ at these different locations. The rank-abundance curves of the outlet and confluence links exhibit clear concavity, resembling their basin-scale counterparts (Fig. 6), while that of the source stream is almost a straight line. Accordingly in the histograms, as one moves downstream, the numbers of species belonging to low-abundance (i.e. rare) classes increase more rapidly in comparison to higher-abundance classes.

This can be put in the context of rarification (see Section 3.1). First, at the source streams (the net propagule exporters), the effects of rarification are hardly felt; the patterns are qualitatively identical to those expected in the non-aggregative habitat with non-directional dispersal (see Figs. 10 and 5). The difference comes as one moves downstream; the rarification effects are apparent at the confluence and outlet links, represented by the concave rank-abundance curves.

4. Discussion and conclusions

The stochastic, discrete, structured metapopulation model developed in this paper is the first such model applied to biodiversity dynamics and patterns in river networks. The system considered in the present model is a leaky metapopulation consisting of local communities of various sizes connected to one another through directional dispersal controlled by hydrologic and geomorphic characteristics of the river network. Dispersal is leaky because propagules are constantly transported out of the system; that is, the edge effect is explicitly included. Under this environment, the directional dispersal and aggregative structure of the river network make the effective colonization rate of a riparian species spatially heterogeneous and thus modify the biodiversity patterns. The following paragraphs summarize some important findings and their implications.

The results have shown that the combined effects of directional dispersal and aggregative structure make the rank-abundance curves concave, corresponding to higher percentages of rare species, compared to the almost straight line expected for a typical 2-D landscape (Section 3.1). The relationships between dispersal rate and \( \alpha \), \( \beta \), and \( \gamma \) diversities are also altered (Section 3.1); the most striking is that of \( \alpha \) diversity.

In contrast to existing theories (e.g. Hubbell, 2001), in which \( \alpha \) diversity increases as dispersal becomes stronger, the present results suggest that in river networks, increased directional dispersal actually reduces \( \alpha \) diversity. Recall that the altered trend is the result of the combined effects of directional dispersal and aggregative structure. Determining the relative importance of each feature is crucial and certainly part of our ongoing research. Preliminary results seem to suggest that \( \alpha \) diversity is very sensitive to directionality.

Table 2 and Fig. 7 suggest that in river networks, \( \beta \) diversity is not significantly affected by dispersal, unlike its 2-D landscape counterpart. Let us re-emphasize here the various existing definitions of \( \beta \) diversity and the possibility of different trends for different definitions (Section 3.1). With the caveat stated, we still expect the conclusion that \( \beta \) diversity is generally higher in river networks than in 2-D landscapes to be robust for any reasonable definitions of \( \beta \) diversity as long as the dispersal is realistically downstream-biased—given, of course, the same total habitat size, the same level of fragmentation, the same diversification, and the same dynamics, i.e. the neutral model. Note that \( \beta \) diversity is, to some extent, indicative of how vulnerable species in the system are to their local extinction. For example, high \( \beta \) diversity means that most species are present at only a few locations; consequently, the extinction at local communities may put the species at a serious risk of system-wide extinction. Therefore, the results suggest that species in riparian communities in
The results indicate that diversity is lower in river networks than in 2-D landscapes, with all else being equal. We thus conclude that it is not the directional dispersal and aggregative structure that make diversity in riparian zones generally higher than that of the surrounding areas—as usually found in riparian literature (e.g. Gregory et al., 1991; Malanson, 1993); they actually reduce it. This leads us to conjecture that diversification, including both speciation and immigration, in riparian zones is significantly higher than that of the surrounding areas, thereby over-compensating the effects of the directional dispersal and aggregative structure and resulting in the observed higher biodiversity. The conjecture seems to agree with two important features of the riparian zones. First, riparian zones usually receive many inputs from their upland surrounding areas, e.g. organic matter and nutrients, as well as vegetation propagules; this apparently increases immigration. Second, the hydrologic and disturbance regimes, as well as such factors as elevation, temperature, and light availability, in the riparian zones are diverse and produce sharp environmental gradients—both longitudinally (along streams) and laterally (along channel cross-sections)—that can accommodate species of various traits; in addition, these diverse environmental conditions encourage the riparian vegetation to devise different strategies to cope with them, thereby leading to increased speciation. Again, this is only a conjecture; the present model does not prove it. A full test of this conjecture would require a departure from neutrality in the model.

Another important and practical lesson from the model is the potential use of the vegetation spatial patterns (Section 3.4 and Fig. 9) to identify the type of interspecific interaction taking place in river networks. In particular, the results suggest that riparian vegetation species obeying the neutral model exhibit abrupt changes in abundance and diversity where large tributaries confluence, especially when the directionality of dispersal is strong. To develop this interaction-identifying methodology, one needs to study other types of interspecific interactions, e.g. trade-off competition, and compare the emerging patterns to those reported in this paper to see if they differ from each other. However, one must take necessary cautions in applying the methodology; in reality, many other physical processes and properties, examples of which were mentioned in the previous paragraph, exist that are capable of causing such changes, and oftentimes, they, too, change abruptly at confluences. This, along with our model results, points to the potential role of confluences as key sites for conservation and fieldwork study (see Benda et al., 2004; Fernandes et al., 2004).

This paper is merely one of the first steps to explore biodiversity patterns arising from ecological dynamics in atypical habitats with asymmetrical dispersal. We hope that our work has demonstrated some of the important, yet understudied, aspects, issues, and questions related to biodiversity study, which warrant many future research directions—both theoretical and empirical. What is the relative importance of directionality and landscape structure? What are biodiversity patterns associated with other types of interspecific interaction? Are the patterns seen here scale-dependent—would they be different in larger river networks? How could we verify these patterns with real data in the field? How sensitive are these patterns to the shape of dispersal kernels, especially the ones that allow cross-basin dispersal? How should we incorporate the effects of other processes and properties such as spatial heterogeneity and temporal fluctuation of precipitation and disturbance (primarily flooding), elevation, temperature, and light availability?

Indeed, we are currently pursuing some of these questions. The analyses performed in this paper are being applied to the strictly hierarchical competition-colonization trade-off model. The comparative study of the two models—neutral and trade-off—will potentially shed light on the problem. We are also developing models to study the relative importance of directionality and landscape structure, and analysing high resolution remote sensing data to infer the actual riparian biodiversity patterns of a river network.

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Appendix A. Estimating the occupancy distribution with a beta distribution

Given $c$ cells and $b$ balls, how many cells will be occupied by the balls if the balls are placed at random and one cell may contain more than one ball? In our present case, the balls are incoming propagules and the cells are available empty sites. The number of occupied sites is thus a random variable following the occupancy distribution (Johnson and Kotz, 1969). The mean and variance of this distribution are

$$
\mu = c - (c - 1)^b c^{1-b},
$$

$$
\sigma^2 = (c - 1)(c - 2)^b c^{1-b} + (c - 1)^b c^{1-b} - (c - 1)^{2b} c^{2-2b}.
$$

To accelerate the computation, we estimated the occupancy distribution by a beta distribution with identical mean and
of propagules. Then, we allow the dispersal to redistribute the propagules and analyse the resulting pattern. As described in Section 2.3, as one moves away from the link of origin, the numbers of the dispersed propagules—after the redistribution of dispersal—decays on the average by a factor of $d$ and $u$ in the downstream and upstream directions, respectively. In Fig. 11, in which a streamlink is represented by its upstream node, the value at each node represents the average ratio between its number of propagules and that at the link of origin. Since the sum of the dispersal kernel values in this infinitely large Cayley tree must add up to one, the normalization constant, $C$, is basically the inverse of the sum of the values at all nodes in Fig. 11. That is,

$$1/C = 1 + 2T + (d + d^2 + d^3 + \cdots)$$

$$+ (dT + d^2T + d^3T + \cdots)$$

$$= 1 + 2T + (1 + T)(d + d^2 + d^3 + \cdots)$$

$$= 1 + 2T + (1 + T)\frac{d}{1 - d},$$  \hspace{1cm} (B.1)

where, as observed in Fig. 11,

$$T = u + 2u^2 + 4u^3 + 8u^4 + \cdots$$

$$= u(1 + 2u + (2u)^2 + (2u)^3 + \cdots)$$

$$= \frac{u}{1 - 2u}. \hspace{1cm} (B.2)$$

Thus,

$$C = \frac{(1 - 2u)(1 - d)}{1 - ud}. \hspace{1cm} (B.3)$$

Fig. 11. Illustration of an infinite Cayley tree and the sketch of how the normalization constant of the dispersal kernel is derived. In this figure, each node represents the upstream node of a streamlink. The value at each node represents the ratio between its number of propagules and that at the link of origin, after dispersal. The values next to the enclosures (the dashed lines), e.g. $T$, $dT$, and $d^2T$, represent the sum of the values at all nodes contained in the corresponding enclosures.
Consequently, for any finite river network, the sum of the dispersal kernel values is less than one as some of the propagules are dispersed out of the system and considered lost. In addition, note that in the case of non-directional dispersal, i.e. \( u = d = p, \)

\[
\frac{1}{C} = \frac{1 - p^2}{(1 - 2p)(1 - p)} = 1 - 2p,
\]

which is consistent with the basic result in percolation theory (Stauffer and Aharony, 1994).

References


