

River networks as ecological corridors: A complex systems perspective for integrating hydrologic, geomorphologic, and ecologic dynamics

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[1] This paper synthesizes recent works at the interface of hydrology, geomorphology, and ecology under an integrated framework of analysis with an aim for a general theory. It addresses a wide range of related topics, including biodiversity of freshwater fish in river networks and vegetation along riparian systems, how river networks affected historic spreading of human populations, and how they influence the spreading of water-borne diseases. Given the commonalities among various dendritic structures and despite the variety and complexity of the ecosystems involved, we present here an integrated line of research addressing the above and related topics through a unique, coherent ecohydrological thread and similar mathematical methods. Metacommunity and individual-based models are studied in the context of hydrochory, population, and species migrations and the spreading of infections of water-borne diseases along the ecological corridors of river basins. A general theory emerges on the effects of dendritic geometries on the ecological processes and dynamics operating on river basins that will establish a new significant scientific branch. Insights provided by such a theory will lend themselves to issues of great practical importance such as integration of riparian systems into large-scale resource management, spatial strategies to minimize loss of freshwater biodiversity, and effective prevention campaigns against water-borne diseases.

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1. Introduction and Objectives

[2] Natural systems, despite their seemingly infinite variety, are built around a surprisingly few general structural types, and dendritic structure, or tree-like branching, is one of them. Indeed, there is a plethora of dendritic structures of great importance in nature, examples of which include human pulmonary systems, plants and many more. The dendritic structure that is the central theme of this paper concerns drainage networks in river basins. They are both practically important and theoretically challenging, and lessons learned from them have implications for dynamical systems taking place in other dendritic structures in nature.

[3] It is clear that river networks provide supporting landscapes for many processes essential to human life and societies. Historical human settlements followed the river

networks for the necessary water resources [Ammermann and Cavalli-Sforza, 1984]. The river networks provide hierarchical habitat features for freshwater fish [e.g., Matthews, 1998; Master et al., 1998] as well as pathways of such life-threatening water-borne diseases as cholera [e.g., Codeço, 2001; Pascual et al., 2002]. River networks are also seen as metaecosystems that affect the metabolism of terrestrial organic carbon in freshwater ecosystems, an important part of the global carbon cycle [see Battin et al., 2003, 2008]. Moreover, the amount of nutrients removed from streams and reservoirs is affected by the network structure and dynamics and ecological processes therein [e.g., Alexander et al., 2000, 2002; Darracq et al., 2008].

[4] Rivers carve fascinating landscapes characterized by general scaling laws and deep symmetries [Rodriguez-Iturbe and Rinaldo, 1997] that are shaped by climate, hydrology, geology, geomorphology, biology and ecology. The topography of river basins is shown to control the interaction between surface and subsurface hydrological dynamics, residence time distribution [Haggerty et al., 2002; Wörman et al., 2007; Boano et al., 2007] and geochemistry [Kirchner et al., 2000] of ecosystems around it. Riparian zones along the networks harbor riparian vegetation, which further regulate flows of energy, water, nutrients and sediment in the rivers and their neighboring upland areas [see Gregory et al., 1991; Malanson, 1993;

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Naiman and Décamps, 1997; Lowrance et al., 1984; Peterjohn and Correll, 1984; McClain et al., 2003]. The profound commonalities existing among all types of river basins and their drainage networks, together with the key roles that the dendritic structure plays in all the above processes, allow for the hope that general statistical signatures will be present in a variety of phenomena of crucial interest.

[5] The above questions have been separately addressed in a wide range of fields, from epidemiology to ecology and geography. However, most of the models that describe the relevant processes do not consider spatial configurations in an explicit manner. Stochastic space-time evolution of living communities in explicitly spatial landscapes is a relatively new subject [see, e.g., Tilman and Kareiva, 1997]. Among the foremost mechanisms relevant to the spatial dynamics are the very configurations of communities imposed by the river networks and the induced anisotropy in the spreading of species, pathogens or other agents of interest along the waterways [Campos et al., 2006; Bertuzzo et al., 2007; Muneepetarakul et al., 2007b]. Such anisotropy proves essential, as shown by exact solutions of the front speed propagation in 2D landscapes and networks [Bertuzzo et al., 2007]. The network configuration per se is likely to exert its own effects on the spatial dynamics and patterns of the mentioned phenomena [Muneepetarakul et al., 2008c]. In addition to the network configuration and spreading anisotropy, we believe that the hydrologic controls accompanying river basins play central roles in the spreading of species, water-borne disease, or populations in other ways. Such mechanisms dictate the spatial distributions of streamflow rate and velocity, which, besides the degree of anisotropy, regulate the amount of available resources, and thus sustainable community sizes, as well as the severity of disturbances. The combined effects of all these mechanisms are expected to give rise to interesting, perhaps unexpected, dynamics and patterns.

[6] Such an approach toward the integration of the hydrologic, ecologic, and geomorphologic dynamics of river basins is fundamentally different from a more common effort that focuses on the implementation of the most important specific processes taking place in the various domains and relating them through a number of shared variables. This is a perfectly valid approach, which uses a large number of functional and empirical relationships and by necessity a very large number of parameters. In terms of classical hydrologic modeling, such an approach is similar in spirit to that of rainfall-runoff models that by design focus on the best possible representation of runoff production and routing in the different spatial units of a specific basin, given that the modeler has at hand all the necessary information. To be sure, these are useful tools, which are used throughout the world for a variety of purposes. They are not the most fruitful for pursuing fundamental, generalizable results, however. Such a pursuit is more challenging when we try to link hydrologic, ecologic, and geomorphologic dynamics. Einstein [1950] posed that “new theories are first of all necessary when we encounter new facts which cannot be explained by existing theories,” but he went on to stress that “there is another more subtle motive of no less importance.” This is the striving toward unification and simplification of the premises of the theory as a whole. As pointed out by Guth [1997], “unification has

been the inspiration for many of the greatest achievements in the history of science.” We firmly believe it is crucial to aim at this type of goal also in hydrologic science.

[7] In this paper we outline a vast field of research oriented toward the pursuit of general signatures linking the hydrologic, ecologic, and geomorphologic dynamics of river basins. One key element of this pursuit is the dynamics of transport through river networks, which has a commanding influence on all these intertwined domains. We usually employ the simplest possible models thought to be meaningful for the general description of the key elements of the dynamics taking place. We are not focusing our effort on the prediction of specific behaviors of a particular river basin that calls for many individual parameters to be identified and quantified. Instead, we search for commonalities across river basins in the statistical structure of some important descriptors of their ecological, geomorphological, and hydrological dynamics. We are confident that the discovery of such common signatures and their linkage across domains and spatial scales will also result in a vast improvement in our abilities to manage and predict the overall functioning of river basins.

[8] Our ultimate goal is a comprehensive theory of how dendritic structure, its associated features and its interaction with external forcings (e.g., hydrological stochasticity) shape the emergent properties of various complex systems. Such a theory would help us address a wide variety of important questions: from conservation plans for freshwater ecosystems to optimal prevention campaigns for containing water-borne disease epidemics to proper inclusion of riparian systems into large-scale resources management. This paper attempts to bring together diverse efforts that have been recently published by the authors in journals of different disciplines under the unified perspective. While providing what we believe is a useful review, the novelty of this paper lies in its global vision of a research area where hydrology, ecology, and geomorphology intersect and where we feel that important advances and their applications will be made in the near future. This is by no means a definitive statement of the roles of river networks as ecological corridors. Throughout the paper, we suggest research areas that look to us particularly exciting.

[9] This paper is organized as follows. Section 2 summarizes some general geomorphological and hydrological signatures of river basins relevant to the governing dynamics of the transport processes. Section 3 aims to demonstrate some results from simple theoretical models that is part of the basis of our motivation. Section 4 discusses results from more realistic models that include the effects of local community size distribution, and importantly, comparison to empirical evidence of spatial biodiversity patterns. In section 5, we discuss possible methods of characterizing sizes of riparian areas, which are ecosystems situated along river networks. In section 6, we provide examples and explore research directions regarding the controls that hydrological external forcing has on ecological systems. Section 7 shows how water-borne disease dynamics is tied to the dendritic structure and anisotropy of river networks, thus demonstrating the possible versatile applications of the general theory we seek. The paper ends in section 8 with a particular vision and outline of where we believe some of

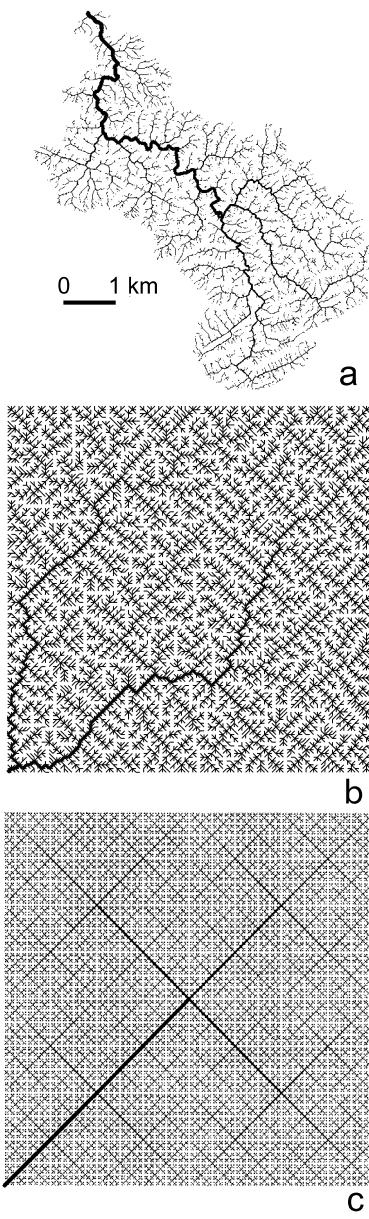


Figure 1. Examples of networks: (a) a real river network, the Dry Tug Fork (California), suitably extracted from digital terrain maps; (b) a single-outlet optimal channel network (OCN); (c) Peano’s construction [after Bertuzzo *et al.*, 2007].

the most exciting research lies ahead at the boundaries of hydrology, ecology and geomorphology.

2. Inferences From the Geomorphological Organization of River Basins

2.1. Signatures in Hydrologic Dynamics

[10] The general mathematical scheme adopted by most models presented here utilize reactive nodes and transportation links, which in this case are identified by the connected fluvial pattern. Reaction may involve individual organisms, species or pathogens of water-borne disease. The river network is modeled as an oriented graph constituted by nodes connected through edges. An oriented graph is a

directed graph (i.e., a graph whose edges have inborn direction) without symmetric pairs of directed edges. In the case of riparian corridors, edge direction is gravity driven and thus uniquely defined from physical features. Nodes could be thought of as patches of species population or communities (e.g., cities with human population) located along the rivers, portions of channels and riparian zones that are habitat for riverine species, etc. Edge directions are chosen accordingly to the flow direction that could bias transport processes. Organisms can either move by their own energy (active dispersal) or be moved by water or wind (passive dispersal). Movements along the flow direction would most likely be favored for passive dispersers, but perhaps not so for active dispersers such as freshwater fish.

[11] Models of ecological corridors are obtained by coupling two submodels: (1) a local reaction model at the nodes and (2) a transport model between nodes through the edges. Different choices of the submodels, along with the relevant temporal and spatial scales involved, are selected to represent and characterize the processes in different cases.

[12] Consider propagules that can locally originate, die and react at the nodes. Let $\rho(i, t)$ be the probability of finding a propagule at node i at time t and P_{ij} the probability that it moves from node i to node j in a given time step τ . The temporal evolution of the probability $\rho(i, t)$ for each node of the network ($i = 1, \dots, N$) can thus be described by the following master equation:

$$\rho(i, t + \tau) = \rho(i, t) + \sum_{j=1}^N P_{ji}\rho(j, t) - \sum_{j=1}^N P_{ij}\rho(i, t). \quad (1)$$

[13] Note that if we consider many realizations of independent processes (i.e., a large number of propagules that do not interact with one another during the transport process), $\rho(i, t)$ is proportional to the number of propagules at nodes i at time t . Operational ergodicity is always assumed. Equation (1) describes only the transport processes, local reactions/interactions at nodes are modeled by introducing additional terms or implementing stochastic interacting particles schemes. It is possible to consider either closed or open systems: all the particles remain in the system after dispersal in the closed systems, whereas the open systems allow particles to exit through parts or all of their boundaries. In an environmental matrix defined by the river network, the main boundaries can be identified by all the source nodes and the outlet. Reactive transport processes have been successfully modeled by means of continuous time random walk schemes, especially in hydrologic applications. For instance, this framework has been applied for stream transport of solutes [e.g., Boano *et al.*, 2007] which helped define enhanced residence times due to hyporheic transport through soil. Other applications, unrelated to the main focus here, have dealt with transport in heterogeneous geological formations [e.g., Berkowitz *et al.*, 2006].

[14] In order to analyze signatures of geomorphological organization of river basins one needs empirical representations of natural forms and their mathematical models [e.g., Rodriguez-Iturbe and Rinaldo, 1997]. We are specifically concerned here with geomorphic features that might affect ecological processes on networks. Self-similar properties

appearing at different scales of observation, or the looplessness of the structure are examples of such features [Rinaldo *et al.*, 1998, 2006].

[15] For general numerical calculations of the structure of topological and metric properties relevant to the functions of ecological corridors, we employ empirical and model representations (see Figure 1). For the latter we use extensively the features of Optimal Channel Networks (OCNs) [Rodriguez-Iturbe *et al.*, 1992a, 1992b; Rinaldo *et al.*, 1992, 1993; Rodriguez-Iturbe and Rinaldo, 1997], local minima of functionals of the network configuration. They hold fractal characteristics that are obtained through a specific selection process known to closely conform to the scaling of real networks over arbitrary ranges of scales and boundary conditions [Rinaldo *et al.*, 1998]. Notably, OCNs have been shown to be exact solutions to the steady state of the general (small gradient) landscape evolution boundary value problem [Banavar *et al.*, 2000, 2001; Rinaldo *et al.*, 2006]. To derive exact results, instead, we resort to special recursive constructions like the Peano network. The latter is a deterministic fractal [Mandelbrot, 1983] whose main topological and scaling features can be computed analytically [Marani *et al.*, 1991; Colaiori *et al.*, 1997].

[16] Also of importance are the ecological implications of the spatial distribution of tributaries, which are related to the availability of flow and extent of riparian zones [Muneepeerakul *et al.*, 2007a; Convertino *et al.*, 2007]. For example, riparian zones, which play many important roles in regulating ecosystem function within streams, surrounding environments, and upland areas, are closely tied to the stream width or topographically concave areas, which in turn relate to landscape-forming discharges. The very definition of the confluence of a stream with a tributary depends on what we define as a sizable tributary, i.e., the threshold area for channelization and the size of the confluent basin that defines a geomorphologically meaningful tributary. A link is only defined as a stream section separating two consecutive tributaries, and this depends on an arbitrary threshold used to define a tributary. This issue has been addressed by Convertino *et al.* [2007] where the probabilistic structure of the distances between tributaries with areas larger than a threshold area a has been studied (see Figure 2a). We denote as D such random distance. We term $P(D \geq d)_a$ the probability of D exceeding a given length d conditional on the threshold area, a . The collapse of all $P(D \geq d)_a$ when plotted against $d/a^{H/(1+H)}$ or $d/\langle a \rangle^d$ (depending on whether the draining boundary is a mainstream or a multiple-outlet line boundary), where $\langle a \rangle$ indicates the mean area of all tributaries whose area is larger than a , defines a general feature with interesting ecological implications. Note that the geomorphological organization is summarized by the elongation (or Hurst) exponent, H ($0.65 \leq H \leq 1$) and by the fractal dimension characterizing the sinuosity of individual streams, d_f ($1 \leq d_f \leq 1.2$).

[17] An important signature is the universal behavior of $P(D \geq d)_a$ against d/a^ψ (or, equivalently, $d/\langle a \rangle^\phi$, with appropriate ψ and ϕ depending on the draining boundary, see Table 1 of Convertino *et al.* [2007]). In fact, the collapse of $P(D \geq d)_a$ for different values of a onto a single universal curve suggests that the relationship $P(D \geq d)_a \sim F(d/a^\psi)$ is valid for all distances and thresholds and is thus seemingly

of general nature (Figure 2b). The specification of the cutoff function F differs between multiple-outlet boundaries and mainstreams due to the fact that allowing drainage from either side naturally shortens the distance between comparable (or larger) confluences. The proposed analytic form for the scaling function is $F(x) = C \exp(-\beta x)$ where $\beta = 1/x_c$ is the exponent estimated by the plot between $F(x)$ and x in a semilog scale. In such case x_c acts as a cutoff value of the distribution of $d/\langle a \rangle^\phi$; physically, x_c can be thought of as a threshold of streamlink length beyond which such long, uninterrupted streamlinks become highly unlikely. The numerical estimates for C and x_c are described by Convertino *et al.* [2007]. The distribution of along-stream distances between tributaries of a given size is thus a distinctive geomorphological signature which bears implications for biodiversity and ecosystem services provided by the river basin.

[18] The geomorphic organization of the network is also fully reflected in the hydrologic response of a river basin. Bankfull or landscape-forming discharges, characterized by a return period of roughly 1 to 2 years, are a byproduct of this organization and affect important ecological characteristics including local habitat sizes. The form of the residence time distributions, the core of the hydrologic response, may be characterized by some parameters of clear physical meaning like mean travel times. In this context, surface-subsurface hydrologic interactions play a major role, on a continuum of scales for basin-scale transport [e.g., Wörman *et al.*, 2007]. For hillslope-channel transitions, however, it is customary to assume the existence of well-defined timescales, postulated by the use of exponential probability density functions [Rodriguez-Iturbe and Valdes, 1979]. Alternatively, the equivalence of water fluxes at control section with residence time distributions may be used to derive the features of interest from the equations of motion [e.g., Rodriguez-Iturbe and Rinaldo, 1997].

[19] Travel time distributions are identified by an analysis of the detailed motion of water particles in space and time along a channel network and its hillslopes. Indeed a complex catchment entails a nested structure of geomorphic states, quite different from one another, where hydrologic transport occurs. Transitions from one geomorphic state to the next is gravity driven and thus uniquely defined by topographic gradients. Typically one thinks of hillslopes (where runoff production occurs) and channel states (where routing occurs). We thus need to define the collection Γ of all individual paths $\gamma \in \Gamma$ that a particle may follow up to the basin outlet. A path $\gamma = \{x_1, x_2, \dots, x_\Omega\}$ (where we define Ω as the closure of the catchment) consists of the set of all feasible routes to the outlet, that is $x_1 \rightarrow x_2 \rightarrow \dots \rightarrow x_\Omega$. If A_i , $i = 1 \dots N$, is the number of overland states whose total area covers the entire catchment (say, we neglect the actual surface of channelized patterns), and c_i defines any channel link of the catchment (N is the total number of links), all the paths are supposed to originate within hillslopes, i.e., $A_i \rightarrow c_i \rightarrow \dots \rightarrow c_\Omega$.

[20] The residence time spent along any one of the above paths is composed by the sum of the residence times of a (large) set of independent particles within each of the states composing the considered path. The time T_x that a particle spends in state x ($x = A_i$ or c_i) is a random variable, which can be described by probability density functions (pdf) $f_x(t)$.

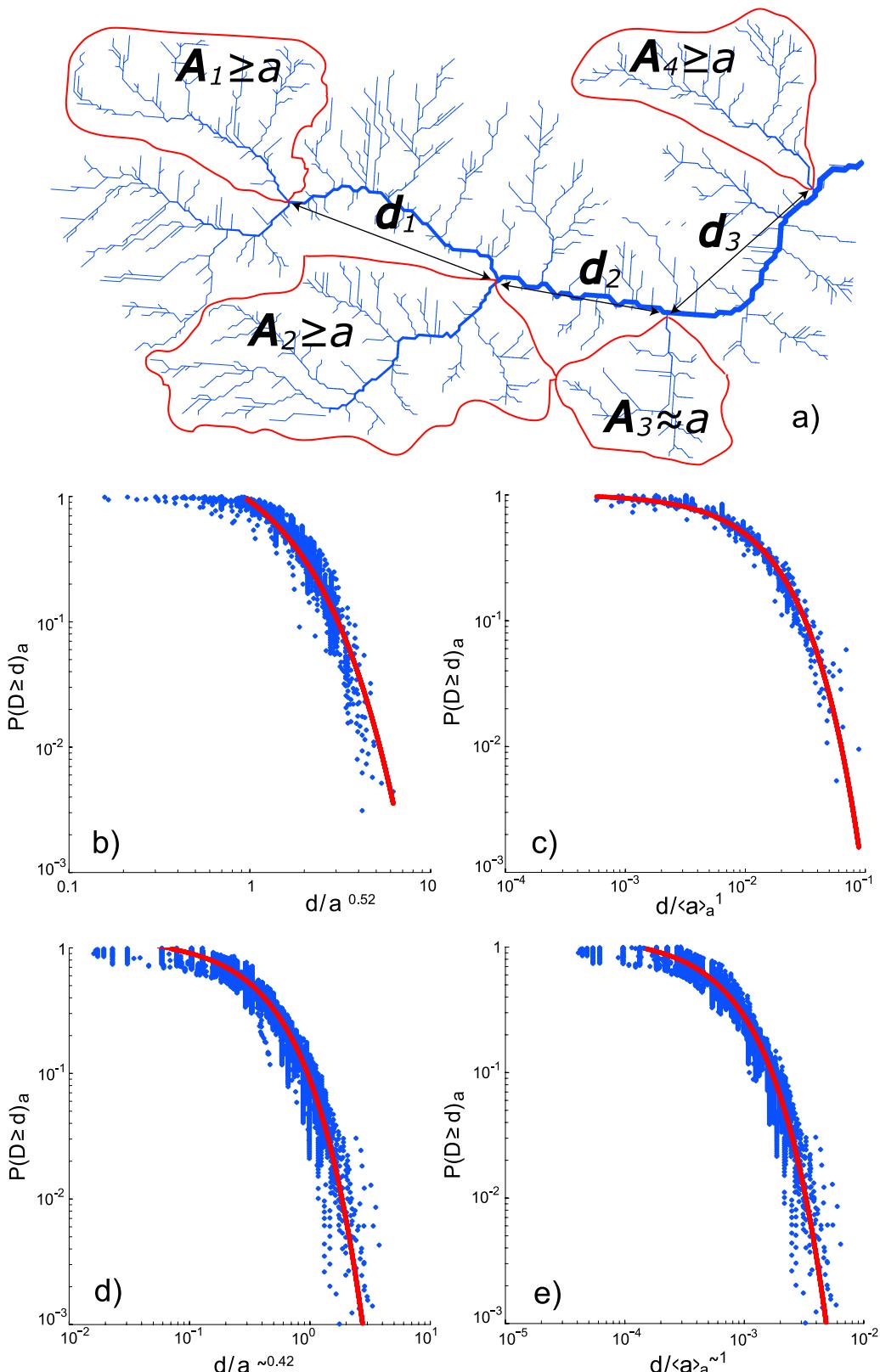


Figure 2. (a) Sketch of the distances between tributaries with areas larger than a threshold area a . (b–e) Collapse tests for $P(D \geq d)_a$. Figures 2b and 2d show the collapse of $P(D \geq d)_a$ is tested as a function of $\frac{d}{a^{1+\beta}}$. In Figures 2c and 2e the collapse is tested as a function of $d/\langle a \rangle_a^H$ or $d/\langle a \rangle_a^{d_f}$ depending on boundary conditions. Here we show Figures 2b and 2c for OCNs and Figures 2d and 2e for the Tanaro river network (Italy) [after Convertino et al., 2007].

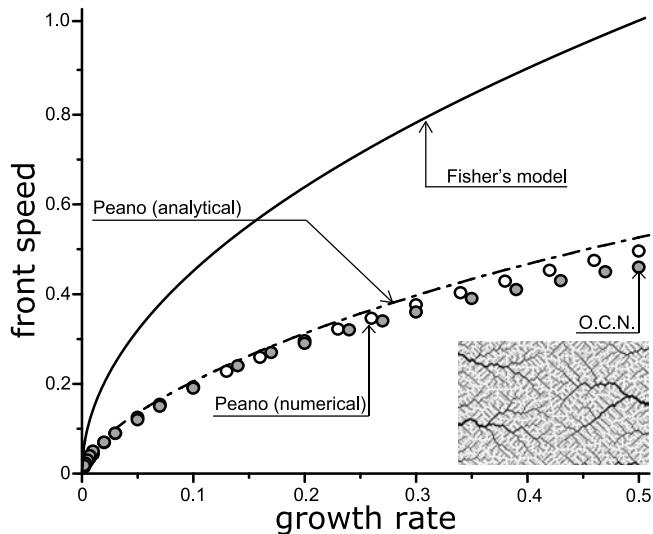


Figure 3. Front speed as a function of the growth rate of the logistic equation (redrawn from Campos *et al.* [2006]). Solid line is the exact solutions of the continuous one-dimensional Fisher's model. The dashed line and the circles represent exact and numerical values for propagation along Peano and OCN [after Bertuzzo *et al.*, 2007].

For different states x and y , T_x and T_y have generally different pdf's ($f_x(t) \neq f_y(t)$) and we assume that T_x and T_y are statistically independent for $x \neq y$. For a path $\gamma \in \Gamma$ defined by the collection of states $\gamma = \{x_1, \dots, x_k\}$ (where $x_1, \dots, x_k \in \{A_1, \dots, A_\Omega, c_1, \dots, c_\Omega\}$), we define a travel time T_γ through the path γ as: $T_\gamma = T_{x_1} + \dots + T_{x_k}$. From the statistical independence of the random variables T_{x_i} , it follows that the derived distribution $f_\gamma(t)$ of the sum of the (independent) residence times T_{x_i} is the convolution of the individual pdf's: $f_\gamma(t) = f_{x_1} * \dots * f_{x_k}$, where $*$ denotes the convolution operator. With the above assumptions, travel time distributions $f(t)$ at the outlet of a system whose input mass is uniformly distributed over the entire domain are obtained by randomization over all possible paths

$$f(t) = \sum_{\gamma \in \Gamma} p(\gamma) f_\gamma(t), \quad (2)$$

where γ is a randomly selected path and f_γ is the path travel time distribution; $p(\gamma)$ is the path probability, i.e., $\sum_{\gamma \in \Gamma} p(\gamma) = 1$, defining the relative proportion of particles in γ [Rinaldo *et al.*, 2006]. Whether or not one needs to modify travel times into residence time distributions (because initial storage impacting the rainfall is nonnegligible) or linking them to the intensity of the hydrologic events depends on the modes of hydrologic transport, e.g., when dominated by storage rather than kinematic effects, but the basic formal machinery remains unaffected. Many papers have addressed the characterization of travel and residence times and the related hydrological processes, including transport; we do not attempt to review them here. In this framework, one can determine the exact relation between the variance of the arrivals at the control section to the morphology of the river network. This has been termed geomorphologic dispersion [Rinaldo *et al.*, 1991] because the variability of the geometric pathways leading to the control section induces

much larger variations in the arrival rates than those induced by hydrodynamic dispersion along single paths. In a sense, the usual hierarchy of dispersive processes where the next scale beclouds the processes at lower scales (say, from molecular to turbulent to shear-flow dispersion) is complemented at large scales by a geomorphologic dispersion produced by the heterogeneity in the geometry of pathways [Rinaldo *et al.*, 1991; Haggerty *et al.*, 2002; Berkowitz *et al.*, 2006; Wörman *et al.*, 2007].

2.2. Geomorphological Signatures in Network Dynamics

[21] The role of the geomorphological organization of river networks in modeling hydrochory or human range expansions (how populations migrate when settling into new territories) emerges through models of reactive dispersion along fractal networks [Méndez *et al.*, 2004a, 2004b; Campos *et al.*, 2006; Bertuzzo *et al.*, 2007]. Migrations are processes of great social, biological or physical importance that involve river basins as substrates [Ammermann and Cavalli-Sforza, 1984] where an essential ingredient is the fact that settlers or colonizing species do not occupy space isotropically, but rather follow fluvial patterns as corridors and pathways.

[22] A notable geomorphological signature concerns the strong controls that network topologies exert on the speed of the traveling wave that is known to form in reaction-diffusion models of transport [Murray, 1993]. Figures 3 and 4 illustrate recent results by Campos *et al.* [2006] and Bertuzzo *et al.* [2007] concerning a reactive random walk (RRW) process through Peano and OCNs. In short, a particle at an arbitrary node of the network jumps, after a waiting time τ , to one of its z first adjacent nodes with probability $1/z$ for unbiased lattices (and through weighted probabilities for biased lattices). During the waiting time τ , the particles react following the logistic equation with growth rate parameter a [T^{-1}]. Figure 3 shows that the one dimensional reaction front (Fisher's model) propagates much faster than the wave constrained by a treelike pathway. This proves that geometrical constraints embedded in fractal networks impose strong corrections on the speed of the travelling fronts. Quite surprisingly, however, Peano and OCNs lead to quite similar results showing that the front speed is controlled by topological features, chiefly the bifurcation structure, that is indeed quite similar for all of the (rather different otherwise) networks shown in Figure 1 [see, e.g., Rodriguez-Iturbe and Rinaldo, 1997; Rinaldo *et al.*, 1998, 2006].

[23] The model proposed by Campos *et al.* [2006] assumes simple diffusive transport. This seems indeed reasonable in the case of population migrations: water supply serves settlers regardless of the flow direction. Bertuzzo *et al.* [2007] wondered whether adding a bias to transport properties changes things considerably. In fact, many ecological agents (propagules or infective agents of water-borne diseases for instance) would likely be affected by the flow direction while propagating within the network. Movements along the flow are typically favored, although movements against flow directions are completely admissible because of various ecological or physical factors like active transport. Exact solutions for biased transport show that the corrections imposed by the fractal networks on the

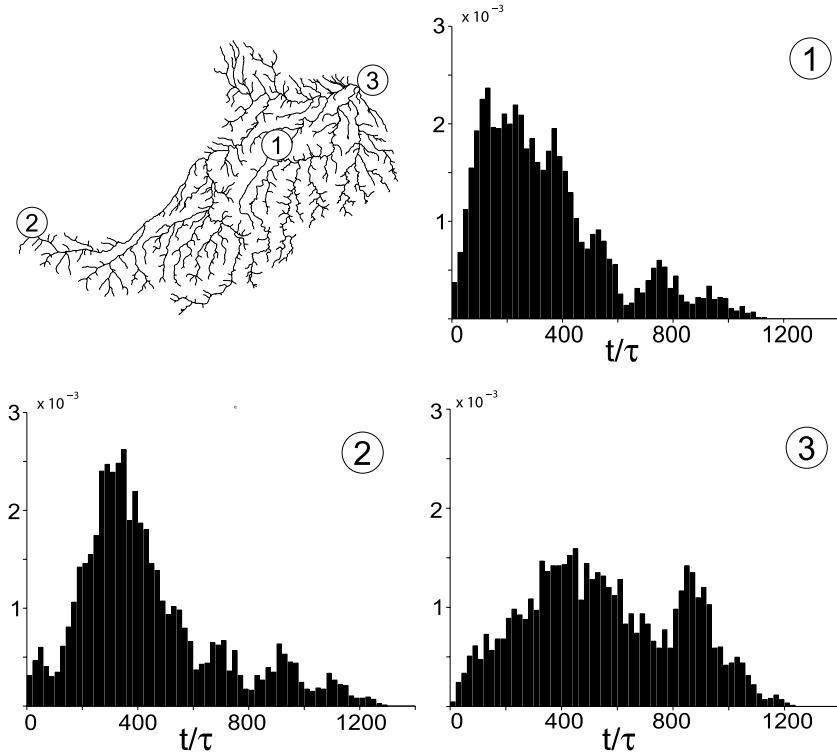


Figure 4. First colonization time distributions of all network sites starting from three different nodes. The positions of the three nodes in the network are shown. The upstream and downstream front speeds employed to compute the travel time refer to values representing a downstream bias of 0.4 and $a\tau = 0.3$ [after Bertuzzo *et al.*, 2007].

speed of traveling fronts can be enhanced or smoothed by the bias.

[24] Another interesting geomorphological signature is the travel time distribution from any given source node to any other node in the network. Ideally, this defines a colonization (or ecological) diameter of the fluvial network. Figure 4 shows the first colonization time distribution from three different starting nodes to all the others for a large river network [Bertuzzo *et al.*, 2007]. Subtle interplays of structural and dynamic controls are thus shown to operate at the network level. Indeed, if the travelling particles in this example were infective agents or propagules, thereby accounting for reactions different from the logistic growth considered here, a definite hydrological role in the ecological colonization would have resulted.

3. Roles of Directionality and Network Structure on Ecological Organization

[25] In reality, many factors other than network configuration and transport anisotropy (see section 1) are of course in place and play different roles. However, inclusion of all factors, no matter how realistic, is hardly a good starting point for pursuit of generalizable signatures. Our research philosophy is to start from simple settings from which fundamental insights can be gathered and to later add complications whose effects would then be distinguishable. In that spirit, we show in this section results from some simple theoretical models focusing on the fundamental differences between river basins and 2D landscapes. From now on, we shall refer to 2D landscapes as “savannas” only

for easier mental link to the real world, as our model does not include all features of real savannas. These results form the basis of our theoretical motivation upon which additional realistic complications will be built.

[26] Specifically, we will study spatial biodiversity patterns of communities obeying the neutral theory [Hubbell, 2001], which assumes that all species are competitively equivalent at a per capita level. The neutral theory offers one of the simplest mechanisms capable of maintaining biodiversity. Despite its bold assumptions, the neutral model has been tested extensively against empirical data in the sense that many aspects of real systems do not require a more complicated model [Hubbell, 2001; Condit *et al.*, 2002; Volkov *et al.*, 2003, 2007; Etienne and Olff, 2005; Dornelas *et al.*, 2006; Walker and Cyr, 2007]. Furthermore, Purves and Pacala [2005] show that patterns predicted by the neutral theory can also arise from nonneutral interspecific dynamics in the presence of some stochasticity and high species richness, thus widening the range of applicability of the theory. Despite its success, it is crucial to recognize that the neutral theory is by no means a panacea for all ecological problems. For example, species-specific information is certainly required when one wishes to study the dynamics of particular species and interaction among them. In any event, employing the neutral theory seems well justified as long as the steady state biodiversity patterns, which are a focus of this paper, are concerned [see also Chave *et al.*, 2002]. In this section, we implement the neutral theory in savannas and river basins under two different frameworks, namely an individual-based contact

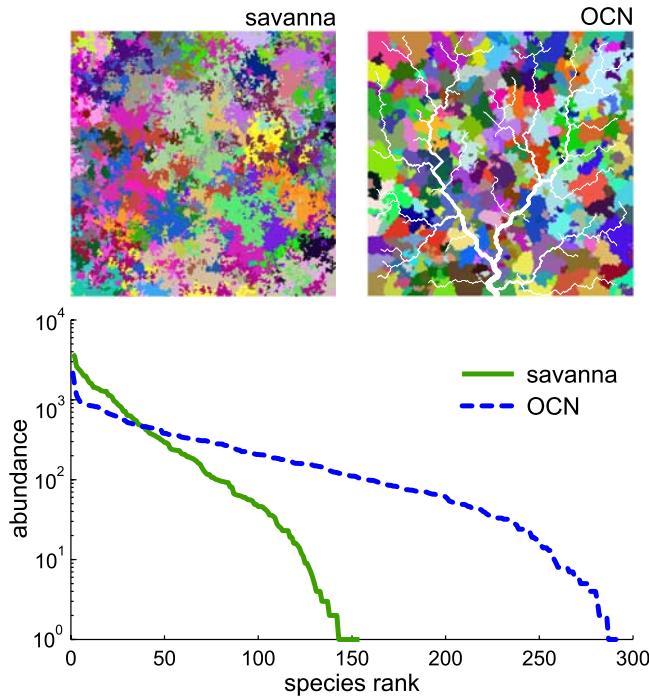


Figure 5. Comparison between biodiversity patterns in a savanna and in a network landscape represented by species spatial patterns and species rank-abundance curves. The simulations are run on a 250×250 lattice with $\nu = 10^{-4}$.

model and a metacommunity model, and investigate the differences between the two types of landscapes.

[27] In our neutral individual-based model, a savanna is represented simply by a square lattice in which each site, or pixel, is occupied only by one individual, say, a tree. As for the river network landscape we use a space-filling optimal channel network built in a lattice of the same size as the savanna. In a space-filling network, all sites are channelized (Figure 1b). The dynamics at each time step is as follows. A randomly selected individual (i.e., a pixel) dies. With probability ν , termed diversification rate, this site is occupied by a new species; with probability $1 - \nu$, the site is colonized with equal probability by an offspring of one of the neighbors. The two landscapes differ in the definition of neighbors. For the savanna the offspring that colonizes the empty site is chosen among the individuals that occupy the four nearest neighbor (von Neumann neighborhood); boundary effects at the edges of the lattice are removed by implementing the genetic algorithm proposed by Rosindell and Cornell [2007]. For the network landscape, the neighborhood of a pixel is constituted by either only its nearest pixels connected to it through the network or all neighboring pixels with larger probabilities being assigned to those connected through the network. Notice that all pixels, except for the outlet, have only one downstream neighbor; source pixels have no upstream neighbors, whereas all the others have one or more upstream neighbors. The process is iterated until it reaches a stationary state.

[28] The two upper insets of Figure 5 illustrate the resulting spatial biodiversity configuration in the two landscapes: pixels of the same colors represent individuals of the same species. Figure 5 (bottom) shows typical results

for the associated rank-abundance curves. The results are remarkably different. It can be noticed that the configuration of the space and the directionality of the dispersal imposed by the network landscape determine a higher species richness. Moreover the spatial configuration of the patches of the same species in the network landscape have sharp boundaries that resemble the boundaries of subbasins. Differences arise in this case only because of the different connectivity imposed by the two landscapes. Adding another factor typical of the dispersal in network landscape such as biased transport (e.g., offsprings preferably colonizing downstream) would enhance the observed differences.

[29] The results from the neutral individual-based model are not to be taken as fully representative of reality. Instead, they demonstrate the differences that may arise in key biodiversity features caused by the presence of the drainage network. These potentially fundamental roles played by the drainage network warrant more refined modeling schemes to investigate other important issues. In that light, we present here another set of results from a neutral metacommunity model [Muneepeerakul et al., 2008c]. In this model, each local community (LC) is assumed to have the same number of sites, and each site contains only one individual. At each time step, an individual, randomly selected from all individuals in the system, dies. With probability ν , the diversification rate, this will be occupied by a new species; with probability $1 - \nu$, the empty site will be colonized by an offspring of a species already existing in the metacommunity. In the latter case, the probability P_{ij} that the empty site in LC i will be colonized by a species from LC j is determined as follows:

$$P_{ij} = (1 - \nu) \frac{K_{ij} H_j}{\sum_{j=1}^N K_{ij} H_j}, \quad (3)$$

where K_{ij} is the dispersal kernel, the fraction of offspring produced by an individual at LC j that arrives at LC i after dispersal; H_j is the habitat size of, or the number of sites in LC j (which is now assumed to constant), and N is the total number of LCs. All individuals in LC j have the same probability of colonizing the empty unit in LC i where the death took place. The neutral assumption is extended to dispersal as well; that is, the dispersal kernel of every species is assumed to be the same. In the context of metacommunity models, the dispersal kernel K_{ij} contains the information on the landscape spatial structure and how individuals move about. Therefore, the key difference between savanna and river network metacommunities lies in their respective dispersal kernels. The dispersal kernels are assumed to take the form of exponential decay whose mathematical expression is omitted here. The interested reader is referred to Muneepeerakul et al. [2008c] for details and specific references. Note that unlike in contact models, an offspring can now travel farther than its immediate neighbors in each time step.

[30] In a metacommunity model, biodiversity patterns are measured by α , β and γ diversities. Here, α diversity is a local description of biodiversity and γ a global one, both inventory measures because they refer to the number of species. β diversity is a differentiation diversity measuring the rate of change in, or the turnover of, the species,

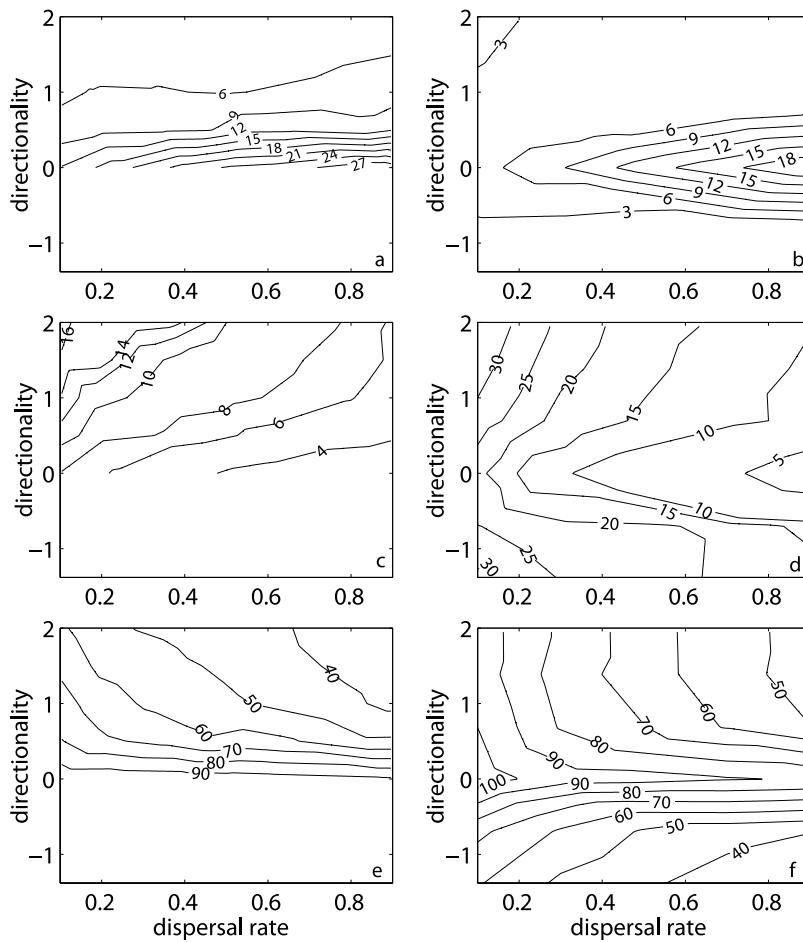


Figure 6. Contours of $\langle \alpha \rangle$, β , and γ diversities of the savannas and river networks under different settings: (a) $\langle \alpha \rangle$, savanna; (b) $\langle \alpha \rangle$, river network; (c) β , savanna; (d) β , river network; (e) γ , savanna; and (f) γ , river network. The x axis represents the dispersal rate, or the fraction of offspring that is dispersed away from their birth local community, and the y axis represents the dispersal directionality (see Muneeparakul *et al.* [2008c] for details). Taken and modified from Muneeparakul *et al.* [2008c].

measuring how species compositions in local communities differ from one another.

[31] In the following, γ diversity is defined as the total number of species in the entire metacommunity. α diversity is a number of species in a randomly chosen LC; it is also useful to consider its mean value averaged across all LCs, denoted by $\langle \alpha \rangle$. The between-community diversity, or β diversity, is a conceptual quantity that can be defined in many ways, all of which share the same general idea: the higher the β diversity, the more different the local communities. Here, it is defined as $\gamma/\langle \alpha \rangle$.

[32] The results (not shown here), namely the rank-abundance curves and exceedance probability plots of abundance, from the metacommunity model are in general qualitative agreement with the contact model, confirming the importance of network configuration of local communities. We further investigate how network structure and dispersal anisotropy affects the diversity measures. Figure 6 shows the contours of $\langle \alpha \rangle$, β and γ diversities of savannas and river networks under different dispersal settings. Here, the dispersal rate is defined as the fraction of propagules that is dispersed away from their birth local community and the directionality is defined as the natural logarithm of the

ratio between the fractions of propagules at the nearest neighbors in the preferred and opposite directions of dispersal (see Muneeparakul *et al.* [2008c] for details). All three diversity measures, in both types of landscapes, appear to be quite sensitive to dispersal anisotropy. This implies that predictions of changes in these diversity measures based solely on the dispersal rate may not be accurate. River networks result in metacommunities with higher β diversity, i.e., more localized and heterogeneous ecosystems. This is due to a containment effect [Muneeparakul *et al.*, 2007b]: in river basins, cross-subbasin dispersal is hindered by topographical divides, resulting in subbasins being more dissimilar from one another. For a detailed discussion the reader is referred to Muneeparakul *et al.* [2008c].

4. Network Metacommunity Models in Heterogeneous Environment

[33] The constant local community sizes and the back-to-back exponential dispersal kernels explored in the previous section were chosen on the grounds of their simplicity, clarity, ease in result interpretation and some analytical tractability. Of course, these do not constitute the most realistic situation, and consequently it may be difficult to

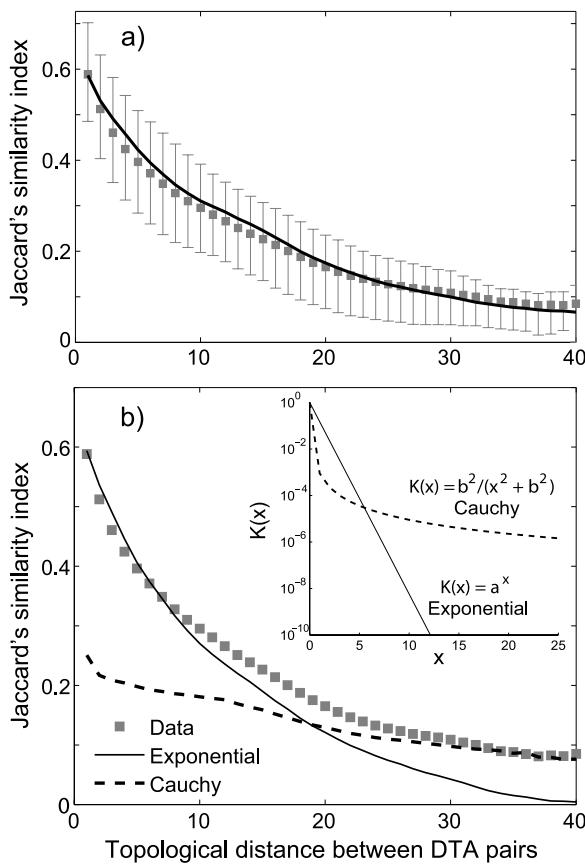


Figure 7. Jaccard's similarity index (JSI) as a function of topological distance between direct tributary areas (DTA) pairs: (a) the empirical JSI pattern and that from the best-fit parameters and (b) the comparison of the JSI patterns associated with the exponential and Cauchy kernels. The overall spatial decay of JSI with the distance is considered as the characterization of β diversity [see Condit *et al.*, 2002]. JSI is defined for any pair of DTAs as $S_{ij}/(S_i + S_j - S_{ij})$, where S_{ij} is the number of species present in both i and j and S_i is the total number of species in DTA i . Taken from Muneepakul *et al.* [2008a].

find compatible empirical evidence to support or test the hypotheses/speculations posed above. In this section, we slightly modify some aspects of the neutral metacommunity model by allowing for varying local community sizes and different dispersal kernels. Importantly, we compare the model results with empirical data.

[34] Muneepakul *et al.* [2008a] implemented the neutral metacommunity model in the Mississippi-Missouri River System (MMRS) with the aim to reproduce the empirical spatial patterns of its freshwater fish diversity, showing that the river network “acts as an effective template for characterizing spatial attributes of fish biodiversity.” There, the fundamental dynamics is essentially the same as that of the neutral metacommunity model in section 3, with two important modifications: (1) the habitat capacity of a local community (i.e., local community size, see below) is assumed to be proportional to the average annual runoff production (AARP) (W. A. Gebert *et al.*, Average annual runoff in the United States, 1951–80, 1987, available at <http://aa179.cr.usgs.gov/metadata/wrdmeta/runoff.htm>)

resulting from the directly contributing area and (2) the dispersal kernel (still assumed to be the same for all species) exhibits a heavy tail character. Here, a local community (LC) corresponds to what they refer to as a direct tributary areas (DTA), which is equivalent to a USGS HUC-8 scale subbasin [U.S. Environmental Protection Agency and U.S. Geological Survey, 2006]. The interested reader is referred to Muneepakul *et al.* [2008a] for more detailed description of the model and data set as well as the fitting procedures.

[35] The model results show very good fits to several empirical biodiversity patterns derived from the freshwater fish occurrence data [NatureServe, 2004] and river network structure derived from the National Hydrography Database Plus (NHDPlus). They capture the general trend and fine structures of the profile of local species richness (LSR), of α diversity, as well as the bimodal character of LSR frequency distribution. They reproduce the relatively straight line character (in a semilogarithmic plot) of the rank-occupancy curve and very well match the spatial pattern of the Jaccard's similarity index (JSI) (Figure 7a), which is another way to characterize the between-community (β) diversity [see, e.g., Condit *et al.*, 2002], or rather in this case, the between-community similarity.

[36] The fits of several empirical patterns constitute a stringent test for theoretical models [Grimm *et al.*, 2005]. The reported simultaneous good fits thus legitimize the neutral metacommunity model, with an appropriate characterization of habitat capacities and dispersal, as a good analog of the real-world ecosystem, at least as far as spatial biodiversity patterns are concerned. A caveat is in order here: as Purves and Pacala [2005] have put it: “neutral pattern does not imply neutral process.” Consequently, different approaches may be needed to predict transient

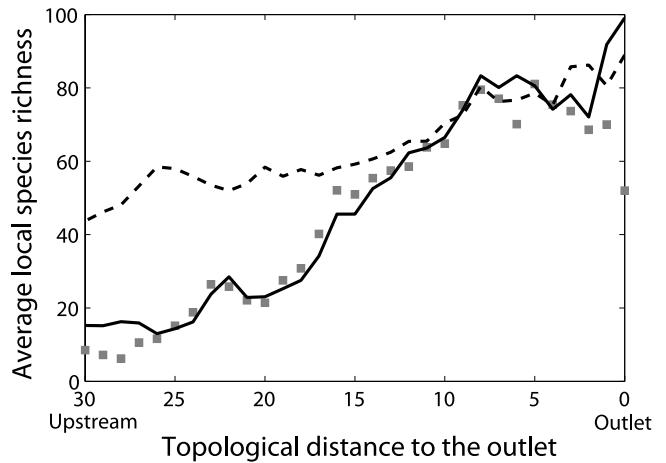


Figure 8. Effects of network structure and climatic gradient on the spatial profile of local species richness (LSR), where squares represent the mean empirical LSR at a given distance to the outlet, the solid line represents the model results with the habitat capacity distribution that incorporates the climatic gradient, and the dashed line represents the model results with constant habitat capacity at every DTA. The climatic gradient clearly steepens the LSR profile. Taken from supplementary information of Muneepakul *et al.* [2008a].

dynamics of the system or to understand patterns and dynamics of particular species. Nonetheless, this does not diminish the significance of this useful tool that can be used to study and differentiate the effects of various factors with a good degree of confidence. Importantly, the current model requires only a few (five in the most general case) parameters [Muneepeerakul *et al.*, 2008a], which significantly limit the amount of field work needed to verify and quantify them. This is precisely the kind of tool we need for investigating the intertwined dynamics of hydrology, geomorphology, and ecology in river basins.

[37] The contribution of the converging character of the river network and the climatic spatial variability may be seen from the general increasing trend in the downstream direction of the LSR profile. In fact, the model with the same set of best-fit parameters but with constant habitat capacities (thereby removing the effects of the climatic spatial variability) produces the results shown in Figure 8. The increasing trend can be caused by the network structure alone and is steepened by the dry-wet climatic gradient. This conclusion is also confirmed by an analysis of empirical data, in which LSR of every DTA is compared to its immediately downstream DTA (see supplementary information of Muneepeerakul *et al.* [2008a]).

[38] The best-fit dispersal kernel also provides us with clues regarding the general behavior of fish. Specifically, it suggests that the spreading of fish offspring is approximately symmetric and unbiased either in downstream or upstream directions; and that on average, the majority of the fish travel locally but a nonnegligible fraction travels great distances [Muneepeerakul *et al.*, 2008a]. The dispersal kernel used in this case can be mathematically expressed as

$$K_{ij} = C \left[a^{L_{ij}} + \frac{b^2}{L_{ij}^2 + b^2} \right], \quad (4)$$

where K_{ij} is the probability that a fish unit produced at DTA j arrives at DTA i after dispersal; C is the normalization constant; L_{ij} is the effective distance, defined as $ND_{ij} + w_u NU_{ij}$, where ND_{ij} and NU_{ij} are the numbers of downstream and upstream steps comprising the shortest path from DTA j to DTA i , and w_u is the weight factor modifying the upstream distance; $w_u > 1$ implies downstream-biased dispersal, thereby characterizing dispersal directionality; $a (<1)$ and b characterize the exponential (i.e., fast decay) and Cauchy (i.e., heavy tailed) decays, respectively. Here, the normalization constant is determined numerically such that, for every species j , $\sum_i K_{ij} = 1$; that is, no fish can travel out of the network. Furthermore, the model enables us to study the dependence of the JSI pattern on the spreading behavior of fish in river basins. Figure 7b presents two JSI patterns associated with two dispersal kernels, namely back-to-back exponential and Cauchy, which are components of the final combined kernel. The dispersal kernel in equation (4) combines the good performance of the exponential kernel at short distances and that of the Cauchy kernel at large distances. Certainly, other types of kernels can be implemented and studied in the same fashion. It is worth noting that with $w_u = 1$ as in the case of the MMRS, the number of parameters required by the model is only four.

[39] Under this framework, one can characterize effects of environmental changes on biodiversity patterns in a more direct and quantitative way. Examples were provided by Muneepeerakul *et al.* [2008a]: changes in precipitation patterns reflected as changes in habitat capacities in the model, and changes in connectivity among local communities incorporated as suitable modifications of the dispersal kernel. In addition, with further model developments it might be possible to even match the spatial distribution of real species to that obtained from the model results. The matching procedure could be done by maximizing the similarity between real and predicted species range size and geographic position. Examples of spatial patterns of individual species for both data and model results obtained through the matching procedure are shown in Figure 9. Through these types of applications, this modeling approach could potentially lend itself well for conservation campaigns and large-scale resource management.

[40] Let us now turn our attention to another crucial inhabitant of river networks, namely riparian vegetation. Here, riparian vegetation is broadly defined as the vegetation situated along streams and rivers and affected by their hydrology. Riparian vegetation is directly and indirectly responsible for the many ecological goods and services that riparian systems provide (see section 1 and Muneepeerakul *et al.* [2007b]). Comprehensive biodiversity data of large spatial extent are hard to come by in general; such is particularly true for riparian systems. Consequently, attempts have been made to infer biodiversity from remote sensing data [Gould, 2000; Nagendra, 2001; Held *et al.*, 2003; Cingolani *et al.*, 2004; Zhang *et al.*, 2006; Foody and Cutler, 2006; Marani *et al.*, 2006b]. Recently, Muneepeerakul *et al.* [2008b] have analyzed the remote sensing data of Sand Creek, a river basin in Oklahoma, (approximate location: $36^{\circ} 30'N$, $99^{\circ} 06'W$) taken by the QuickBird satellite on 18 July 2006 under zero cloud cover conditions. Sand Creek was selected primarily because it is located in a semiarid region in which riparian zones can be easily distinguished [see Muneepeerakul *et al.*, 2008b, Figure 1].

[41] A set of criteria was used to identify the riparian areas, whose 2.4×2.4 m pixels are then classified into functional groups, namely spectral groups (SGs), using an unsupervised classification scheme based on the reflectance data (see Muneepeerakul *et al.* [2008b] for details). The spatial structure of α diversity of the SGs in the riparian areas of the Sand Creek was studied under the network framework; the results are summarized in Figure 10. Note that here the definition of α diversity is slightly different from that in the previous sections: here it is defined as the number of SGs normalized by the riparian area of the streamlink (in pixel units). The average α diversity is then calculated, according to this new definition, for all links located at the same distance from the outlet measured throughout the channel network. The average α diversity seems to be higher in the downstream reaches, a trend similar to that of the fish case, and more fluctuating: keep in mind that the increment in distance from the outlet is determined differently here (see Muneepeerakul *et al.* [2008a, 2008b] for comparison). The series also exhibits long-range correlation and power law power spectrum, as clearly seen in Figures 10b and 10c, where the power spectrum follows a power law, $S(f) \sim f^{-1.3}$. Muneepeerakul

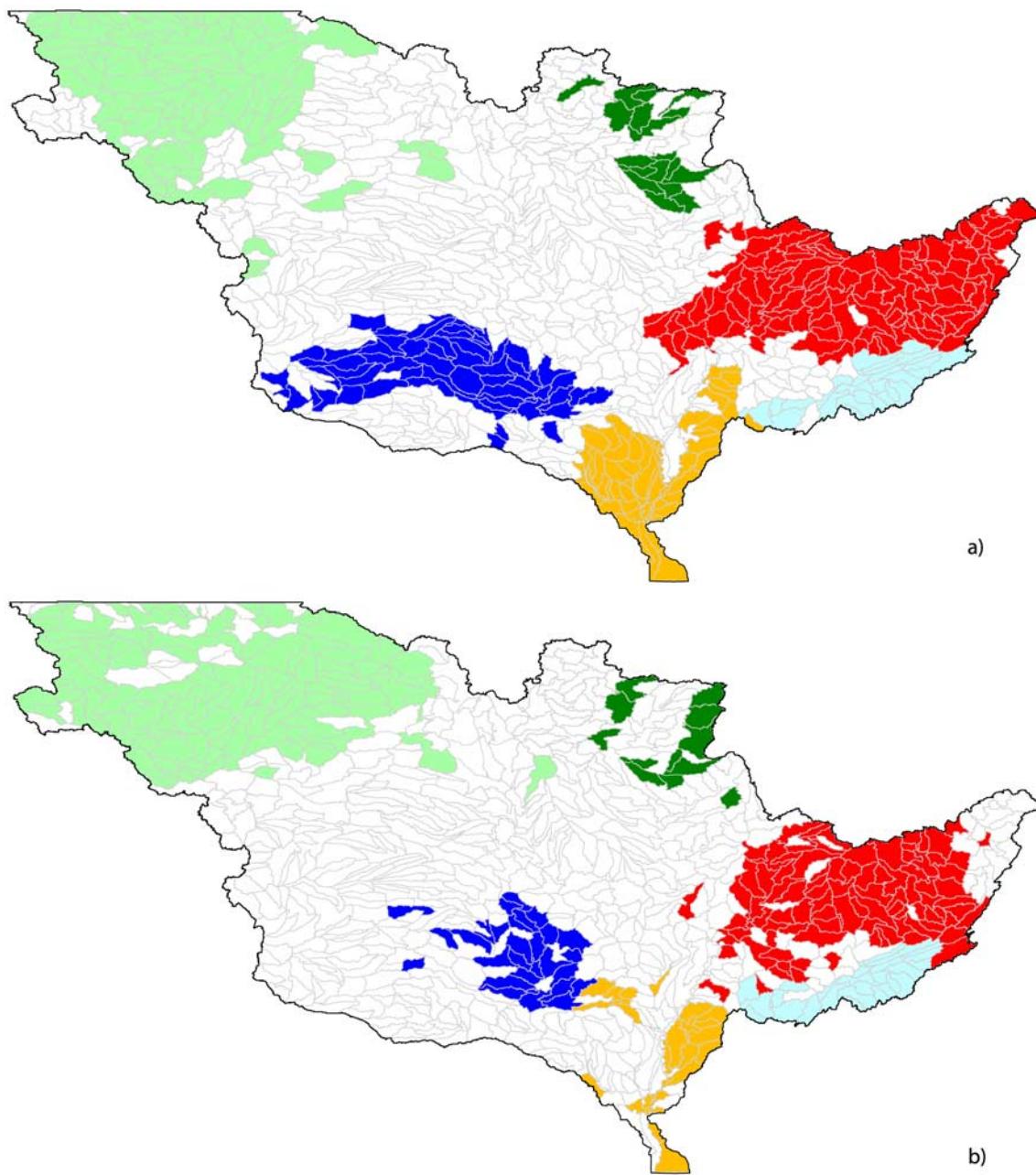


Figure 9. A representative example of comparison between geographic range of individual species obtained (a) from the data and (b) from the model results through the matching procedure.

et al. [2008b] hypothesized that “these characteristics suggest long-range communication of diversity information (likely via such processes as long-distance dispersal)” in the riparian systems of river basins and speculated that this could have an “impact on the resilience of riparian systems to natural and anthropogenic disturbances.” However, the exact mechanisms behind these patterns are not yet clear and their explanation would become a part of the general theory we seek.

[42] In addition, the exceedance probability plots of the α diversity, whose definition now includes the variation of riparian habitat capacity, exhibit a power law character, which seems to imply a high likelihood of biodiversity hot spots. Such feature is not found in the neutral meta-community model in section 3 in which the local commu-

nity sizes are fixed. This is yet another manifestation of the necessity of appropriate characterization of habitat capacity.

5. Hydrologic and Geomorphologic Signatures of Riparian Habitat Capacity

[43] The need for appropriate characterization of habitat capacity is clearly highlighted in the previous section. In the case of the MMRS freshwater fish, the amount of available water seems to be a good representative measure of the fish habitat capacity, but it may not be so for other kinds of living organisms in ecosystems, e.g., riparian vegetation. In many ways, the habitat capacity of riparian vegetation in each local community (a streamline, in this case) may be more complex to determine than that of the fish. This is

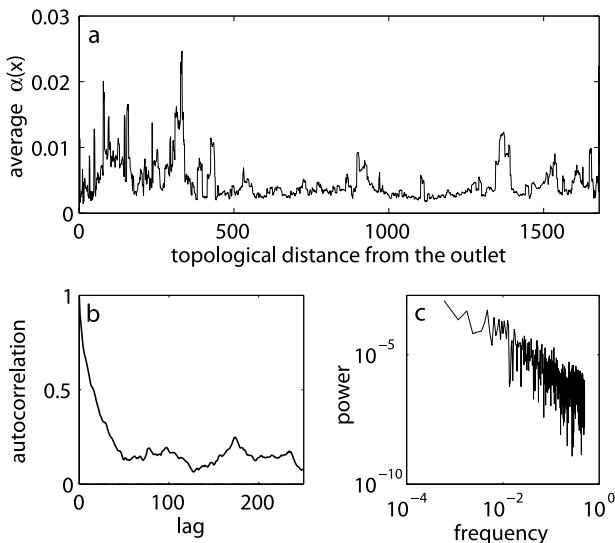


Figure 10. Spatial series analysis of average spectral group (SG)-based α diversity for the case of 61 SGs: (a) the spatial series of stream links at a given distance from the outlet, (b) its correlogram, and (c) its power spectrum. Here, a “step” occurs when one or more links are included in or excluded from the averaging of α diversity. Taken from Muneepetarakul *et al.* [2008b].

because it is controlled by the intertwined responses between geomorphological patterns of channel geometry, topography of river basins, hydrological fluctuations, surface-subsurface hydrological interaction, nutrient transport through landscape and biological characteristics of the riparian vegetation. As such, it is interesting to note that the emerging body of research on surface-groundwater interaction and its effects on residence time and biogeochemistry [Kirchner *et al.*, 2000; Haggerty *et al.*, 2002; Wörman *et al.*, 2007; Boano *et al.*, 2007; Battin *et al.*, 2008] may be incorporated in the sought after theory by way of their influence on the habitat capacity.

[44] Let us now revisit the remote sensing data of Sand Creek with an eye for this issue. The analysis by Muneepetarakul *et al.* [2008b] shows that there is no clear trend of riparian area with stream magnitude; if anything, there may be a weak increasing trend for low stream magnitudes (Figure 11a). However, when analyzed as a group regardless of spatial position, the riparian area seems to follow an exponential distribution (Figure 11b), a pattern that warrants further investigation. More analysis of this type is needed for other river basins to confirm or refute these patterns. Nevertheless, from these results, one may characterize the riparian areas by making the simplest assumption that size of the riparian area associated with a streamlink is a random variable independent of the stream magnitude and thus on the average the riparian areas are the same throughout the network. Or one may assume such relationship as $H \sim A^a$, where H is the habitat capacity and A is the drainage area of a streamlink under consideration. In fact, the latter is the approach taken by Muneepetarakul *et al.* [2007b] who determine the exponent a on the basis of a number of well-established geomorphological relationships [Leopold *et al.*, 1964; Rodriguez-Iturbe and Rinaldo, 1997]. However reasonable, these approaches are not very satis-

factory in the sense that there is no explicit linkage to the relevant dynamics.

[45] Recently, different approaches have been proposed that are potentially useful for characterizing the habitat capacity of riparian vegetation. Camporeale and Ridolfi [2006] presented a framework for the estimation of the distribution of biomass of riparian vegetation based on meaningful biological and hydrological parameters. Their model was modified by Muneepetarakul *et al.* [2007a] to address the problem of the relationship of riparian width and vegetation biomass with the geomorphological structure of river basins. There, the dynamics of vegetation biomass situated at elevation η is assumed to be described by

$$\frac{dV}{dt} = \begin{cases} -\alpha_1 V^n & , h \geq \eta \\ \alpha_2 V^m (1 - V/V_c)^p - \alpha_3 V^q & , h < \eta, \end{cases} \quad (5)$$

where V is the riparian vegetation biomass; V_c is its carrying capacity; α_1 and n represents the rate and exponent of vegetation decay due to inundation; α_2 represents the intrinsic growth rate and the exponents m and p determine the nonlinearity of the growth and intraspecific competition, respectively; α_3 and q represent the rate and exponent of vegetation decay due to water stress caused by low water table; and h is the free water surface, which is assumed to be the same as the water table.

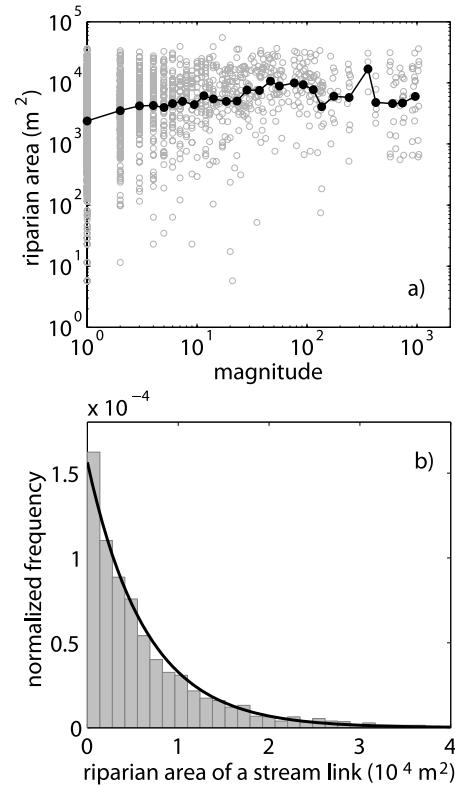


Figure 11. Distribution of riparian areas of stream links: (a) its (lack of) trend with stream magnitude and (b) its probability density function. The exponential distribution with parameter $\lambda = 1.56 \times 10^{-4} m^{-2}$ (the inverse of the mean riparian area of $6396 m^2$ of the population of 2077 links) fits the empirical distribution extremely well. Taken from Muneepetarakul *et al.* [2008b].

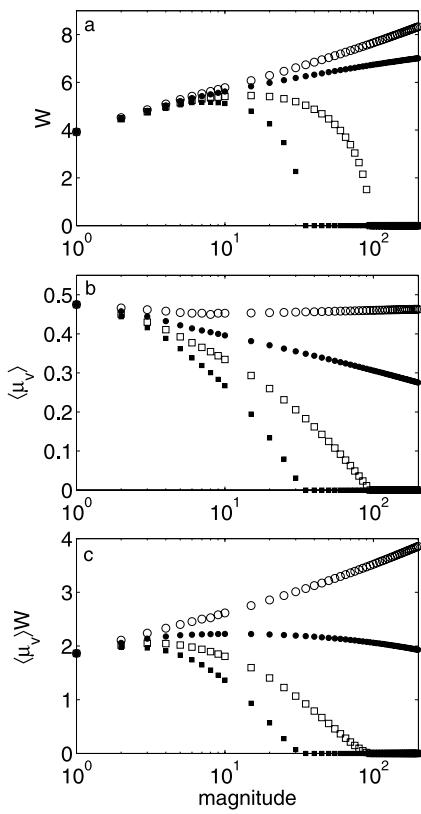


Figure 12. Trends with the stream magnitude of the (a) riparian half width W , (b) average dimensionless biomass (i.e., the biomass normalized by the carrying capacity) per unit width $\langle \mu_v \rangle$, and (c) total dimensionless biomanss $\langle \mu_v \rangle W$ for various values of s , where s is the scaling exponent of the σ_Q as in $\sigma_Q \sim A^s$. Solid squares represent $s = 1$, open squares represent $s = 0.85$, solid circles represent $s = 0.7$, and open circles represent $s = 0.5$. See Muneepetarakul et al. [2007a, Figure 4] for parameter values. Taken from Muneepetarakul et al. [2007a].

[46] By making the rates of decay functions of the water level h and relating the probability distribution of flows with that of h through a typical channel shape, Muneepetarakul et al. [2007a] provide mathematical expressions to determine the upper and lower bounds, and thus the width, of the riparian area. The riparian width is then related to the geomorphological structure of the river basin through the relationships linking several variables, e.g., width of channel, average water depth, mean and variance of flow and slope of stream banks, with the total contributing area (which is equivalent to the stream magnitude) of the link under consideration.

[47] Under the assumption of a scaling relationship between the standard deviation of the flows and the drainage area, i.e., $\sigma_Q \sim A^s$, it is found that the scaling exponent plays an important role in determining the patterns of the riparian width and vegetation biomass. Specifically, increasing trends of riparian width with stream magnitude are found to be associated with low values of s and decreasing trends with high values of s . Figure 12 shows an example of these results for a particular set of parameters. Typical values of s are around or less than 0.7 [e.g., Gupta and Waymire, 1990] and thus most commonly we expect an

increase in the riparian width in the downstream direction. This trend of riparian width is in general agreement with that of Sand Creek as shown in Figure 13.

6. Hydrologic Controls and Organization of Vegetation in River Basins

[48] An important question with crucial implications concerns similarities and departures among large-scale vegetation patterns existing in savannas and river basins. Here we address two important mechanisms. The first is the concept of local-scale interactions driving large-scale pattern formation frequently observed in nature [e.g., Bascompte and Solé, 1998; Scanlon et al., 2007]; this suggests the possible existence of characteristic patterns across a broad range of environmental conditions. Local interactions are crucial for the development of community structures and, as shown in section 3, are most likely to be different between a 2D savanna and a river basin. The second mechanism is the optimization of resource use subject to the constraints imposed by hydrologic controls. Here, we will focus on such mechanisms in river basins and compare them to their savanna counterparts where appropriate.

[49] In river basins, the geomorphological structure plays a key role in the spatial organization of vegetation where the drainage network acts as a template around which the systems of hillslopes impose global and local constraints on the internal dynamics of the system. Caylor et al. [2004, 2005] examined the mechanisms leading to the organization structure of vegetation, in both hillslopes and riparian areas, in semiarid river basins under the controlling influence of water stress. As discussed in section 2, there exist a number of unifying principles and common statistical signatures behind the infinite variety of shapes and forms one observes in drainage networks and the three-dimensional geometry of river basins. The basic question is now whether or not the

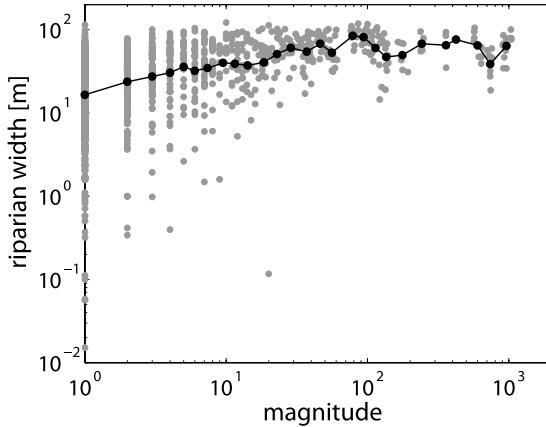


Figure 13. Empirical relationship between the stream magnitude and the riparian width of Sand Creek (Oklahoma) derived from remote sensing data. The solid circles connected by a line represent binning average values. Only stream links longer than 120 m are included in the plot as the determination of the riparian width becomes less reliable for short stream links. Note that a power law with a scaling exponent of approximately 0.3 seems to fit the plot reasonably well for stream magnitude ≤ 100 . Taken from Muneepetarakul et al. [2007a].

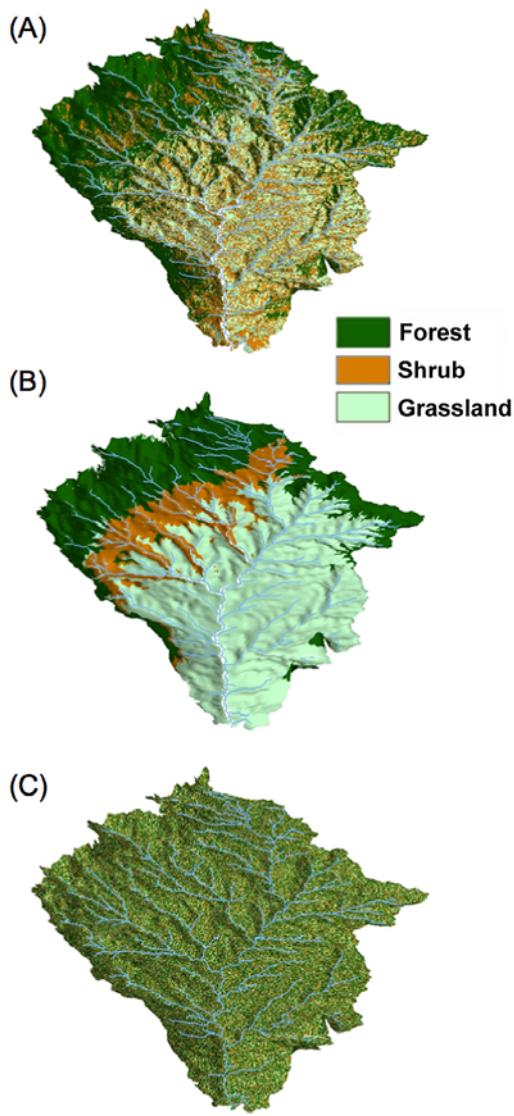


Figure 14. Vegetation spatial patterns in Rio Salado river basin: (a) empirical pattern, (b) “ideal” pattern (see text); and (c) “random” pattern. Taken from *Caylor et al. [2005]*.

interaction of vegetation, soils, and climate may also display some unifying characteristics among the very different patterns they exhibit in natural watersheds.

[50] Using available geospatial data, *Caylor et al. [2005]* assigned soil types, climate, and vegetation properties across the Upper Rio Salado river basin near Sevilleta in New Mexico, USA. The organization of vegetation in the basin was then studied through the analysis of the spatial patterns of the steady state soil moisture probability distribution calculated through the framework developed by *Rodríguez-Iturbe et al. [1999]* and *Laio et al. [2001]*. A comparison was carried out between the observed vegetation patterns and those resulting from two alternative dynamics. The first is the vegetation pattern that results from a simple random assignment of vegetation type at each location within the basin, under the constraint that the proportions of overall vegetation composition are preserved. The second hypothetical pattern results when at each pixel one assigns the vegetation type that exhibits the lowest dynamical water stress. From a water stress perspec-

tive, the second pattern represents the optimal distribution of vegetation.

[51] Figure 14 shows the vegetation patterns resulting from these two alternative dynamics, as well as the actual pattern observed within the Rio Salado basin. It is clear that the actual vegetation pattern “contains elements of both the highly organized large-scale ideal pattern and the characteristic small-scale variation associated with the random pattern” [*Caylor et al., 2005*]. Moreover, as shown in detail by *Caylor et al. [2005]*, the water stress spatial characteristics of the real river basin fall between those of the higher stress configurations of the random vegetation assignment and the lower stress configurations corresponding to the ideal vegetation configuration described before, although it should be noted that they are much closer to those of the ideal case. The results of *Caylor et al. [2005]* suggest that the actual vegetation pattern is configured in such a way that it is well constrained between the two extremes of vegetation organization. Moreover, it seems likely that the vegetation patterns of water-controlled ecosystems in river basins tend to approach a configuration controlled by a global hydrologic condition (e.g., minimization of water stress in this case), but are subject to important and decisive random contingencies of an altogether different character.

[52] Conceptually, this is not different from the notion of feasible optimality arising from the organization of vegetation that is constrained by the stochastic nature of local interactions mediated by the network organization. This hypothesis was investigated by *Caylor et al. [2004]* through two simple cellular automata models. The models were implemented in the Rio Salado river basin starting from a random vegetation pattern, in which each of the vegetation types (i.e., trees, shrubs and grass) occupies one third of the river basin. The initial random vegetation mosaic undergoes changes because of local interactions between adjacent cells. Specifically, the vegetation at cell i can replace the vegetation at cell n with probability $1 - [\theta_i / (\theta_i + \theta_n)]$, where θ_i is the modified dynamic water stress [see *Caylor et al., 2005*] of cell i . The principal difference between the two cellular automata models is the definition of adjacent neighborhood. In the “neighbor” model, the cell under consideration interacts with a cell randomly selected from all the cells that are adjacent to the cell. In the “network” model, the cell under consideration can only interact with its direct downstream cell. In both models, the probabilistic replacement continues until no further replacements occur; that is, the system reaches a steady state.

[53] *Caylor et al. [2004]* then investigated the $\bar{\theta}$ profiles resulting from both models. A $\bar{\theta}$ profile is defined as the average θ of all cells located at the same distance from the outlet measured along the drainage network. They found that the $\bar{\theta}$ profile of the neighbor model coincides, as expected, with that associated with the ideal vegetation configuration described earlier, while the empirical θ profile is in good agreement with that of the network model [*Caylor et al., 2004*]. These results confirm that drainage networks act as a template in which geomorphology, hydrology and ecology interact and give rise to the observed spatial distribution of vegetation in river basins. Furthermore, these findings exemplify how the local-scale interactions and optimality principle may operate in such a geomorphologic template.

[54] As mentioned at the beginning of this section, local-scale interactions can indeed drive large-scale patterns. A striking example, and a savanna counterpart, was provided by *Scanlon et al.* [2007]. Through the use of high-resolution satellite imagery, they have documented the power law character of the size distribution of vegetation clusters in the Kalahari savannas: most patches of vegetation are very small but a few are much larger than what would be expected from peaked distributions (e.g., lognormal or gamma). Such power laws are a fingerprint of self organization in the internal dynamic processes driven by local interactions [*Solé*, 2007]. They show that the emerging spatial patterns in the Kalahari result from local-scale positive spatial feedbacks, in which the probability of establishment increases with local tree density, and the probability of mortality increases with greater open space in the vicinity of the tree. Water availability is indeed hypothesized to be the main driver of positive feedbacks, as below canopy areas remain wetter in savanna ecosystems owing to reduced bare soil evaporation from shading. Such local-scale interactions interplay with the global-scale hydrologic control, namely the regional rainfall, which controls the overall amount of tree cover. Simple cellular automata models that captures these local and global effects indeed yield the power law distributions of tree canopy cluster sizes observed in the satellite images.

[55] Moreover, *Kéfi et al.* [2007] also observed power law distribution of cluster sizes in Mediterranean arid ecosystems with more intense grazing leading to departures from the power law behavior, with large patches of vegetation becoming less and less common. Indeed it was noted that models consistently predicted that such changes in size distribution might be warning signals of a transition to the desert state. The seriousness of such a possibility is highlighted by the fact that some of these transitions are catastrophic and largely irreversible [*Solé*, 2007]. Interestingly, power law distributions of cluster sizes of vegetation were also found for water-controlled halophytes where the selective pressure is related to tidal hydroperiods inducing potential suffocation due to excess soil moisture owing to periodic flooding [*Marani et al.*, 2006a, 2006b].

[56] Regarding the optimal use of resources, it has been shown that in savannas the temporal dynamics of grass cover optimizes the use by vegetation of limiting resource, i.e., soil moisture [*Scanlon et al.*, 2005]. Specifically, they showed that such grass cover dynamics minimizes both the total water stress and the total amount of water lost from the base of the root system (thereby unexploited by the savanna vegetation) across the different locations of the Kalahari transect. These examples, namely the spatial organization of vegetation in the river basin and the temporal dynamics of grass in the savanna, clearly demonstrate the ubiquity of the thrive to optimality in natural ecosystems, which should be taken into account in the general theory we are developing here. In addition, *Battin et al.* [2008] have recently combined geophysics, microbial ecology and organic geochemistry to show that geophysical opportunities and microbial capacity greatly enhance the net heterotrophy in streams, rivers and estuaries. Hydrological storage and retention zones extend the residence time of organic carbon during downstream transport creating opportunities for microorganisms to develop as attached biofilms or suspended

aggregates, which in turn metabolize organic carbon for energy and growth of vegetation, and fish alike. These findings may lend themselves as a more mechanistic way to incorporate the optimality principles in studying meta-ecosystems in fluvial networks.

7. River Networks as Corridors for Water-Borne Disease

[57] Our discussion and empirical data have so far centered around spatial patterns. In this section, we show that temporal dynamics is also strongly influenced by features of river networks. Specifically, we will focus on the study of how river networks, acting as environmental corridors for pathogens, affect the spreading of water-borne diseases by following the work by *Bertuzzo et al.* [2008] on cholera epidemics. Because water-borne disease dynamics apparently differs from the dynamics behind biodiversity patterns discussed above, such demonstration will suggest the wider applicability, and thus the necessity, of understanding the effects of river networks on various ecological dynamics. The theoretical tools are not fundamentally different to those used in the previous sections of this paper with the novelty lying on the nodal reactions describing the dynamics of cholera. The bacterium that causes the disease (*Vibrio cholerae*) is transported through the river network, which serves as links between different human communities and enables the reaction between pathogens, environment and human hosts.

[58] The spatial and temporal patterns of cholera epidemics are strongly related to the environmental matrix within which the disease can spread. There exist useful mathematical models of cholera dynamics such as those by *Capasso and Paveri-Fontana* [1979], *Codeço* [2001], *Pascual et al.* [2002], and *Hartley et al.* [2006]. Nevertheless, these models do not consider space explicitly: the spatial distribution of the communities and how they interact are crucial to understanding the spreading of epidemics into a disease free region.

[59] *Bertuzzo et al.* [2008] study the spreading of epidemics on the environmental matrix defined by the oriented graph whose nodes are human communities in which the disease can diffuse and grow, and edges are hydrologic links between communities. The edge direction follows that of the stream. The model is assembled by coupling two models: (1) a transport model for the infective agents through the edges and (2) a local epidemic model at the nodes of the graph. The transport model uses the framework described in section 2: the infective agents (equivalent to propagules in section 2) can move from a node to one of its neighbor nodes following either an outward or an inward edge with probability proportional to P_{out} and P_{in} , respectively. Thus the probability for an infective agent to be transported from node i to node j can be expressed as follows:

$$P_{ij} = \begin{cases} \frac{P_{\text{out}}}{d_{\text{out}}(i)P_{\text{out}} + d_{\text{in}}(i)P_{\text{in}}} & \text{if } i \rightarrow j \\ \frac{P_{\text{in}}}{d_{\text{out}}(i)P_{\text{out}} + d_{\text{in}}(i)P_{\text{in}}} & \text{if } i \leftarrow j \\ 0 & \text{if } i \leftrightarrow j, \end{cases} \quad (6)$$

where $d_{\text{out}}(i)$ and $d_{\text{in}}(i)$ are, respectively, the number of outward and inward edges of node i .

[60] *Bertuzzo et al.* [2008] use as local dynamics a continuous model of the SIR (i.e., susceptible-infected-recovered) class with a reservoir of free-living infective agents. The three state variables at every node of the network are the number of susceptible individuals (S), the number of infected (I), and the concentration of *V. cholerae* in the aquatic environment (B). The vibrios are removed at every node with a certain rate l (day $^{-1}$) and transported through the network. The equations describing the process at every node are thus given by the following system of equations:

$$\begin{aligned} \frac{dS_i}{dt} &= n(H_i - S_i) - a \frac{B_i^*}{1 + B_i^*} S_i \\ \frac{dI_i}{dt} &= a \frac{B_i^*}{1 + B_i^*} S_i - (r + m + n) I_i \\ \frac{dB_i^*}{dt} &= n_B B_i^* + \frac{p}{K W_i} I_i - l B_i^* + \sum_{j=1}^N l P_{ji} B_j^* \frac{W_j}{W_i}, \end{aligned} \quad (7)$$

for $i = 1, 2, \dots, N$, where N is the number of nodes, and all the parameters are node independent except for the population size H_i and the water volume W_i (the latter represents the entire water supplies for that community, not only the one provided by the river). Susceptible individuals are born and die on average at a rate n . Newborn individuals are considered susceptible. Susceptibles become infected at a rate $aB/(K + B)$, where a is the rate of contact with contaminated water and $B/(K + B)$ is a logistic dose-response curve that links the probability of becoming infected to the concentration of vibrios in water, B . $B^* = B/K$ is a dimensionless concentration. The number of infected people (the second equation of equation (7)) decreases at a rate that is the sum of neutral mortality n and disease-caused mortality m , and recover with a rate r . The third equation of equation (7) describes the dynamics of the free-living infective propagules in the reservoir. The concentration of the vibrios in the aquatic environment is reinforced by the contamination rate p/W , where p is the rate of bacterial production per infected person that reaches the water body of volume W . The growth rate n_B of the free living bacteria in the water body is negative because mortality in natural environments usually exceeds reproduction. The last two terms of the third equation apply the described transport model to the vibrios.

[61] *Bertuzzo et al.* [2008] applied the above model to a well documented case of cholera epidemic that occurred in South Africa where the largest outbreaks took place in the summers of 2000–2001 and 2001–2002, involving 135,000 cases among a population of about 8.5 million inhabitants. The network acts as links through which different sets of water supplies of different communities can be connected and contaminated. River networks were derived from GIS data: all the channels of perennial rivers are considered as edges, and all the endpoints of these channels are considered as nodes. A full description of the parameter estimation procedures and the details of the model application to the largest river basin in the region (i.e., Thukela watershed) are given by *Bertuzzo et al.* [2008].

[62] Figure 15 shows the comparison between the data and model predictions of the temporal dynamics of the

weekly and cumulated cholera cases in the whole Thukela river basin. Figure 16 compares the spatial distribution of observed infection cases with that obtained from the model, from which we infer that the model is capable to reproduce the main features of the space and time distributions of cholera. Admittedly, the model is not completely reliable in reproducing the secondary peaks of infections in the tails of both annual outbreaks. This is likely due to the simplified modeling of the seasonality of the *V. Cholera* dynamics (which was assumed to be sinusoidal). Improvements of the model of the bacterium ecology will be the subject of future work.

[63] The above clearly shows the significant role of ecological corridors defined by waterways and networks in the transportation and redistribution of the free-living infective pathogens, which can be considered as a special case of ecological dynamics involving direct interactions with humans. The general perspective synthesized in this paper for the integration of hydrological, ecological and geomorphological dynamics allows for the formulation of what we are confident will constitute an exciting and important theme for interdisciplinary future research.

8. Search for General Scaling Laws Integrating Hydrology, Ecology, and Geomorphology

[64] An exciting frontier of research on the intertwined hydrological, ecologic and geomorphological dynamics lies in the scaling of biodiversity in river basins. Little of general character has been done in this area where explicitly spatial aspects of the drainage network play a fundamental role.

[65] A stumbling block in this problem is the lack of appropriate data linked to the river basin geomorphology over extended spatial scales. *Muneepeerakul et al.* [2008b, 2008a] have addressed this problem through the use of high-resolution satellite data in the case of vegetation and an extensive spatially extended data set for freshwater fish species in the Mississippi-Missouri river system (MMRS). In the case of riparian vegetation diversity inferred from remote sensing data, the drawback is that one is not really dealing with different species but rather with different spectral groups (see section 4). In the case of the MMRS freshwater fish, the data set indeed characterizes actual biologically different species, but, although quite extensive in its spatial coverage, it is not of such spatial resolution that one can link different elements of the network structure (e.g., stream links) with specific species. Moreover the data set refers only to presence or absence of the species, not to their abundance. Because the spatial structure of river basins is such an important factor for biodiversity dynamics, we believe the most promising approach to quantitatively tackle the linkage of hydrological, geomorphological, and ecological dynamics is through the use of the results produced by the model presented in sections 3 and 4. Such a model has been shown to reproduce quite well all the key spatial patterns related to fish biodiversity in the MMRS. Moreover, one can also obtain from the model the hard to collect information regarding the relative abundance of species at each link of the network. Inspired by the fish biodiversity case, this is how we suggest to proceed in the search for scaling laws of biodiversity in river basins.

[66] Through digital elevation maps (DEMs) one can objectively define the river network at the scale of resolu-

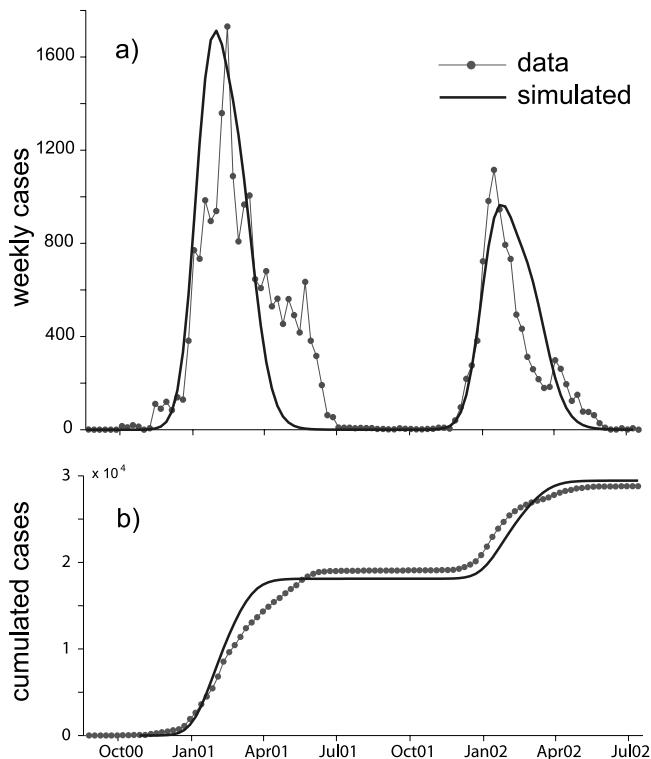


Figure 15. Temporal evolution of (a) weekly cholera cases and (b) cumulated cases for the Thukela river basin. Circles represent data, and solid lines represent simulation. Taken from *Bertuzzo et al.* [2008].

tion of the DEM [e.g., *Rodriguez-Iturbe and Rinaldo*, 1997]. Moreover, one can aggregate the DEM at coarser spatial scales and derive new drainage networks from these river basins of coarser resolution, while still preserving the potential energy embedded in the geomorphological landscape. The neutral metacommunity model can then be implemented, using the networks at these different scales, and full descriptions of biodiversity patterns can be obtained in each case.

[67] In general, one can look for two types of scaling: community-level scaling and species-level scaling. Examples of the first kind include:

[68] 1. The scaling behavior of the species-area relationship in which the area is defined as a subbasin in the river basin.

[69] 2. The dependence of the local species richness on the geomorphological characteristics of the stream link under consideration (e.g., its magnitude or its mean geomorphological diameter) and the changes in such dependence with the scale of the analysis.

[70] 3. The dependence on scale of the relationship between local species richness and distance to the outlet. For example, one could average local species richness at all links located at the same distance from the outlet, measured through the network, and study the shape and fluctuations of this species richness function. With a proper normalization of the measured distances, one can then pose such questions as: what characteristics of this function are independent of scale? Or, more specifically, are there common statistical signatures in its power spectrum?

[71] 4. The dependence on scale of measures of β biodiversity, e.g., spatial patterns of the Jaccard's similarity index [e.g., *Muneepeerakul et al.*, 2008a].

[72] 5. The dependence on scale of rank-occupancy and rank-abundance curves.

[73] In a similar fashion, one may consider for the species-level patterns, say, the scaling behavior of the abundance of a particular species with subbasin areas or areas within a certain radius from a focal link, with the latter being analogous to the cluster dimension in a fractal analysis framework [see, e.g., *Rodriguez-Iturbe and Rinaldo*, 1997].

[74] In all the above analyses it is important to clarify the role played by the dispersal kernel. What is the role of the kernel structure and the directionality, or the lack of it, in the scaling relationships described above? Are there optimality criteria which make a heavy-tailed dispersal kernel more attractive than, say, an exponentially decaying one? Or is it some combination of both? Indeed, there are numerous evidences for heavy-tailed dispersal for biological organisms [see, e.g., *Kot et al.*, 1996; *Nathan et al.*, 2002; *Nathan and Muller-Landau*, 2000], including human [*Brockmann et al.*, 2006]: how may such dispersion affect the spreading and spatial patterns of ecological agents and infectious diseases?

[75] It is also important to note that in the above analyses the concept of scale is more meaningful and richer than the simple scale related to absolute size of cells in a 2-D lattice. To begin with, in this case, there are two notions of scale, namely “coarse-graining scale” and “subbasin scale.” The former is basically the spatial resolution or grid size of the DEM representing the landscape under consideration. For a given coarse-graining scale and with a certain threshold, the drainage network can be defined on the basis of the fact that water flows along the steepest descent. As the coarse-graining scale changes, the drainage network is accordingly redefined. Given a fixed drainage network, one can discuss changes with the second kind of scale, the subbasin scale, which is simply defined as the area that drains through a particular location of interest. The subbasin scale changes in an entirely different manner from that of the 2-D lattice due to the converging character of the network. These two types of scale can be used to investigate different suites of patterns. For example in the list above, the coarse-graining scale is used in items 2–4, while item 1 uses the subbasin scale.

[76] Likewise, the implications of the sought after scaling behaviors based on the two types of scale also differ. The coarse-graining scaling behavior may imply that one can infer the patterns at a given scale from those at a different scale. This would greatly facilitate the information exchange between studies, which oftentimes are carried out at different scales. The subbasin scaling behavior may imply that one can infer the patterns of an entire river basin by studying much smaller subbasins. Let us recall that the success of quantitative geomorphological analyses in unraveling the deep symmetry and general scaling laws of river basins (as summarized in section 2) proceeds from two basic principles: (1) the criteria behind OCNs, e.g., a network structure that minimizes total energy expenditures, and (2) changes in scale (coarse graining) of the landscape in such a way that potential energy is conserved [*Rodriguez-*

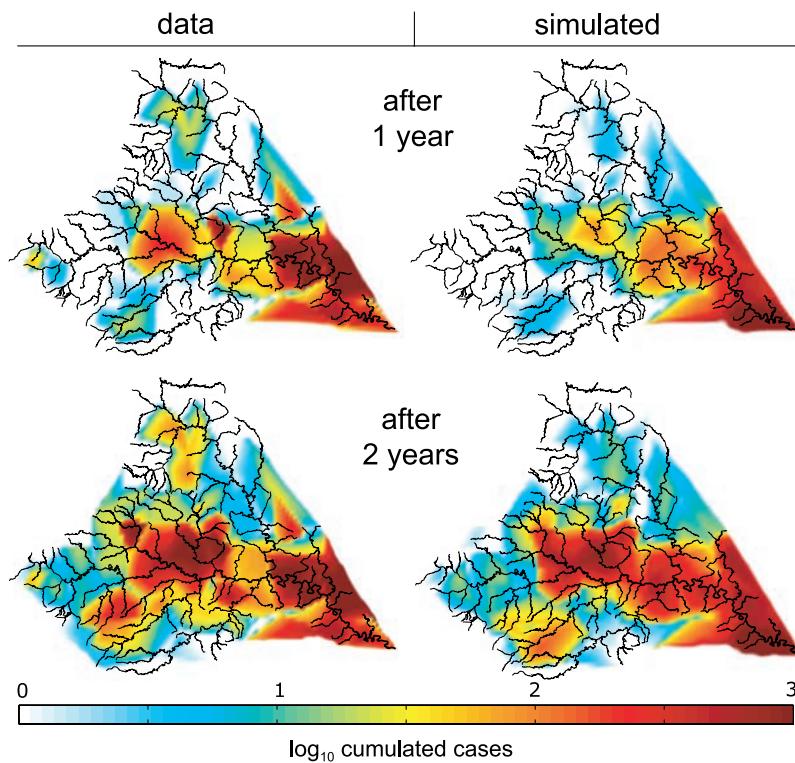


Figure 16. Spatial distributions of empirical and simulated cumulated cholera cases after the first and second epidemic outbreaks. Taken from Bertuzzo *et al.* [2008].

[*Iturbe and Rinaldo, 1997*]. Here we seek similar simple, powerful principles for biodiversity patterns in river basins.

[77] As mentioned earlier, the surface-groundwater interaction in river basins and its biogeochemical consequences may affect spatial heterogeneity and temporal fluctuation of habitat capacity. How do scaling characters found in these processes [e.g., Kirchner *et al.*, 2000; Wörman *et al.*, 2007] interplay with ecological processes in river basins? Would they lead to some scaling behaviors in biodiversity patterns and processes, e.g., clustering and lifetime distribution of species? These are the types of questions that will constitute an important research topic in the future, in terms of both theoretical development and appropriate data acquisition.

[78] Throughout much of this paper we have focused on ideas involving the use of neutral metacommunity models of ecological dynamics influenced by hydrological and geomorphological processes. One may wonder if such neutral models are appropriate for the objectives being pursued. We believe they indeed are so when one is not interested in the dynamics of any particular species, but rather general signatures of the spatial patterns of multiple populations comprising the ecosystem. We now provide some reflections on this.

[79] From a general perspective, genetics explains evolution by four basic factors driving the changes through successive generations of the composition of populations [*Cavalli-Sforza, 2007*]: (1) mutation, or rare random changes of DNA; (2) natural selection, the ensemble of changes in the composition of populations determined by their inherited characters; (3) random genetic drift, chance mechanisms controlling the number of progeny;

and (4) migration, space-time displacements that generate genetic exchanges between populations of the same species.

[80] Neutral theory is a dynamical framework of community assembly fundamentally based on three mechanisms which govern the presence/absence and the abundance of species in communities over local to global scales [*Borda-de-Agua *et al.*, 2007*]. These mechanisms are speciation, ecological drift or demographic stochasticity, and dispersal. According to neutral theory, the differences in abundances of different species arise basically from demographic stochasticity and the accidents of dispersal.

[81] Although they pursue different goals, it is interesting to look at the neutral perspective of biodiversity through the lens of genetic evolutionary theory. Speciation in the neutral framework can be thought of as resulting from the mutation in the framework of evolutionary theory. The role of chance, i.e., genetic drift, is a fundamental one in the evolutionary process especially under the light that the majority of mutations are selectively neutral. This role is played in the neutral model of biodiversity by the ecological drift or demographic stochasticity. In both frameworks the expansion of successful species takes place through migration or dispersal processes. Neutral theory does not attempt to incorporate the role of natural selection, which provides different evolutionary paths among the individual species in the population.

[82] In studies at local scales, the specific trade-off mechanisms and particular characteristics of the different species play a commanding role in answering all types of ecological questions, which are heavily conditioned by the relationship between the specific environmental conditions and the unique properties of each species. In studies at

regional scales, basin scales and other larger scales, the locally different dynamics and the highly nonlinear interactions between many of the local components are typical of complex systems, which tend to self-organize toward some general statistical signatures. It is not that at these scales the trade-off dynamics and similar interactions are nonexistent; they are in fact present, but many of the patterns arise from statistical regularities that do not depend on the specific details of the interactions among the system components [e.g., *Marquet et al.*, 2007]. This is the basic reason of the finding of *Purves and Pacala* [2005] encapsulated in the phrase that “neutral pattern does not imply neutral dynamic.”

[83] As shown throughout this paper, hydrological and geomorphological dynamics are crucial for the study and characterization of biodiversity in river basins. They are commanding forces in the demographic stochasticity as well as in the dispersal dynamics, which together with speciation drive the spatial patterns of biodiversity in the domain configured by river networks. In all three of these dynamics, namely hydrological, ecological and geomorphological, there is an abundance of power laws for both functional and statistical characters. These power laws are the signatures of a dynamics found in scale invariant processes. The search for these general laws and their associated dynamical explanation as well as the links between the signatures is at the core of the search for the scaling of biodiversity in river basins.

[84] As final remarks, we briefly summarize some limitations of our proposed approaches as well as several related issues that remain unaddressed to date. The neutral metacommunity approach primarily addresses steady state macroecological patterns. Admittedly, it does not lend itself well to studies of patterns or dynamics of particular species. There have been attempts to marry stochasticity, which is at the heart of the neutral theory, to classical niche theory, i.e., stochastic niche theory [see *Tilman*, 2004; *Purves and Pacala*, 2005], to overcome such limitation. It remains to be seen whether the benefit of such integration would outweigh the inevitably more demanding requirement of parameters, which is in contrast to the attractive parametric parsimony and effective simplicity of the neutral theory. It is worth noting, nonetheless, that once properly established, such a theory can be easily implemented in the metacommunity approach as proposed here. On another frontier, much work is also in dire need for the dynamical aspect of the neutral theory [see *Azaele et al.*, 2006], which is key to understand the possible responses of ecosystems to external forcing and their resilience to various types of perturbations. This is particularly true if the proposed approach is to be applied to ecological agents that exhibit such behavior as organized motions and seasonal migration. Theoretical developments for such systems call for more detailed monitoring of spatial patterns at various snapshots, the type of data that is currently lacking. Yet another interesting research direction is to address the feedbacks between ecosystems, mainly vegetation, and landscape, namely how the plant communities and river basins coevolve [see, e.g., *Istanbulluoglu and Bras*, 2005]. These issues are only a small sample of what lies ahead. Questions and issues presented throughout this paper and in this final paragraph,

as well as others inspired by them, are certain to deliver significant contributions to modern biogeosciences.

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