Key Points:
- We compute the metapopulation capacity of evolving channel networks
- Species viability increase with optimal network selection
- Landscape evolution improve ecological suitability

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Metapopulation capacity of evolving fluvial landscapes

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Abstract The form of fluvial landscapes is known to attain stationary network configurations that settle in dynamically accessible minima of total energy dissipation by landscape-forming discharges. Recent studies have highlighted the role of the dendritic structure of river networks in controlling population dynamics of the species they host and large-scale biodiversity patterns. Here, we systematically investigate the relation between energy dissipation, the physical driver for the evolution of river networks, and the ecological dynamics of their embedded biota. To that end, we use the concept of metapopulation capacity, a measure to link landscape structures with the population dynamics they host. Technically, metapopulation capacity is the leading eigenvalue λ_M of an appropriate "landscape" matrix subsuming whether a given species is predicted to persist in the long run. λ_M can conveniently be used to rank different landscapes in terms of their capacity to support viable metapopulations. We study how λ_M changes in response to the evolving network configurations of spanning trees. Such sequence of configurations is theoretically known to relate network selection to general landscape evolution equations through imperfect searches for dynamically accessible states frustrated by the vagaries of Nature. Results show that the process shaping the metric and the topological properties of river networks, prescribed by physical constraints, leads to a progressive increase in the corresponding metapopulation capacity and therefore on the landscape capacity to support metapopulations—with implications on biodiversity in fluvial ecosystems.

1. Introduction

Fluvial landforms empirically (and compellingly) show profound similarities of the parts and the whole across several orders of magnitude regardless of major diversities in their drivers and controls, like geology, exposed lithology, vegetation, and climate [*Rodriguez-Iturbe and Rinaldo*, 1997]. Remarkably, one observes robust, approximate universality in the set of (mutually related) scaling exponents that mathematically describe the self-similar or self-affine metric or topological features of the fluvial landscape [*Rodriguez-Iturbe and Rinaldo*, 1997]. River networks in runoff-generating areas are spanning trees: a unique route exists from every site to an outlet, and no loops are observed. Optimal Channel Networks (OCNs) are trees minimizing a functional describing total energy dissipated along drainage directions by landscape-forming discharges which hierarchically accumulate toward the outlet of the basin [*Rodriguez-Iturbe et al.*, 1992a, b; *Rinaldo et al.*, 1992]. The OCN ansatz and posits, initially assumed, proved exact statements later. Specifically, any loopless network configuration that minimizes total energy dissipation corresponds exactly to stationary solutions of the general landscape evolution equation under reparametrization invariance in the small-gradient approximation [*Banavar et al.*, 2000, 2001; *Rinaldo et al.*, 2006, 2014]. The large variety of dynamically accessible local optima and the universality of their scaling features akin to those observed in nature [*Rodriguez-Iturbe and Rinaldo*, 1997; *Rinaldo et al.*, 2014] suggested several applications ranging from the design of laboratory experiments [e.g., *Carrara et al.*, 2012, 2013] to a variety of explorations on network scaling [e.g., *Briggs and Krishnamoorthy*, 2013].

Recent studies have not only highlighted how the dendritic structure of river networks shows signatures of a self-organized process which tends to minimize total energy dissipation, but also how it controls processes at different levels of ecological organization, from genetic to individual, population and community [*Grant et al.*, 2007; *Rodriguez-Iturbe et al.*, 2009; *Altermatt*, 2013; *Peterson et al.*, 2013]. The tenet of spatial ecology, a well-established one in genetics, population ecology, and adaptive evolution [*Levins*, 1969], is that the spatial structure of ecological interactions affects populations as much as average birth, death, competition, and predation rates do [see e.g., *Tilman and Kareiva*, 1997; *Hanski*, 1998, 1999]. Understanding

the origins, and the needs for maintenance, of biodiversity in dendritic freshwater metacommunities is a primary goal of current ecological studies centered on population demography, population genetics, and community composition. In this context, river networks have been viewed as ecological corridors for species, populations, and pathogens of waterborne disease [*Bertuzzo et al.*, 2007, 2008; *Rodriguez-Iturbe et al.*, 2009]. Such perspective has allowed gaining significant insights especially into the study of spatial biodiversity patterns of communities obeying the neutral theory (where all species are equivalent at a per capita level, *Hubbell* [2001]) and where the effects of spatial connectivity are akin to those of a fluvial network [*Muneepeerakul et al.*, 2008a, 2008b; *Bertuzzo et al.*, 2011; *Grant*, 2011; *Peterson et al.*, 2013]. Interestingly, the theoretical prediction for a key role of dendritic connectivity in shaping biodiversity patterns resists several generalizations, from individual-based to metacommunity models and for interactions/migrations ranging from nearest neighbors alone to long distances [*Muneepeerakul et al.*, 2008b; *Rodriguez-Iturbe et al.*, 2009]. Replicated experimental evidence that connectivity per se shapes diversity patterns in protist microcosm metacommunities supports such tenet [*Carrara et al.*, 2012, 2013]. Empirical evidence to that end also exists [e.g., *Fagan*, 2002; *Benda et al.*, 2004; *Grant*, 2011]. Spatially constrained dendritic connectivity is thus accepted now as a key factor for community composition and population persistence in environmental matrices commonly found in many natural ecosystems, such as streams and watersheds [e.g., *Fagan*, 2002; *Benda et al.*, 2004; *Bertuzzo et al.*, 2011; *Suweis et al.*, 2012; *Grant*, 2011; *Peterson et al.*, 2013]. Such habitats are structured in linear, hierarchic arrangements where landscape structure and physical flows determine the directions and the range of organismic dispersal [e.g., *Haddad*, 1999; *Grant et al.*, 2007].

In this paper, we investigate how minimization of dissipated energy, the physical driver for the evolution of river networks, relates to the ecological dynamics of the embedded biota. To that end, we borrow concepts from metapopulation ecology [*Hanski*, 1998, 1999] which views landscapes as networks of idealized, connected habitat patches (fragments, or local ecosystems) in which species occur as local populations connected by dispersal or migration. A core topic of metapopulation ecology concerns the study of the conditions leading to regional persistence of species with fluctuating local populations. This is achieved by balancing the effects of basic rates characteristic of the population with the large-scale dynamic consequences of spatial effects (i.e., migrations and dispersal) involving local populations. This leads to the definition of *metapopulation capacity* (sensu *Hanski* [1999]) as an objective measure to link landscape structures with their capacity to sustain viable populations of species. Because metapopulation capacity can conveniently be used to rank different landscapes in terms of their capacity to support metapopulations, we study how it changes in response to the evolving network configurations of spanning trees.

This paper is organized as follows. Section 2 reviews the methods, namely: the model landscapes we shall use to contrive a synthesis of the evolution of physical and ecological attributes; and the basic theoretical results underlying the concept of metapopulation capacity and its ecological significance. Section 3 presents the results which are then discussed in section 4. A set of conclusions, section 5, closes the paper.

2. Methods

2.1. Optimal Channel Networks

We consider, to no loss of generality, landscapes formed by square lattices with side L with $N = L \times L$ pixels (nodes). Each node has a link to one of its eight nearest neighbors forming a spanning tree with a single root—the outlet. Total contributing area A_i to each pixel i of the tree (the number of upstream pixels connected to i through flow directions) is expressed in pixel units as

$$A_i = \sum_j W_{ji} A_j + 1, \qquad (1)$$

where W_{ji} is the arbitrary element of the connectivity matrix **W** (i.e., $W_{ji} = 1$ if $j \rightarrow i$ and 0 otherwise), and 1 represents the unit area of the pixel that discretizes the surface. A_i provides a proxy of the flow Q_i at point i as the sum of the injections over all connected sites upstream of site i (included): $Q_i = \sum_j W_{ji} Q_j + r_i$ (where r_i is the distributed injection). In the case of uniform injection r_i for landscape-forming events, one has $Q_i \propto A_i$, a commonly accepted hydrologic assumption whose robustness has been tested [*Rodriguez-Iturbe and Rinaldo*, 1997]. The tree configuration is uniquely determined by the set of total contributing areas $s =$

$(A_1, A_2, \cdots, A_N)^T$ at any of the N sites making up the landscape. From equation (1), one has $s = (\mathbf{I} - \mathbf{W}^T)^{-1}$ ($\mathbf{I}$ being the identity matrix). A necessary condition for the existence of s is that the matrix at right-hand side can be inverted. In turn, this corresponds to specific spectral properties of the connectivity matrix $\mathbf{W}$ implying uniqueness of the paths from any site to the outlet i.e., s must be a tree [*Rinaldo et al.*, 1992].

Optimal Channel Networks (OCNs) are spanning trees minimizing a functional describing total energy dissipation $H(s)$ of the aggregate's configuration s. At a local level, say, along the i-th link of the network, energy dissipation is $H_i \propto Q_i \Delta z_i$, which makes use of suitable landscape-forming discharges ($Q_i \sim A_i$) and of the drop in elevation Δz_i along the drainage direction. Theory and field evidence indicate $\Delta z_i \sim A_i^{\gamma - 1}$ with $\gamma = 0.5$ [*Rodriguez-Iturbe et al.*, 1992a; *Rodriguez-Iturbe and Rinaldo*, 1997]. Spanning, loopless network configurations characterized by minimum energy dissipation are thus obtained by selecting the configuration s that minimizes the functional [*Rodriguez-Iturbe et al.*, 1992a, 1992b; *Rinaldo et al.*, 1992]:

$$H_\gamma(s) = \sum_{i=1}^{N} H_i \propto \sum_{i=1}^{N} A_i^\gamma. \tag{2}$$

In the selection process, one needs to choose tree-like configurations consistently. This, in turn, is exactly admissible because every tree is a local minimum of total energy expenditure [*Banavar et al.*, 2000] whenever one has $\gamma < 1$ directly from the physics of the problem recapitulated by a deterministic slope-area relation [*Banavar et al.*, 2001; *Rinaldo et al.*, 2014].

We adopt a simulated annealing strategy [*Bounds*, 1987] to find OCNs [*Rinaldo et al.*, 1992]. The algorithm starts from an initial network configuration chosen to span the whole $L \times L$ landscape toward an imposed outlet (see e.g., Figure 1a), chosen at a single site—at no loss of generality [*Rodriguez-Iturbe and Rinaldo*, 1997]—for sake of simplicity. Every network configuration is completely described by the connectivity matrix $\mathbf{W}$. At every iteration of the optimization process, one pixel is drawn at random and its link is rewired to a different nearest neighbor, provided that no loops are formed. This change affects the matrix' elements W_{ij} and, in turn, the values of the aggregated areas A_i. The change in configuration $s \rightarrow s'$ is always accepted if total energy dissipation is decreased (i.e., $H_\gamma(s') < H_\gamma(s)$). Perturbations to higher values may be accepted, however, with a probability that depends on a parameter T, termed "temperature" owing to the thermodynamic annealing analog. On following a schedule of decreasing values of T, the network resulting from a perturbation is accepted according to the Metropolis rule, i.e., if

$$\exp\left(-\frac{H_\gamma(s') - H_\gamma(s)}{T}\right) < R \tag{3}$$

where R is a random number drawn from a uniform distribution in the interval (0, 1). In this manner, when the temperature is initially high, unfavorable changes are likely to be accepted thus making the algorithm capable of jumping out of structures conditioned by the initial condition. As temperature is reduced, changes are only accepted if they lower total energy dissipation and thus the optimum configuration gets refined and "frozen" around a dynamically accessible minimum.

2.2. Metapopulation Model

To investigate the persistence and the probability of occupancy of species spreading along river networks, we make use of a well-established spatially-explicit metapopulation model [*Hanski*, 1999; *Hanski and Ovaskainen*, 2000; *Ovaskainen and Hanski*, 2001, 2002] which accounts for the fundamental ecological processes of colonization, extinction, and dispersal. Each pixel of the modeled landscape is assumed to be a patch that can be either occupied or not by the species considered. We consider species that are constrained to disperse along the river network and that are not biased by the flow direction. The former assumption makes sense in the context of riverine ecological corridors as it subsumes directional dispersal beyond strictly fluvial pathways. The latter assumption is meant as a proof of concept rather than a specific feature of a species (although it proved valid for large scale patterns of fish biodiversity, see *Muneepeerakul et al.* [2008a]) and could be relaxed to study the conditions of persistence under drift [e.g., *Bertuzzo et al.*, 2007; *Mari et al.*, 2014].
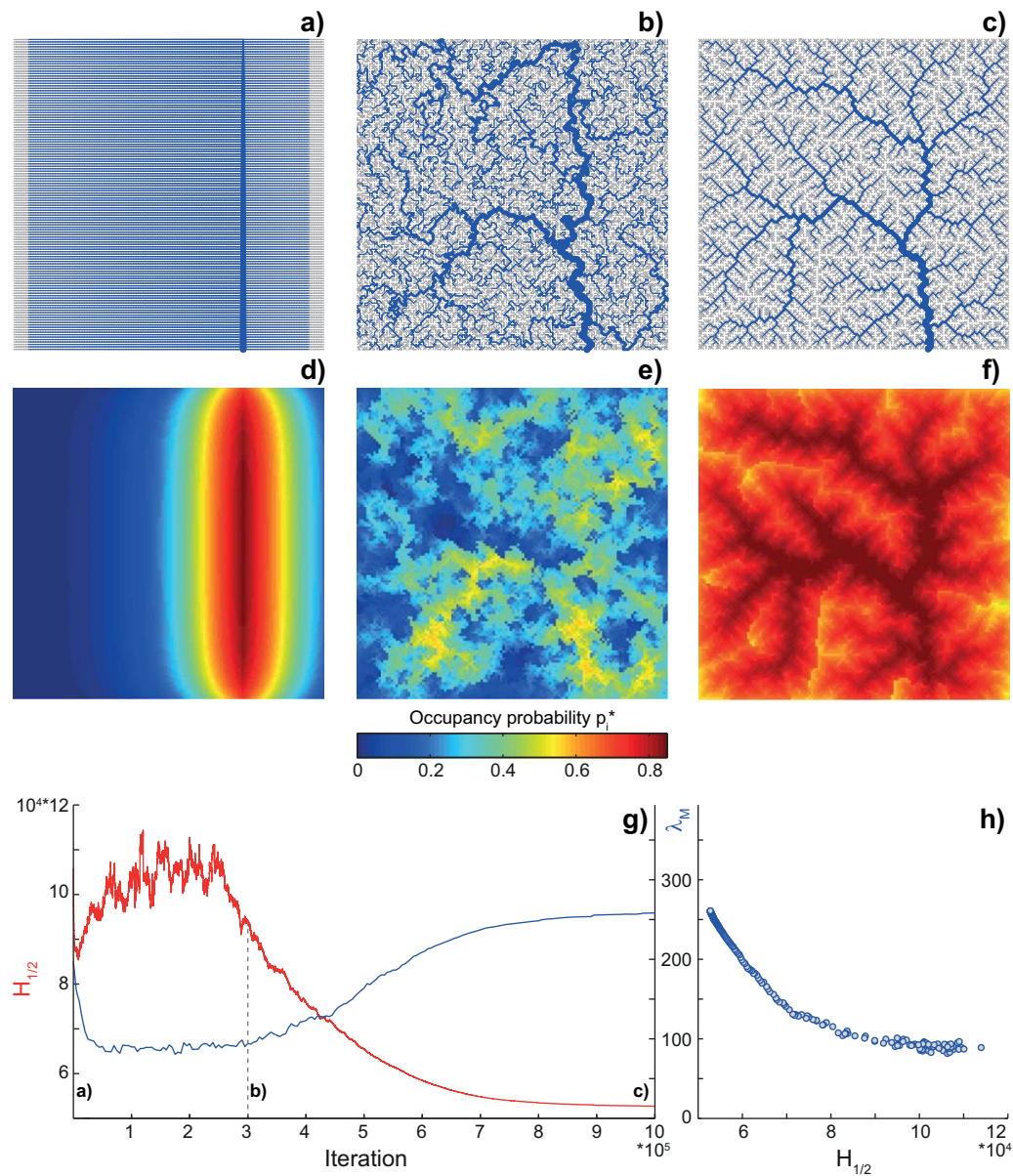
Figure 1. Linkage between the process of minimizing total energy dissipation which leads to an Optimal Channel Network (OCN) and the metapopulation capacity of the embedded fluvial landscape. (a) Initial network configuration, characterized by parallel flow directions collected by a central channel whose outlet is placed at the lower boundary; (b) intermediate state with disordered structure; and (c) final OCN. (d), (e), and (f) Spatial distribution of the equilibrium probability of occupancy p_i^* for network configuration shown in Figures 1a, 1b, and 1c, respectively. (g) Evolution along the iteration of the simulated annealing process of total energy dissipation $H_{1/2}(s)$ (red) and metapopulation capacity λ_M (blue). One verifies empirically that energy minimization of a network configuration results in improved metapopulation capacities, emphasized by the one-to-one relation between λ_M and $H_{1/2}(s)$ (h). Parameters used: OCNs, $L = 128$; simulated annealing, $T = H_{1/2}(0)/2 \cdot 10^5$; Metapopulation model, $\delta = 50$, $1/\alpha = 10$.

In the spatial metapopulation scheme, the evolution of the probability $p_i(t)$ of the focus species being present in patch i at time t is a balance between colonization and extinction forces [*Hanski and Ovaskainen*, 2000]:

$$\frac{dp_i(t)}{dt} = C_i(t)[1 - p_i(t)] - E_i(t)p_i(t), \tag{4}$$

where $E_i(t)$ is the extinction rate of the existing populations in patch i and $C_i(t)$ is the colonization rate of patch i when empty ($p_i = 0$). The effective colonization rate (first term of the right-hand side of equation (4)) accounts for the probability that the patch is empty ($1 - p_i(t)$).

Species spreading along river networks encounter patches with highly heterogeneous habitat suitability and habitat capacity depending on a variety of environmental conditions. However, all these drivers act on top of the unavoidable constraints provided by connectivity, whose imprinting is argued to be relevant in general [*Muneepeerakul et al.*, 2008b; *Carrara et al.*, 2012]. In order to single out the effect of landscape connectivity, we specifically assume that all pixels are equivalent in terms of habitat suitability and habitat capacity. It follows that the extinction rate can be assumed as constant and uniform $E_i(t) = e$ and that the colonization rate of patch i is a function of all possible contributors, i.e.,

$$C_i(t) = c \sum_{j \neq i} \mathrm{e}^{-\alpha d_{ij}} p_j(t) \tag{5}$$

where d_{ij} is the distance (measured along the network) between sites i and j; $1/\alpha$ is the mean distance of dispersal, here assumed to be exponential [*Hanski and Ovaskainen*, 2000], and c is a constant. Depending on the focus species and its life cycle, colonization can be achieved through migration, movement, or dispersion of propagules. In the following, we will generally refer to dispersal processes and dispersal distance.

Under the above assumptions, equation (4) reads:

$$\frac{dp_i(t)}{dt} = c \sum_{j \neq i} \mathrm{e}^{-\alpha d_{ij}} p_j [1 - p_i(t)] - e p_i(t). \tag{6}$$

A key parameter is thus $\delta = e/c$, the ratio of extinction and colonization rate parameters. Equation (5) is simplified with respect to the original approach [*Hanski*, 1999] in that "patches" are assumed of equal area and equal habitat suitability and spanning the whole lattice whereas the connectivity of the system directly affects the key metrics d_{ij}, i.e., the distance of pixel i from any other site j.

The state $\mathbf{p_0}$ characterized by $p_i = 0$ for any i is a global extinction equilibrium for model 6. Metapopulation persistence is related to the stability of such equilibrium. If $\mathbf{p_0}$ is unstable, a small perturbation (e.g., the introduction of a few individuals) leads to a positive stable equilibrium $\mathbf{p}^*$ with $p_i > 0$ for any i. On the contrary, if $\mathbf{p_0}$ is stable the species cannot persist and any population is doomed to extinction. The condition for the extinction equilibrium to switch from stable to unstable is that the leading eigenvalue of the Jacobian matrix $\mathbf{J}$ of system 6 linearized around $\mathbf{p_0}$ switches from negative to positive. If we define a matrix $\mathbf{M}$ consisting of elements $m_{ij} = \sum_{j \neq i} \mathrm{e}^{-\alpha d_{ij}}$ for $i \neq j$ and $m_{ii} = 0$, the Jacobian reads $\mathbf{J} = c\mathbf{M} - e\mathbf{I}$ and the stability condition becomes [*Hanski and Ovaskainen*, 2000]:

$$\lambda_M > \delta, \tag{7}$$

where λ_M, termed metapopulation capacity, is the leading eigenvalue of the matrix $\mathbf{M}$. Because $\mathbf{M}$ is a nonnegative square and irreducible matrix, according to the Perron-Frobenius theorem it has a positive and simple maximum eigenvalue λ_M and a unique positive eigenvector associated to it.

The inequality 7 therefore provides the condition for long-term persistence of a species in a given landscape as a function of parameters proper to the species considered (δ and α). To compute λ_M for a given landscape, what matters is just the spatial scale of connectivity (set by the average dispersal distance $1/\alpha$) and the spatial locations of the habitat patches, here identified as any pixel of the fluvial landscape. For a given species, λ_M is a measure of the ecological suitability of the landscape and it has powerful implications as it allows comparisons of differently connected landscapes where the relative contribution of any site to all others is accounted through d_{ij}, i.e., the distances available to ecological dispersal.

Hanski and Ovaskainen [2000] have also shown that an appropriately weighted average $\bar{p}^*$ of the equilibrium occupancy probability $\bar{p}_i^*$ values can be approximated by $\bar{p}^* = 1 - \delta/\lambda_M$. Therefore, when the conditions for persistence are satisfied, the higher the metapopulation capacity, the higher the expected occupancy of the population. Metapopulation capacity can be used specifically to rank different landscapes in terms of their capacity to support viable metapopulations. We shall employ such concept to analyze evolving fluvial landscapes to probe the parallel evolution of their capacity to support long-term persistence of arbitrary metapopulations.

3. Results

Figure 1 shows the results of a computational experiment carried out on a 128×128 lattice starting from an initial condition characterized by parallel-flow channeled hillslopes draining onto an orthogonal
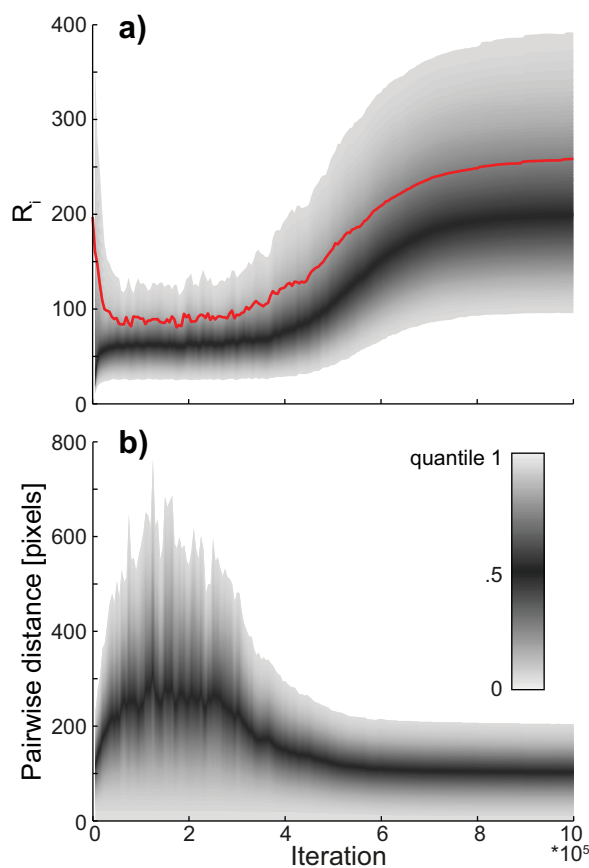
Figure 2. (a) Evolution of the distribution of values of $R_i = \sum_j \exp(-\alpha d_{ij})$, $i=1, N$, along with the optimization process shown in Figure 1. Gray-scale code shows quantiles of the distribution. The red line represents the evolving value of λ_M, which is theoretically predicted to lie between the maximum and the minimum value of R_i (see text). (b) Evolution of the distribution of pairwise distance d_{ij} measured along the network. Color code as in Figure 2a.

collecting channel (Figure 1a). The whole process of optimization is illustrated, including the high-T phase where many changes were accepted even if the related energy was increased. Figure 1b shows an intermediate configuration along the minimum search process, characterized by a value of total energy dissipation comparable to the initial one. Figure 1c shows the OCN obtained after the algorithm has converged toward a local minimum of energy dissipation. Even at eyeball, one recognizes the similarity of the parts and the whole that endows OCNs with features indistinguishable from natural forms distinctively marked by intertwined scaling exponents differently by chance-dominated trees [*Rodriguez-Iturbe and Rinaldo*, 1997; *Rinaldo et al.*, 1999]. Interestingly, along the process of minimizing total energy dissipation by shifting and sorting landscape matrices, the metapopulation capacity of the resulting landscapes increases. The evolution of λ_M mirrors, with changed sign, the convergence of total energy dissipation toward its local minimum. Figure 1 also shows the spatial distribution of the equilibrium occupancy probability p_i^* of the population of a species spreading in the corresponding networks. Note that the chosen intermediate state in the process of optimization, lowering only marginally the initial value of H_γ, is characterized by a disordered aggregation process far from locally optimal either in terms of energy dissipation or in terms of metapopulation
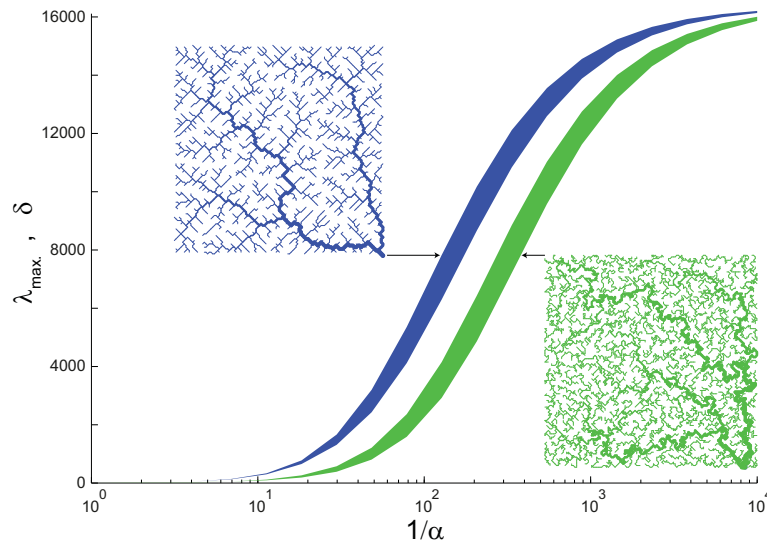
capacity. The occupancy probability of the OCN matrix is instead characterized by vastly improved values indicating higher chances of species persistence and occupancy. Another pattern is clearly distinguishable in Figure 1, occupancy probability increases moving from headwaters downstream, although with a final decrease toward the outlet of the catchment.

Figure 2 elucidates the mechanisms underlying the results presented above. It shows how the probability distribution of $R_i = \sum_{j \neq i} \exp(-\alpha d_{ij})$, i.e., the sum along the rows of the landscape matrix **M**, changes along with the optimization process leading to an OCN. Row sums R_i of **M** are convenient indicators because **M** is a nonnegative, irreducible square matrix and a corollary of the Perron-Frobenius theorem states that, under those conditions, one has

$$\min_i R_i \leq \lambda_M \leq \max_i R_i. \tag{8}$$

This corollary's implication is shown in Figure 2a, where the red line represents the evolving value of λ_M. The physical meaning of R_i is that of the potential for a population occupying node i to disperse to any other site or, conversely (**M** being symmetrical), the potential of the population occupying any other site to reach node i. R_i can thus be thought of as a measure of the network closeness at i and its distribution over all sites measures a collective closeness of the landscape. One sees that as energy is lowered, the amount of habitat that a population with a specific dispersal ability may reach from any given site increases. A similar result can be observed analyzing the evolution of the distribution of the distance d_{ij} among all possible pairs of nodes in the network, a metric which is independent of the dispersal distance

Figure 3. A comparative analysis of the metapopulation capacity λ_M for OCNs and random spanning trees as a function of the dispersal distance $1/\alpha$. Blue: OCN, green: random trees. Shaded areas represent the envelopes containing the relationships between λ_M and $1/\alpha$ for 100 different realizations (see text). Other parameters as in Figure 1. A species characterized by parameters δ and α can be thought of as a point in the illustrated space. Its population is predicted to persist if this point lies below the curve of a specific landscape ($\lambda_M > \delta$).

and it is often used to characterize the overall network closeness [*Newman*, 2003]. Along the network, evolution mean and variance of the pairwise distance distribution decrease indicating a more compact network (Figure 2b).

Figure 3 illustrates how the previous result depends on the dispersal distance $1/\alpha$. It shows the plot of the metapopulation capacity λ_M computed from 100 OCNs started from the same initial condition (Figure 1a) but choosing at random each outlet's position, for various values of the average dispersal distance $1/\alpha$. The shaded area highlights the variability obtained for the various realizations, that, although dependent on the schedule of decreasing temperature assumed, is deemed realistic in general. The green area in Figure 3 shows the metapopulation capacity λ_M for 100 random spanning trees, generated performing $10N$ iterations of the search algorithm described in section 2.1 but accepting all changes regardless of the implied energy value, provided that they maintain a tree structure. The convergence of λ_M for very large and very small dispersal distances regardless of the landscape matrix conforms with theoretical predictions. In fact, $1/\alpha \to \infty$ implies mean-field conditions with infinite dispersal. For any landscape thus equation (6) reduces to $dp_i(t)/dt=(N-1)cp_i(t)[1-p_i(t)]-ep_i(t)$, $\forall i$, whose stability condition reads $(N-1)>e/c=\delta$, i.e., $\lambda_M=N-1$. On the other extreme, $1/\alpha \to 0$ implies no dispersal at all and equation (6) reduces for any landscape to $dp_i(t)/dt=-ep_i(t)$, $\forall i$, according to which the extinction equilibrium is always stable and no population can persist, i.e., $\lambda_M=0$. For all intermediate cases, metapopulation capacities of OCNs are greater than those of random trees. Overall, it is clear that forms whose landscape matrix implies both chance and necessity at work produce higher viability for metapopulations to persist with respect to chance-dominated ones.

Figure 1 shows how minimizing energy increases metapopulation capacity. One thus wonders whether a local minimum of total energy dissipation, prescribed by the OCN search, corresponds to a local maximum of λ_M. This turns out to be not the case, as demonstrated in the following. Figure 4 shows the results of the process of maximization of λ_M starting from an OCN as initial state. Significantly, maximizing metapopulation capacity results in an even higher metapopulation capacity and, in turn, in a distribution of the occupancy probability whose mean is higher and overall makes for a more supportive landscape for metapopulations to persist. Crucially, we note that the aggregation structures produced by maximization of metapopulation capacity are not akin to the forms that we observe in nature for river networks, nor it implies lower total energy dissipation. The former statement is supported by the probability distribution of contributing area A_i (Figure 4f), well known to be a power-law of nearly universal character for real basins and OCNs [*Rodriguez-Iturbe and Rinaldo*, 1997]. Therein, the kind of regularity (especially at small scales) selected by maximization of metapopulation capacity produces a nearly-exponential distribution
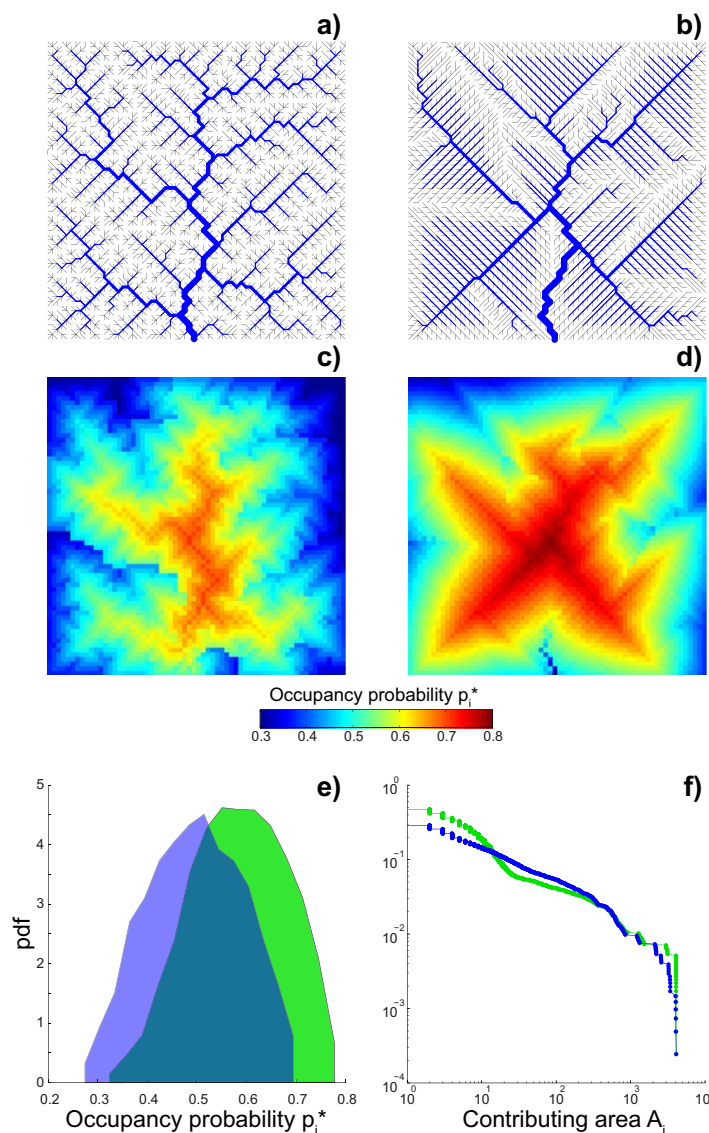
Figure 4. Selection of network configurations that maximize the metapopulation capacity by accepting changes only if they improve its value. (a) OCN, here assumed as initial condition; (b) network configuration obtained by maximizing λ_M. (c) and (d) spatial distribution of the equilibrium probability of occupancy p_i^* for network configuration shown in Figures 4a and 4b, respectively. (e) Probability density function of p_i^*: blue refers to Figure 4c, green to Figure 4d. (f) Exceedance probability distribution of total contributing area A_i for the networks in Figure 4a (blue) and Figure 4b (green). Parameters used: $L = 64$, $1/\alpha = 10$, $c = 1$, $e = 100$.

characteristic of parallel flow directions, in turn dependent in the value of $1/\alpha$. This result was somehow expected, in that the process has a well-defined characteristic scale—the dispersal distance—that breaks the scale-free nature shared by all river networks. We note that the numerical procedure has been greedy, i.e., only favorable changes are accepted corresponding to a $T = 0$ Metropolis scheme, to which one owes the impossibility of radical alterations of the initial large-scale aggregation structure which would require large and coordinated efforts to be modified significantly. This is reflected in the tail of the probability distribution of A_i which preserves memory of the initial condition. Overall, while it is clear that OCN shapes match all linked scaling exponents observed in nature (the sole condition for truly distinctive network comparisons *Rinaldo et al.* [1999]), the network shapes obtainable by maximization of metapopulation capacity are unsuitable to describe real river landscapes.

4. Discussion

Our analysis shows that the physical processes responsible of landscape evolution (the chief landforming processes like fluvial erosion, hillslope diffusion, and geologic uplift) drive the landscape toward a stationary state which is characterized by a minimum of total energy dissipation. The network configurations at local stationarity of the energy functional are unavoidably trees, that is, a unique path from any source to the outlet exists in runoff-producing areas where a concave slope-contributing area relation applies. The requirements, and the impediments, of landscape evolution are thus prescribed solely by physical constraints. As a by-product of physical evolution, landscapes develop vastly improved conditions for the persistence of populations of species spreading along the river network. The results are not necessarily limited to aquatic organisms living in the river but can be thought as valid, at large scales, also for species whose dispersal could be ecologically controlled by altitude or physical impediments like valley and ridges. While increased metapopulation capacity is not prescribed nor required, it simply occurs as a by-product of geomorphological evolution. Any process that forces the evolution of a network configuration by lowering its total energy dissipation, out of compelling

physical reasons, produces fluvial ecosystems whose viability for long-term species persistence systematically increases. Thus an improved ecological viability is not seen as a driver for landscape evolution, but rather an unintended consequence of the physical processes underlying landscape evolution.

Metapopulation theory focuses on population dynamics and viability of a single species. However, it also proved a powerful tool to study biodiversity patterns. A remarkable example is the study of the species-area relationship (i.e., the relationship between the number of species and the area of observation) in heterogeneous and fragmented habitats [*Rybicki and Hanski*, 2013; *Hanski et al.*, 2014]. Therein the model bridges the single-species view which we have employed here for OCNs with the multispecies community perspective by neglecting interspecific interactions but assuming differences in the ecological traits of the species. In our context, this assumption translates into considering a community assembled by many species characterized by different parameters δ, the ratio of extinction and colonization rate, and average dispersal distance $1/\alpha$. A first straightforward result is that landscapes with higher metapopulation capacity host the larger number of species, i.e., they have the higher regional species richness (γ-diversity). This can be visualized in Figure 3 where every species can be represented by a point in the space (δ, $1/\alpha$). Considering a large number of species with random parameters, it follows that the OCNs can sustain the larger share of species (points below the curves, $\lambda_M > \delta$).

The same framework can be applied to investigate how river network organization controls patterns of local species diversity (i.e., α-diversity). In fact, the higher the probability of occupancy p_i^* of a node, the higher the probability of simultaneously hosting a larger number of species, and thus the higher the local species richness. Our results show that the p_i^* peaks at intermediate levels of network organization with lower values toward headwaters and outlet, a behavior that mirrors patterns of species richness supported by theoretical and experimental evidence [*Vannote et al.*, 1980; *Carrara et al.*, 2012] and consistently found in empirical observations across different taxa (e.g., fish [*Muneepeerakul et al.*, 2008a] and macroinvertebrates [*Finn et al.*, 2011; *Altermatt et al.*, 2013]), although exceptions exist [see e.g., *Besemer et al.*, 2013]. This points toward a more theoretically sound metric for this general pattern, which has so far been related to loosely defined measures of network centrality [*Convertino et al.*, 2009; *Carrara et al.*, 2012; *Altermatt*, 2013]. Another well-established pattern in riverine macroecology is that diversity in community composition (i.e., β-diversity) among headwaters is higher than among higher-order streams [*Vannote et al.*, 1980; *Bertuzzo et al.*, 2009; *Brown and Swan*, 2010; *Finn et al.*, 2011; *Carrara et al.*, 2012], which implies that headwaters disproportionately contribute to regional species richness and should thus be targeted for conservation strategies [*Finn et al.*, 2011]. However, the simplifying assumptions of our analysis, chiefly neglecting interspecific interactions, do not allow us to reproduce nor to investigate this pattern, which indeed calls for fully fledged spatially explicit network metacommunity models, i.e., models that simultaneously account for the population dynamics of many species as well as their interactions [e.g., *Muneepeerakul et al.*, 2008a, 2008b; *Bertuzzo et al.*, 2009; *Carrara et al.*, 2012, 2013]. The method's limitations notwithstanding, therefore, we deem that the result subsumed by the evolution of the single-species metapopulation capacity works as a powerful proof of concept.

In our analysis, we have assumed uniform habitat suitability and unbiased dispersal to single out the effects of connectivity provided by the river network structure. However, there exist other environmental variables, which are known to affect biodiversity patterns of riverine communities, that change predictably with river network structure. Habitat size and altitude are among the most relevant. Habitat size can effectively be linked to geomorphological properties of rivers [*Carrara et al.*, 2013; *Muneepeerakul et al.*, 2007] and its direct effect on species richness derives from the simplest and most universal ecological principle: the number of observed species increases with increasing habitat size [*Rosenzweig*, 1995], often referred to as the "closest thing to a rule in ecology" [*Lomolino*, 2000]. The elevation field of a fluvial landscape can be reconstructed from the distribution of contributing areas and the contributing area-slope relationship [*Rigon et al.*, 1994] and it is therefore univocally linked to the river network configuration. Altitude is a proxy for temperature and energy [*Lomolino*, 2001] and it has long been studied in relation to species richness [see *McCain and Grytnes*, 2010 for a review] also in riverine contexts [*Altermatt et al.*, 2013]. When focusing on specific species or taxa, the habitat suitability of a river reach can be related to other hydrologic variables (e.g., flow velocity, depth, bottom shear stress) that can be estimated for the whole network starting from first hydrologic principles [*Ceola et al.*, 2014]. These drivers are certainly at work in shaping biodiversity patterns of fluvial landscapes. However, they act on top of the unavoidable constrains provided by

connectivity, whose imprinting is argued to be relevant in general. All these determinants should be accounted for in future research to develop a comprehensive theory of biodiversity in river networks.

5. Conclusions

We have objectively examined the relation between energy dissipation, the physical driver for the evolution of river networks, and their metapopulation capacity, a powerful measure derived from rigorous theoretical arguments to link landscape structure with the population dynamics it hosts. It has been shown that the process of total energy minimization shapes progressively refined network configurations which at stationarity reproduce all scaling features observe in nature, and implies a parallel process increasing metapopulation capacity. Thus the ensemble of geomorphological processes that force landscape evolution, and thus the embedded river network configuration, produces fluvial ecosystems whose viability for long-term species persistence systematically increases.

The evolutionary processes that govern river network configurations prescribe a lowering of the energy functional and they also obtain systematic improvements of the viability of the landscape for species persistence regardless of details on the species' attributes, in particular the average dispersal distance relative to the system's size. The converse is not true, however, maximizing metapopulation capacity, and thus the capacity of the landscape to support long-term occupancy of a species, does not lead to lowering of total energy dissipation nor generates realistic network shapes.

Improved ecological viability is not suggested to be a driver for landscape evolution, but rather an incidental but inevitable consequence of the physical processes underlying landscape evolution. While we recognize the abstract character of our results, precisely for their a specific prescriptions and their exact nature they seem to support a possible general tenet and suited to pave the way for a number of more specific studies employing more realistic ecological assumptions.

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