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Key Points:

- Fluctuations of drainage density matter for a species' metapopulation dynamics owing to related changes on local habitat size and network connectivity
- Viability of the focus species is determined by the value of the maximum eigenvalue of a suitable landscape matrix depending on drainage density
- The range of metapopulation capacities of flowing river network scales with mean total active contributing area measuring time-changing connectivity

Supporting Information:

Supporting Information may be found in the online version of this article.

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A Note on the Role of Seasonal Expansions and Contractions of the Flowing Fluvial Network on Metapopulation Persistence

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Abstract Does a dynamic drainage density have a role on species persistence in the river basin? The general viability of a focus species under time-varying hydrologic connectivity and habitat quality is a topic gaining traction in view of recent advances in our understanding of flowing fluvial network dynamics and of ecological interactions occurring on directed trees. Here, we combine metapopulation dynamics and scaling theory to investigate how the structure of river networks and time-changing hydrological and geomorphological attributes control local metapopulation survival. This is done by introducing seasonal fluctuations of the drainage density subsuming overall time-changing connectivity and distributed changes in habitat quality of the fluvial domain. Suitable replicas of channel networks within an assigned domain are used to compute the statistics of evolving metapopulation capacities, properties of a landscape matrix measuring the viability of the focus species. To obtain consistent replicas of the substrate for ecological interactions, we employ constructs whose suitability for the task has long been established. We find that the river network structure blends the fluctuations into a nontrivial scaling of the metapopulation capacity with the sum of total active contributing sites at any point of the flowing network. The latter is proportional to the mean distance to the outlet of the flowing dendrite and to the tree diameter—a measure of the overall connectivity of the active stream links. Scaling emerges as a robust ensemble property that enables the linkage of ecological patterns across a river network to clearly identified hydrological and geomorphological factors.

Plain Language Summary Contractions and expansions of the active flowing river networks matter for the persistence of ecological species owing to the related changes on local habitat suitability. The general viability of a focus species is determined here by the value of the so-called metapopulation capacity, the maximum eigenvalue of a suitable landscape matrix, which depends on the extent of the active network. The range of metapopulation capacities experienced by a dynamically changing flowing river network is shown to scale with total contributing area, a result that bears implications on our ability to predict the connection of hydrology and ecology.

1. Introduction

Despite evidence of the major biogeochemical and hydrologic relevance of the fluctuations of the flowing extent of a river network (Basu et al., 2011; Battin et al., 2009; Bertuzzo et al., 2019; Botter & Durighetto, 2020; Godsey & Kirchner, 2014; van Meerveld et al., 2019), the ecological implications of the inherent time-changing hydrologic controls remain elusive. Recent theoretical, field, and experimental results have clarified the crucial role of directional dispersal embedded in a treelike substrate for ecological interactions (e.g., Altermatt, Bieger, et al., 2011; Altermatt, Schreiber, & Holyoak, 2011; Carrara et al., 2012; Carraro, Hartikainen, et al., 2018; Carraro, Mari, et al., 2018; Detry et al., 2014, 2016, 2017; Economo & Keitt, 2008; Fagan, 2002; Goldberg et al., 2010; Grant et al., 2007; Holyoak & Lawler, 2005; Ma et al., 2020; Muneeppeerakul et al., 2007, 2008; Ramirez, 2012; Rinaldo et al., 2020). Moreover, intrinsically scaling treelike nested structures posit that local storages and fluxes depend on aggregation, thus bringing fundamental nonlocal interactions into the ecological dynamics (see e.g., Bertuzzo et al., 2019; Rinaldo et al., 2020). In this context, the description of temporary and ephemeral streams, although certainly not new (Bernier, 1985; Day, 1978; Gregory & Walling, 1968), is currently a major focus of ecohydrologic research where field studies aim at quantifying the seasonal and event-based dynamics of the active stream network and

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their implications (Agren et al., 2015; Durigetto et al., 2020; Florianci et al., 2018; Jaeger et al., 2007; Lovill et al., 2018; Malard et al., 2006; Perez-Saez et al., 2017, 2019; Shaw, 2016; van Meerveld et al., 2019; Whiting & Godsey, 2016).

Transient waterscape connectivity has long been the subject of ecological investigation for example (Bertassello, Aubenau, et al., 2020; Bertassello, Bertuzzo, et al., 2020; Bertassello et al., 2019; De Angelis et al., 2005; Dixon, 2003; Lowe et al., 2019; Stoffels et al., 2016; Trexler et al., 2005; Unmack, 2001; Zeigler & Fagan, 2014; Zhou & Fagan, 2017). Specifically, hydrologically driven changes in size, shape, and location of habitat patches, for example, induced by water level rises related to hydrologic responses to the vagaries of precipitation regimes, may generate ecological opportunities owing to transient windows for connectivity, periodic, or altogether changing (Bertassello et al., 2019; Zeigler & Fagan, 2014). One case study of paramount importance to that end proved the Florida everglades (Lodge, 2004). Even short-lived, hydrologically driven windows for connectivity may be exploited by fish (Zeigler & Fagan, 2014) or amphibians (Bertassello et al., 2019; Lowe et al., 2019), where a factor is arguably the restriction posed by habitat size of the permanent water bodies (e.g., Rinaldo et al., 2020). Seasonal fluctuations may possibly affect also terrestrial species, in particular riparian tree species whose recruitment and establishment need suitable seed transport and depositional environments (Dixon, 2003). Within this domain one should mention the issue, not addressed in this study, of the strategies for species survival in ephemeral rivers for example, via estivation (Kerezst et al., 2013; Perez-Saez et al., 2017). Relatedly, the study of the spatial variation in fluvial branch sizes has only recently suggested its key role in promoting metapopulation persistence in dendritic river networks (Ma et al., 2020; Rinaldo et al., 2020).

Clearly, the broad characters of the persistence of specific species to spatially and temporally varying hydrologic connectivity depend on a number of factors centered on the interplay between their dispersal ability and the extent of the fluctuations of the habitat size and its inherent risks (Mari et al., 2014b; Stoffels et al., 2016; Unmack, 2001). Chief among the latter, for example, for small fish, is the risk of getting trapped in isolated patches generated during the retreating phase to the permanent water bodies, that eventually dry out thus generating periodic bouts of mortality.

In quite a few cases, rivers impose significant constraints to aquatic organisms that may strongly affect their movement, like those induced by a strong downstream drift (tending to the limit cases of the passive scalar behavior, i.e., advective along-stream transport). Hydrologic constraints also include minimum stage thresholds that might prevent fish migration (e.g., Tetzlaff et al., 2018). Plants and animals may persist in fluvial ecosystems however, which actually harbor great biological diversity. Mari et al. (2014b) have studied metapopulation dynamics in stage-structured metapopulations capable of exploiting different dispersal pathways depending on their life stage. In this specific case, amphibians were studied that use alternatively (or jointly) along-stream and unchanneled domains. Criteria for metapopulation persistence in arbitrarily complex river networks have consequently been derived. However, such an approach is hardly a candidate for a synthesis of the geophysical controls imposed by a dynamic drainage density. The passive transport of an aquatic organism within a river system is the byproduct of many hydrodynamic effects resulting from the combination of advection and hydrodynamic dispersion blending natural streamflow heterogeneities (Mari et al., 2014b; Rinaldo et al., 2020). The so-called active organismic mobility, that is, the net displacement produced by flying (directly or by other vectors) or swimming/crawling, and the related geomorphological dispersion resulting from the multiplicity of flow sources at any river station (Rinaldo et al., 1991, 2020), further increases the overall macroscopic diffusion of organisms (Mari et al., 2014b). In many cases relevant to streamflow ecology, the latter may become the predominant factor. All these factors act synergistically with the fluvial landscape topology, which is characterized by hierarchical branching geometries and universal scaling features (Rodriguez-Iturbe & Rinaldo, 2001). Stream ecosystems matter, because their branched structure (subsumed by recurrent measures like the distribution of total contributing area at any point of the network) is an important constraining factor for aquatic species that lack life stages that can disperse overland (Fagan, 2002; Zeigler & Fagan, 2014). Moreover, it was shown experimentally (Carrara et al., 2012) how branching structures of the ecological substrates facilitate persistence of populations (Rinaldo et al., 2020).

Our study matters in particular for species where dispersal can occur at different life stages, frequently early in the life history of the focus aquatic organisms (Campbell Grant, 2011). As an example, in a

comprehensive mark-recapture study of two lungless salamander species in stream networks (Campbell Grant et al., 2010), newly metamorphosed (juvenile) salamanders showed high probabilities of dispersing to other stream reaches, thus operating as the primary mechanism for widespread overland connectivity. Therefore, dynamic drainage densities matter because they alter the relative distances to be covered through overland states (dry) versus fluvial ones (wet). Incidentally, it is relatively common to observe freshwater organisms that begin their life cycle as motile and reaching maturity as sessile (e.g., mussels). However, notable exceptions exist. This is the case, for instance, of flatworms and other parasites characterized by complex life cycles involving intermediate hosts with low motility (like freshwater snails, especially of the *Bulinus* genus) and otherwise final hosts characterized by high motility (e.g., fish; Mari et al., 2014b; Rinaldo et al., 2020).

Despite their importance, the joint effects of dispersal, landscape geometry, and stage-dependent movement leading to multiple dispersal pathways have been analyzed only recently for example (Bertassello, Aube-nau, et al., 2020; Bertassello et al., 2019; Fagan et al., 2009; Garbin et al., 2019; Mari et al., 2014b; Stoffels et al., 2016; Zeigler & Fagan, 2014). To yield a description of the conditions leading to the persistence and spread of riverine populations, dendritic geometries have shown their decisive role in a number of ways, including simulation studies of individual-based schemes (Campbell Grant, 2011; Fagan, 2002), or in population models applied to stage-structured populations in connected networks of habitat patches (Goldberg et al., 2010). Relevant analytical results for persistence of populations driven by advection and hydrodynamic dispersion on a tree graph also exist (e.g., Ramirez, 2012).

Here, we pursue a theoretical exercise originating from a simple set of questions: does the variation of the dynamic drainage density of flowing fluvial networks have a role on species persistence? What features of a species' life cycle are affected by seasonally (or event-based) expanding and contracting substrates for ecological interactions? Is there some geomorphological measure that relates directly to persistence features? To address these questions, one avenue is to further our understanding of specific metapopulations whose persistence may be inferred by exploiting observed ecological field observations contrasting spatially explicit models (Casagrandi & Gatto, 2002; Fagan, 2002; Mari et al., 2014b). However, to target general features of metapopulations in dynamic river networks, the candidate approach must search for recursive properties, like scaling features, linking ecological indicators of persistence to directly measurable geomorphological determinants. This is the aim of this study.

This study is organized as follows. A methodological section describes the ecohydrological tools adopted, in particular about the key concept of metapopulation capacity for fluvial networks. It is a measure related to the stability of a focus species' persistence, and thus to the connectivity of the system subsuming the number of sites from where a population going locally extinct may be replaced owing to others' dispersal ability. We then describe our novel result, the statistical study of metapopulation persistence under varying extents of the flowing river network based on a large sample of replicas of optimal channel networks (OCNs), independent realizations of the substrate for ecological interaction within the same domain whose statistical properties are statistically indistinguishable from those of real river networks. A discussion on the results follows, with emphasis on the scaling properties of local measures of stable persistence with metrics of connectivity based on the distribution of contributing area at a point, the master variable of streamflow ecology. An analysis of limits and validity of the proposed approach is also included. A set of conclusions closes then the study.

2. Methods

We study the metapopulation of a focus species (a group of spatially separated populations of the same species which interact at some level Levins, 1969) within a river network belonging in runoff-generating areas as its ecological substrate (i.e., identifiable as a loopless tree structure [Rodriguez-Iturbe & Rinaldo, 2001]). We aim at determining how an arbitrary focus species' survival probability changes, given its ecological determinants therefore, under the time-varying conditions of altered connectivity and habitat size that a seasonal contraction/expansion of the flowing network exhibits. To study geomorphological effects on species persistence, we do so by studying the behavior of a large number of network replicas.

The confined, and yet ambitious, perimeter of our analyses must be stated upfront. More realistic settings may include anthropic interventions like artificial regulations, localized water withdrawals, or barriers (like dams or run-of-river plants) that may alter connectivity or streamflow distributions. Also, no result put forth here holds for strongly heterogeneous conditions, say in locally polluted or regulated rivers, which poses a different problem. Moreover, the design of our experiments excluded at this stage empirical comparisons with both ecological or hydrological evidence to concentrate on theoretical predictions. Further work will address validation, in analogy with inspiring examples of the past (Hanski & Ovaskainen, 2000; Hanski et al., 2015).

A detailed description of the theoretical premises of the metapopulation model and the related materials and methods is in Supporting Information S1, see also Rinaldo et al. (2020). The following methods section describes the essential elements of the mathematical model and of the tools employed to simulate the species and the river landscape as well as the species' features demanded for its capacity of survival.

2.1. Metapopulation Model

We propose to use a well-known model describing a metapopulation of virtual species (Hanski, 1994, 1999; Hanski & Gilpin, 1991; Hanski & Ovaskainen, 2000; Ovaskainen, 2002; Ovaskainen & Hanski, 2001), adapted to a river network domain (Giezendanner et al., 2020; Muneeppeerakul et al., 2008; Rinaldo et al., 2020). A metapopulation portrays the dynamics of a population of one species in a given landscape, and the relation between the subpopulations in the different patches making up the domain. Patches here are thought of as riverine reaches with their geomorphological attributes.

The metapopulation dynamics and its stability properties are driven by two processes: the colonization of new patches from occupied ones, which depends on the dispersal ability of the focus species to move away from a source site and on the distance to its destination; the extinction probability in already occupied patches. Specifically, here a patch is identified with a pixel extracted from a digital terrain map—pixels cover the catchment surface and are the units from which one extracts all relevant discretized geomorphic information like elevation in its centroid, steepest descent directions among neighboring sites, topographic curvature at its center, connectivity features over short and long range largely simplified by the treelike nature of river networks in runoff-generating areas (Rinaldo et al., 2020; Rodriguez-Iturbe & Rinaldo, 2001). Both processes (namely, dispersal-dependent colonization of patches and the extinction of occupied patches) depend on habitat quality, which governs the focus species' fitness, that is, how well it can survive in a given patch. The model is described in some detail in Supporting Information S1.

The equivalent of patches in our context are pixels of a digital terrain map, seen as network nodes (see Section 2.2), that is, the building blocks of the network description obtainable from topographic data. The construction of connected paths along the network structure follows the rule of a spanning tree: a unique path connects every two pixels, every pixel in the landscape is part of the tree, and the network branches are channeled only after some threshold area downstream of the source. From that point on, the branches remain irreversibly channeled (the property of being a loopless tree is general and solidly rooted in physics Banavar et al., 2001, 2007). Figure 1 shows an example of computation of the relevant features.

The local fitness f_i at site i is assumed to be proportional to the volume of flowing water upstream of i , computed as a function of the local active contributing area (Supporting Information S1):

$$f_i \propto A_i^\alpha \cdot A_i^\beta, \quad (1)$$

where A_i is the total flowing contributing area at the i th site (pixel; see Section 2.2 and Supporting Information S1), and the quantities A_i^α and A_i^β are proportional to the width and height of the bankfull channel, respectively (Leopold et al., 1964). α and β are rescaled by the width and the height of the channel at the outlet, that is:

$$\alpha = \log(w_{outlet}) / \log(A_{outlet}) \quad (2)$$

$$\beta = \log(h_{outlet}) / \log(A_{outlet})$$

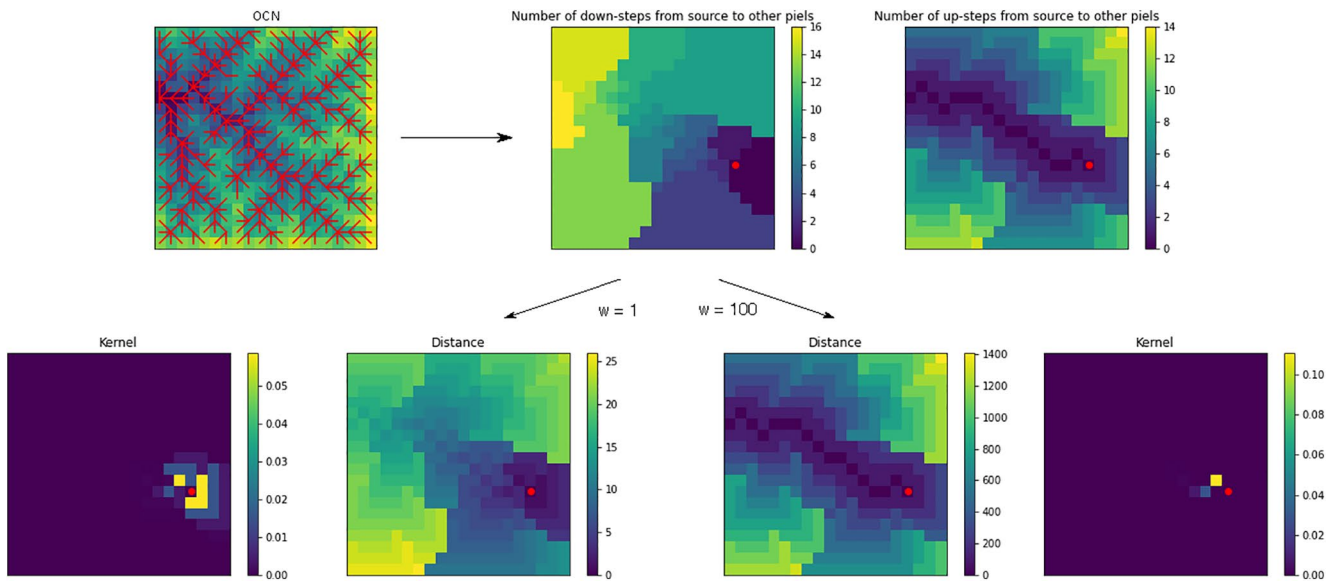


Figure 1. Example of computation of the relevant quantities derived from a single optimal channel network (OCN). First, we define the matrices defining the number of downstream and upstream steps necessary to join every couple of sites (Supporting Information S1). This is a practical way of determining the connectivity of the system as a whole, noticing that if the drift of the streamflow drift (w) is tuned to zero all steps are equally costly. In the example shown, L_{ij} is the effective distance between two patches in the network given as $L_{ij} = ND_{ij} + wNU_{ij}$, where ND and NU are respectively the number of upsteps and downsteps required from one pixel to the next along steepest descent directions, and w a drift factor (Supporting Information S1). In the figure, this is computed from the point highlighted in red to all others and color coded as indicated in the label. The relevant landscape matrix is then computed for different values of w , the drift factor that converts the physical distance between two points into a weighted distance accounting for the energy required for dispersal from one to the other (Supporting Information S1).

The width of the channel at the outlet is an intrinsic property of an OCN (see Section 2.2 and Supporting Information S1), whereas the height at the outlet is arbitrarily fixed, as an example, to 3 m. Suffice here to note that any other choice of fixed height would not have changed the scaling properties discussed in Section 3.

Hanski and Ovaskainen (2000) have proposed a powerful way to compute the capacity of a metapopulation to survive in a landscape based on the interactions between the different sites, by constructing a suitable landscape matrix to subsume the effects of such interactions. The derivation of the metapopulation capacity, first presented in Hanski and Ovaskainen (2000) and explained in full detail by Ovaskainen and Hanski (2001), is presented in Supporting Information S1. Here, only a short summary is reported.

Let λ_i^J ($i = 1, \dots, n$) be the eigenvalues of the Jacobian matrix evaluated in the stationary null solution of the dynamic system (Supporting Information S1). The persistence-free solution is stable if $\text{Re}(\lambda_i^J) < 0$ for all $i = 1, \dots, n$ (where Re indicates the real part of a complex number) and unstable if there is at least one eigenvalue of $\mathbf{J}(0)$ with real part greater than zero. Technical difficulties aside (Supporting Information S1), if the largest eigenvalue of the Jacobian is positive, that is, $\lambda_1^J > 0$, the condition of stability is not satisfied (Supporting Information S1).

The main theoretical advance is that the eigenvalues of the Jacobian of the system can be directly obtained from those of a matrix, say \mathbf{M} , which does not depend on the values of the local extinction and colonization parameters (e and c , see Supporting Information S1).

The elements of \mathbf{M} read

$$\mathbf{M}_{ij} = \begin{cases} f_i f_j K_{ij} & \text{for } i \neq j \\ 0 & \text{for } i = j \end{cases} \quad (3)$$

where K_{ij} (see Supporting Information S1) is the dispersal kernel between patch i and j . Moreover, it can be shown that the landscape matrix \mathbf{M} and the Jacobian of the system have the same eigenvectors (Supporting

Information S1). The onset of instability leads to conditions on the eigenvalues of \mathbf{M} (Supporting Information S1). This implies that the largest eigenvalue of \mathbf{M} must be smaller than elc to insure generalized extinction. In this manner, the eigenvalues of the matrix are computed independently from the extinction and colonization rates of the species. Moreover, \mathbf{M} is symmetric and has a condition number much lower than $\mathbf{J}(0)$ (Supporting Information S1), thus the largest eigenvalue can be computed with a reduced computational effort.

2.2. Optimal Channel Networks (OCNs) and Their Landscapes

To assess general conditions for survival of species in a fluvial ecosystem, we must produce a set of suitable replicas of the substrate for ecological interactions. To that end, we employ OCNs (see Rodriguez-Iturbe & Rinaldo, 2001, for a review of the relevant methods) generated using an R open source package called OCNet (<https://github.com/lucarraro/OCNet>; Carraro et al., 2020). Without loss of generality (Rinaldo et al., 2014), we generated several space-filling OCNs within square lattices (side L , $N = L \times L$ nodes). Each node is connected by a link to one of its eight nearest neighbors (the drainage direction), leading each OCN to form a spanning tree with a single root (the outlet). Other possible features, like multiple outlets, are possible but unsuitable in this context because they would not alter the statistical features of any of the resulting trees and would only ultimately reduce the range of contributing areas under scrutiny.

The master variable of an OCN, whose collection defines uniquely the configuration of the network, is total contributing area at an arbitrary site i , A_i , that stems from the aggregation structure of each tree to characterize each pixel. A_i defines the number of upstream pixels connected to i through the set of assigned drainage directions, is a random variable whose probability distribution is known to be scale free and whose scaling exponent finely discriminates different aggregations (Rinaldo et al., 1999, 2014). In pixel units (i.e., the elementary pixel area $\Delta x \times \Delta x = 1$, where Δx is the length of the pixel side), one has

$$A_i = \sum_j W_{ji} A_j + 1, \quad (4)$$

where W_{ji} is the element of a general landscape connectivity matrix \mathbf{W} (i.e., $W_{ji} = 1$ if $j \rightarrow i$ and 0 otherwise), and the added unit represents the unit area of the pixel that discretizes the surface. A_i is a proxy of the landscape-forming flowrate at point i , as it represents the sum of the local injections over all connected sites upstream of i (included; Rodriguez-Iturbe & Rinaldo, 2001). When the connectivity matrix \mathbf{W} underpins a directed tree configuration, say s , the latter is completely determined by the vector of total contributing areas $s = (A_1, A_2, \dots, A_i, \dots, A_N)$ at each of the N sites. Details on the nature and properties of the connectivity matrix are given elsewhere (Rodriguez-Iturbe & Rinaldo, 2001). The same applies to the ecological significance of several quantities related to total contributing area at a point (Rinaldo et al., 2020).

Briefly, OCNs are spanning trees minimizing a functional describing total energy dissipation of the aggregate's configuration. At the i th pixel 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 along a drainage direction. Theory and field evidence indicate $\Delta z_i \propto A_i^{\gamma-1}$ with $\gamma = 0.5$ (Rodriguez-Iturbe & Rinaldo, 2001). Spanning, loopless network configurations characterized by minimum energy dissipation are thus obtained by selecting the configuration s that minimizes the functional (Rinaldo et al., 1992, 2014; Rodriguez-Iturbe et al., 1992) that is, $H(s) = \min \sum_{i=1}^N A_i^{1/2}$. Details on the selection process, the resulting statistics, and the exact nature of the mathematical problem that comes directly from its physics encapsulated in a deterministic slope-area relation—every tree is a local minimum of total energy expenditure (Banavar et al., 2000)—are reported in the original works and here only briefly summarized in Supporting Information S1. In summary, the exact linkage of OCNs with the set of stationary solutions of the general landscape evolution equation allows us to treat OCNs as independent replicable realizations of spanning trees, planar constructs that reproduce sets of drainage directions statistically indistinguishable to those of real stream networks (Rinaldo et al., 2014).

Also, a 3D landscape topography may be associated uniquely with each planar OCN, because a slope-area law is implied by $H(s)$ that is, the upstream drop in elevation along the drainage direction, Δz_i , scales with A_i via $\Delta z_i = C A_i^{-1/2}$ where C is a suitable constant. Thus, the topographic relief is determined by the planar imprinting—under specific constraints (Balister et al., 2018; Banavar et al., 2001). Starting from the

outlet, whose elevation is set to 0, the landscape-generating algorithm proceeds to label each node with a prescribed elevation by following the upstream drainage directions (e.g., Carraro et al., 2020). Upstream from the outlet, one thus populates the domain: the landscape is uniquely determined by the connectivity matrix because there exists a unique path from any site j to the outlet (Banavar et al., 2001). Thus, a definite topography is uniquely associated with any planar OCN. This is assumed to apply deterministically. Thus, we implicitly assume that it is the inherent variability in the aggregation structure of each replica that prescribes suitably approximate stochastic features to the derived landscapes.

For a proper discussion on limits and validity of the slope–area law not simply restricted to the channeled portion of the landscape, or for the detailed discussion of stringent testing for statistically identical trees, the reader is referred elsewhere (Rinaldo et al., 2014; Rodriguez-Iturbe & Rinaldo, 2001). Here, we also assume that a dynamic drainage density does not affect the landscape elevations.

2.3. Expanding and Retracting Networks

OCNs entail the useful concept of statistically coherent replicas of ecological substrates. To study the influence of landscape alterations materialized in cyclic expansions/retractions of the substrate for ecological interactions (the flowing fluvial domain), we have performed our computational experiments on 39 replicas of OCNs of size 64×64 each, and computed their metapopulation capacity for nine retraction steps in every realization, starting from $t = 0$ and increasing by $dt = \pi/18$ at each time step t .

The simulation of the expansion of each network replica in time is performed here in three steps:

1. Following the procedure described above, we first define the initial contributing area of each pixel as A_i^0 .
2. We then define the pixels to be considered in the contraction of the network with the rule:

$$A_i^0 \cdot \sqrt{dZ_i} > \text{thr}(t), \quad (5)$$

where dZ_i is the slope in pixel i . This is tantamount to applying a variable threshold contributing area because for every pixel j of the flowing river networks one must have $A_j^t > \text{thr}(t)/\sqrt{C^{2/(\gamma+1)}}$. Needless to say, this is justified by the exploratory nature of our quest. More detailed channel initiation models may be in order to portray the relevant dynamic drainage density (Durighetto et al., 2020; Gregory & Walling, 1968; Montgomery & Dietrich, 1988; van Meerveld et al., 2019), and they could be readily implemented at the cost of the introduction of additional parameters.

- 3 Finally, we compute the contributing area A_i^t of the contracting state t only considering the pixels above the threshold value (see Figure 2).

The threshold value is given as a sinusoidal function:

$$\text{thr}(t) = \alpha \sin(t = 0, 1, \dots, \pi/2) \cdot (A_{\min}^0), \quad (6)$$

ranging from the minimum area (A_{\min}^0) to $\alpha \cdot (A_{\min}^0)$, where α is the maximum retraction of the network corresponding to the permanent flowing domain (here arbitrarily set at 10 pixels). To justify the choice of the minimum threshold area (or to employ a sensible criterion for proper mean channel initiation e.g., Montgomery & Dietrich, 1988), in real-life settings one should parametrize the extent of drainage density variation via $CV(L)$, the coefficient of variation of the total of the active channel network (Durighetto et al., 2020). As a reference, one may posit that the observed values of $CV(L)$ vary in the range from 3.5 for arid climates to 0.3 for wet climates (Durighetto et al., 2020). More realistic schemes of time-varying channel initiation may thus be considered by future research, especially if temporary disconnections could be developing in the waterscape. However, the minimalist approach adopted here seems justified by the intent of a first step in the search for rules underpinning the geomorphological inferences of transient connectivity and habitat quality as a consequence of a first-order approximation of the expansion/contraction process.

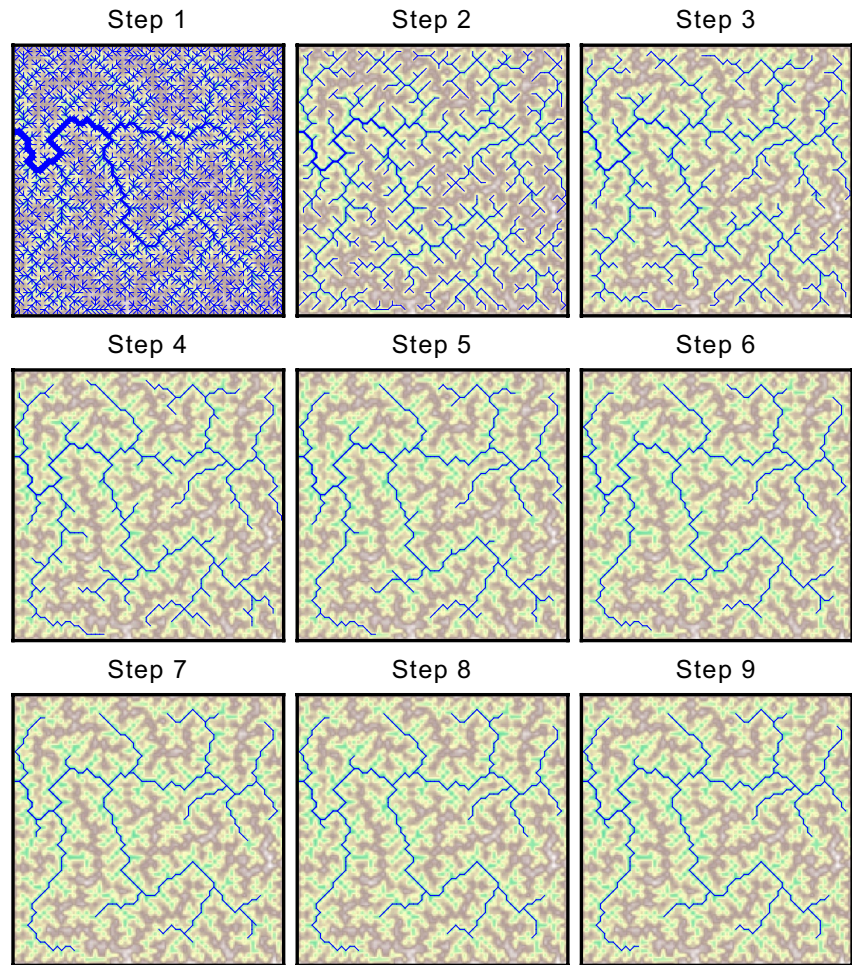


Figure 2. Graphic representation of the volume of water (proportional to the active flowing total contributing area) in each stretch in time at nine steps of the threshold $\text{thr}(t)$ defining the effective support area in each of the computed OCNs. Blue lines indicate the active river network.

3. Results

Figures 3a and 3b show the relation between mean total active contributing area ($\bar{A} = 1/n \sum_{j=1,n} A_j$, where j labels each of the n active pixels (i.e., belonging to the flowing river domain at any given time step t) making up each OCN k , and $A_j = A_j(k, t)$ is computed for each active pixel of the k th OCN at the various contraction/expansion stages t) and the computed metapopulation capacity $\lambda_{k,t}$ for each of the k OCNs at different stages t of retraction/expansion of the active fluvial domain. The physical meaning is immediate. In fact, the quantity $\sum_j A_j$ is known to be proportional to the mean nodal distance from the outlet \bar{L} (computed along stream; Rodriguez-Iturbe & Rinaldo, 2001). In turn, \bar{L} is proportional to the OCN diameter, that is, the mean along-stream distance to the outlet of all tree sites. This follows from (a) the treelike features of OCNs; (b) the property of directed trees, characterized by a unique path connecting any two nodes; and (c) the uniqueness of a configuration s whose vector components are $s = \langle A_1, A_2, \dots, A_j, \dots, A_n \rangle$ in defining the system state (Rodriguez-Iturbe & Rinaldo, 2001). The spread of the relation between the contributing area and the metapopulation decreases while the retraction of the network occurs, possibly indicating a relative homogenization of the aggregations emerging for different OCNs when the contraction limits metapopulation survival to a region near the outlet. Also, no sign of scaling in the coefficient of variation of the clusters of computed metapopulation capacities is detectable. The relation between the two variables is markedly nonlinear, indicating possibly analogous effects of dynamics features, like dispersal, on metapopulation survival.

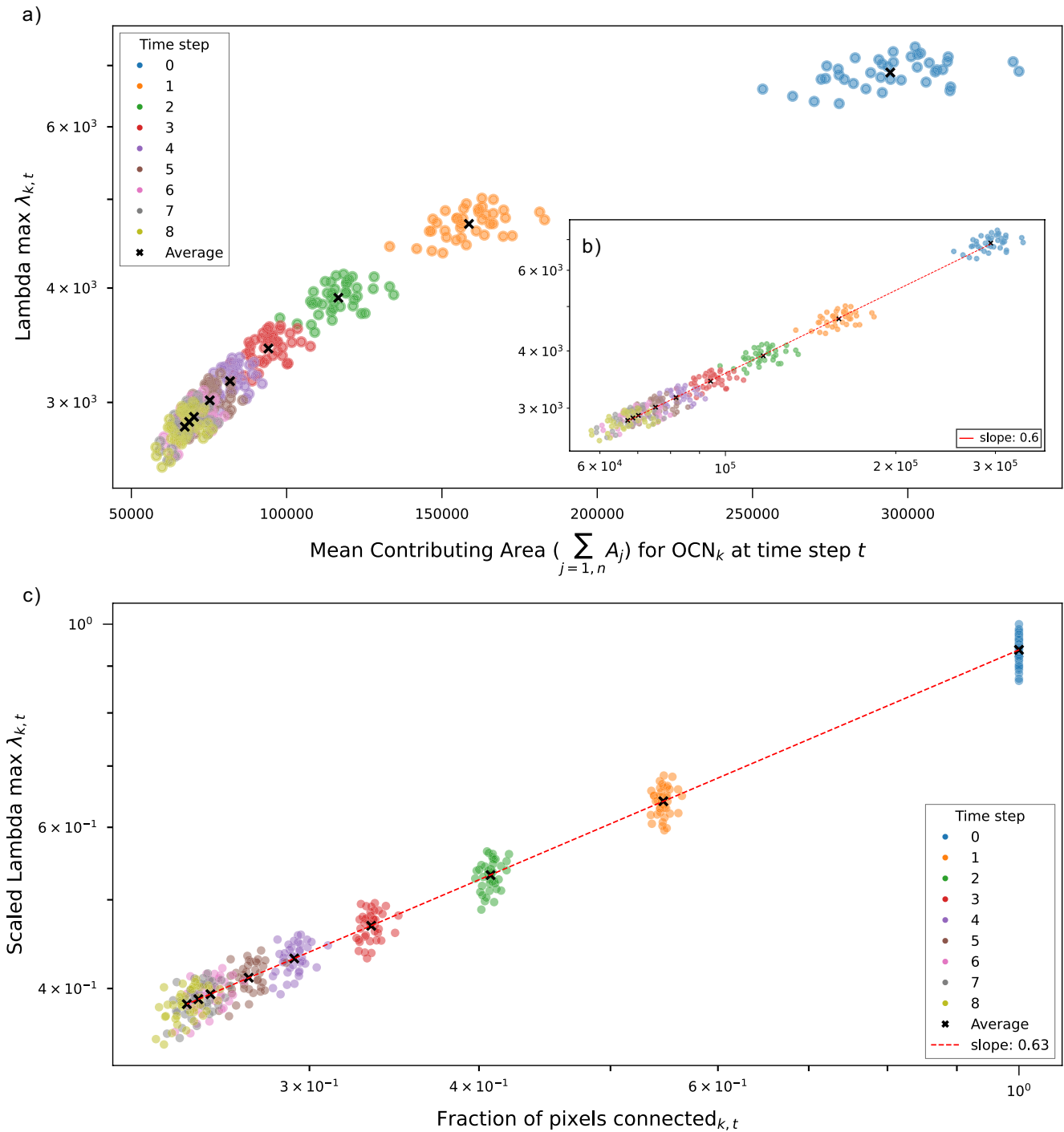


Figure 3. Scaling of species viability with time-varying geomorphic measures: (a) Mean active contributing area $\bar{A} = 1/n \sum_{j=1,n} A_j$ of the flowing river network at various stages t of the network retraction, plotted against metapopulation capacity $\lambda_{k,t}$ for each k th replica OCN at various stages t (i.e., time step). The y-axis is log scaled. Panel (b) same as panel (a) in a log-log plot. The relation between the mean data (dashed line) proves concave in log space with slope $\sim 0.6 \pm 0.05$; (c) Fraction of active pixels connected versus scaled maximum metapopulation capacity ($1/\max(\lambda_M)$) for each OCN at each time step of the retraction, in log-log space.

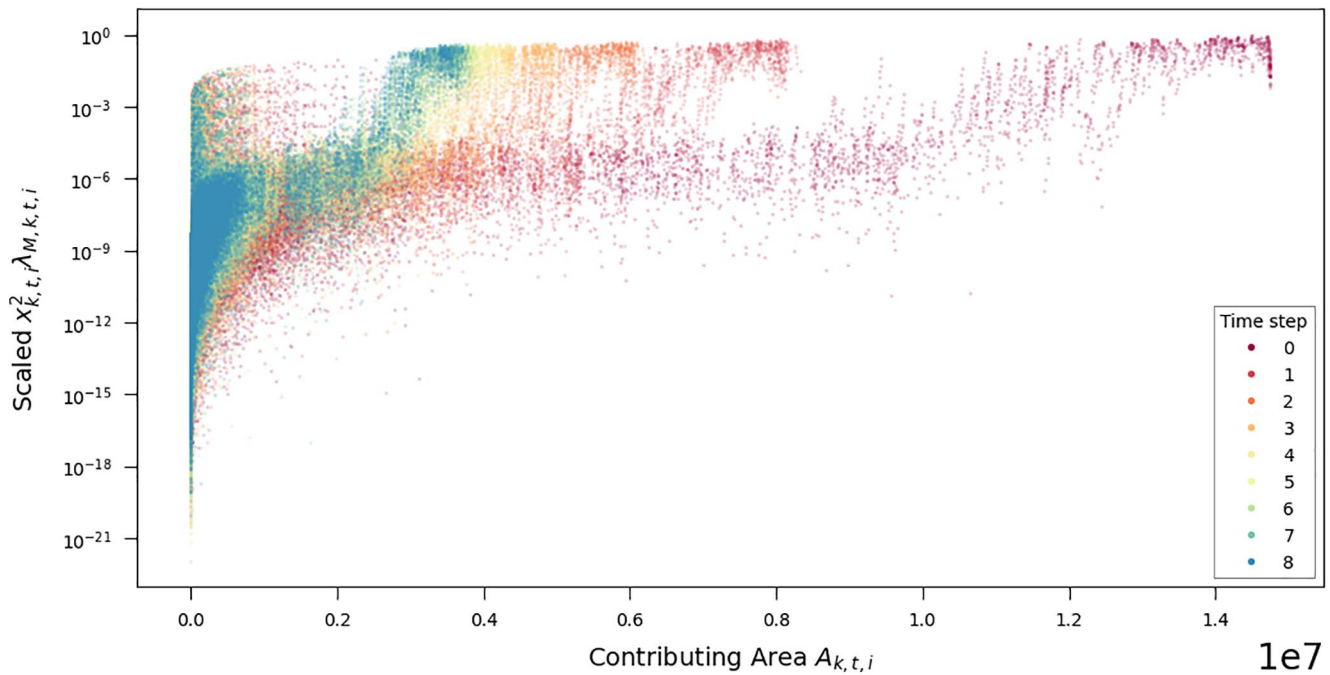


Figure 4. A sample of the variability obtained by replication. Scaled metapopulation capacity (λ_{\max} normalized by $\max(\lambda_{M_i})$) plotted against $A_{k,t,i}$, the total contributing area at each pixel i of each OCN k (for each retraction step t indicated in the inset).

Relatedly, Figure 3c shows the log-log plot of the fractions of active pixels connected against the (normalized) maximum metapopulation capacity ($\max(\lambda_{M_i})$) computed for each OCN and time step of the retraction. The fraction of connected nodes is computed as the number of active pixels (i.e., belonging to the flowing fluvial network) at any retraction step, divided by the total number of pixels in the OCN. The difference with Figure 3a is that the variability inherent in the OCN structure is less apparent for the expanded network, as all OCNs are fully connected. The differences in heterogeneity of the networks become more apparent with the retraction of the network, as suggested by the sublinear spread in the fraction of connected pixels increasing with the expansion steps.

Figure 4 quantifies the reduction in metapopulation capacity due to decreasing effective contributing area in each pixel (i.e., the flowing stream length, and thus the available habitat via at-a-site scaling relations Rinaldo et al., 2020), emphasizing the role of dispersal. This highlights the controls ultimately imposed by the network structure on species survival. This echoes, and provides qualitative evidence for, previous empirical and theoretical results (Fagan, 2002; Hanski, 1999; Ma et al., 2020; Muneeppeerakul et al., 2008; Rinaldo et al., 2020). Specifically, Figure 4 shows the contribution of each pixel to the metapopulation capacity for each retraction step of the network.

Figure 5a provides the breakdown of the results for a single OCN realization. It shows where the focus species would survive when the network contracts for different threshold values. Figure 5b shows the fraction of connected pixels (with flow) versus the number of pixels where the species can survive ($\lambda_{M_i} > e/c$) compared to the number of connected pixels for the different contraction steps. Figure 5b further illustrates the detail of the variability obtained by replication by highlighting the fraction of viable pixels (%) plotted versus the fraction of pixels connected (%) computed in each pixel of one OCN for each retraction time step and different thresholds of e/c . White pixels are unchanneled sites (i.e., outside of the active river network). Red pixels are sites where survival of the focus species is warranted. This would mean that a species could have an occupation area bigger than the one due to dispersal by maintaining subpopulations outside of areas with flowing waters.

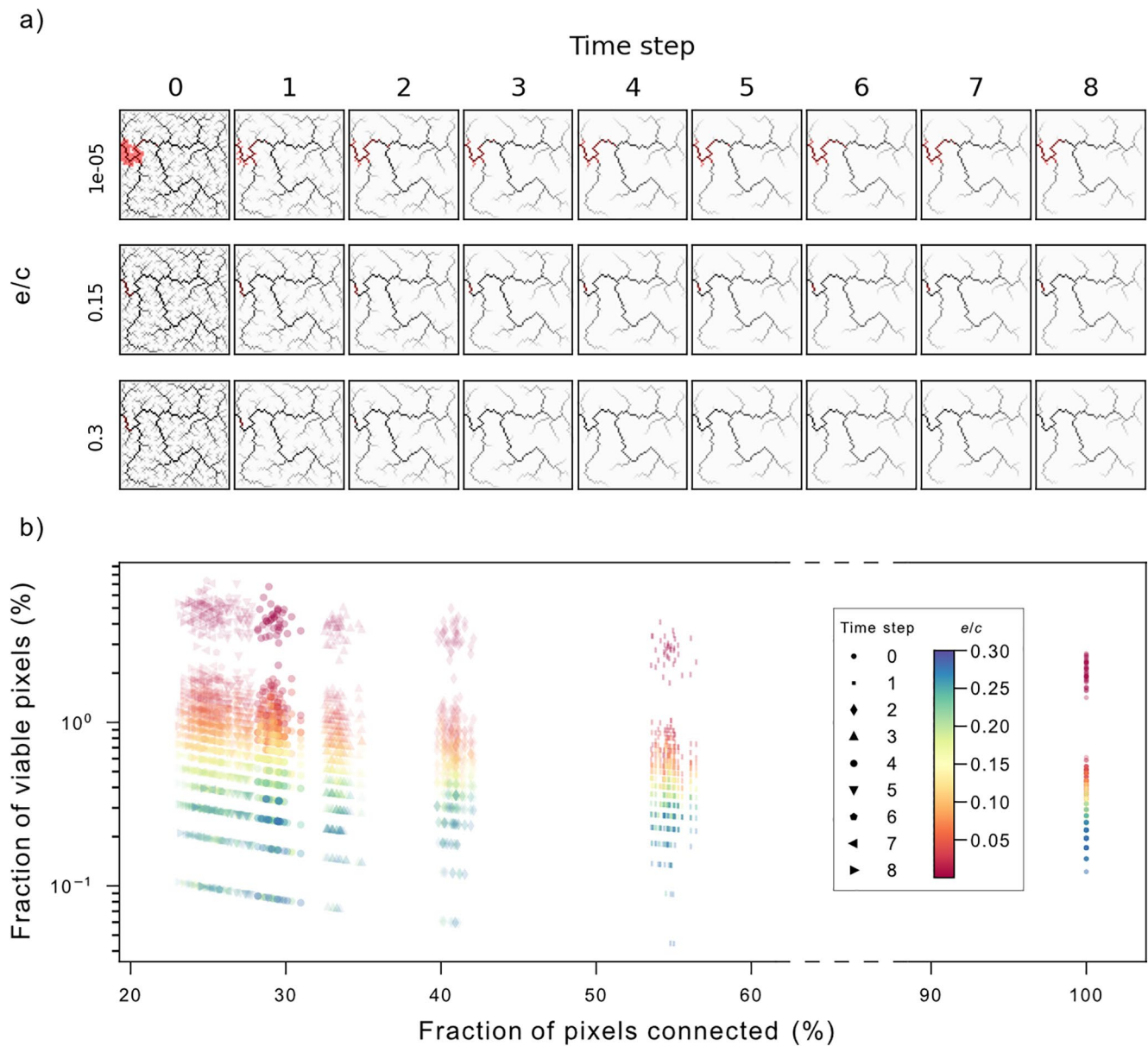


Figure 5. A geography of focus species survival and the range of variations obtained within single realizations: (a) Synoptic view of the fraction of connected pixels (i.e., belonging to the flowing fluvial network, gray) and the fraction of viable pixels (red) per OCN at different time steps t (shapes). The fraction of viable pixels is defined as follows: Number of pixels with contribution to the maximum value of $\lambda_{k,t}$ larger than the ratio e/c ($\lambda_{M_i} > e/c$) divided by the number of active pixels. (b) Breakdown of the fraction of viable pixels (%) plotted versus the fraction of pixels connected (%) computed in each pixel of one OCN for each retraction time step and different thresholds of e/c (y-axis). White pixels are unchanneled sites (i.e., outside of the active river network). Red pixels are sites where survival of the focus species is warranted. This would mean that a species could have an occupation area bigger than the one due to dispersal by maintaining subpopulations outside of areas with flowing waters. The colors code different e/c ratios.

4. Discussion

The notable scaling features of metapopulation capacity versus mean total contributing area at a point (Figure 3) seem to imply that the underlying the aggregation structure of OCNs—reflecting the recursive aggregation patterns found in nature for fluvial networks regardless of climate, vegetation, or exposed lithology—controls metapopulation survival, in particular toward the maximum expansion of the fluvial network. When compared with Figure 3a, these results provide a quantitative tool to quantify the influence of the dynamic drainage densities on metapopulation survival.

The empirical verification that the variation of the number of “patches” (i.e., pixels) in a network, and the variation in the total amount of habitat (seen as the total pooled area of active pixels) do not explain but a fraction of the actually occupied sites averaged in time (Hanski et al., 2015) supports the theoretical result highlighted in Figure 3. Metapopulation theory (Hanski & Ovaskainen, 2000) suggests that the equilibrium value of the occupancy of the i th site, say p_i , is a weighted average of patch occupancy where the weights describe the role of individual sites in the dynamics of the metapopulation. The equilibrium value p_i , the onset of persistence, is shown to be equal to

$$p_i = 1 - \frac{e/c}{\lambda_M}, \quad (7)$$

where λ_M is a suitable average, under the assumptions of the present model, of the metapopulation capacities $\lambda_{k,i}$ in Figure 3. The ratio e/c characterizes the focus species via the extinction and colonization rates (Supporting Information S1), emphasizing that the extinction threshold is a characteristic of the focus species, whereas the metapopulation capacity describes features of the connected network—the relative importance of dispersal rates and the relative distance among all patches is contained in the metapopulation capacity—being the maximum eigenvalue of the landscape matrix \mathbf{M} (Supporting Information S1).

By making standard assumptions about how the landscape structure affects extinction and colonization rates, Hanski et al. (2015) proposed that the equilibrium value p_i at site i is given by

$$p_i = 1 - \frac{e/c}{A_i^x y^Q S_i}, \quad (8)$$

where A_i , Q_i and S_i are respectively the area, quality, and connectivity of patch i , x , and y are parameters. In the same vein, our result would suggest that, should empirical validations support a power law relation between metapopulation capacity and the network diameter (the mean distance between any two sites of the flowing network) subsumed by the mean total contributing area, that is, $\lambda_M \sim \mathcal{K}\bar{L}^{0.6}$ (where \mathcal{K} is a proportionality constant that may be estimated from the data in Figure 3), we may propose for validation a relation of the type:

$$p_i = 1 - \frac{e/c}{\mathcal{K}\bar{L}^{0.6}}, \quad (9)$$

where λ_M is an ensemble time average of the metapopulation capacities of the replica OCNs. Such a relation could be validated by empirical studies if p_i would be measured accurately enough as the fraction of times in which patch i has been occupied. However, the conditions for persistence from the metapopulation theory (Supporting Information S1) deserve much scrutiny in the light of the number of simplifying assumptions made in this study (see below).

Figure 4 highlighted the contribution of each pixel to the metapopulation capacity for each retraction step of the network. It therefore quantifies the reduction in metapopulation capacity due to decreasing effective contributing area in each pixel, that is, flowing stream length and available habitat deduced from the local water volume via Leopold’s relations that is (Leopold et al., 1964; Rinaldo et al., 2020; Rodriguez-Iturbe & Rinaldo, 2001). This in turn underpins the influence of dispersal, and thus the control ultimately imposed by the network structure on species survival. This echoes, and provides scaling evidence for, previous empirical and theoretical evidence (Fagan, 2002; Hanski, 1999; Ma et al., 2020; Muneeppeerakul et al., 2008; Rinaldo et al., 2020).

The main implication of our results, in particular those in Figure 5a, concerns the general distributions of the sites allowing the focus species to overcome the extinction threshold. Specifically, the fraction of connected pixels with flowing waters where the species can survive (in turn, implying sufficient metapopulation capacity) compared to the number of connected pixels for the different contraction steps. The minimal influence exerted when the network retracts, and the increasing importance of dispersal otherwise is manifested (Figure 5).

The scaling property identified by the results in Figure 3 is a complex byproduct of local conditions, reflected in the habitat quality affecting the landscape matrix whose features determine the metapopulation

capacity as a spinoff of the aggregation structure of the river network. This is only possible owing to the consistent ecological substrate replication. Consistency is granted owing to a number of previous scaling studies on independent outcomes of OCNs showing to accuracy statistical features indistinguishable from real-world observations (Carraro et al., 2020; Rinaldo et al., 1999, 2014, 2020; Rodriguez-Iturbe & Rinaldo, 2001). This is a key strength of the present approach.

Self-similar and self-affine features of river networks postulate certain regularities exhibited by our results. In particular, the outlet of the OCN at retraction step 1 may be suitably moved upstream to obtain a subset of that OCN with a smaller diameter, say approximately equal to the diameter of the OCN at retraction step 2. This results in a smaller OCN, yet endowed with the same network properties of the OCN at step 2 (every subcatchment of an OCN is also a local minimum of total energy dissipation Rodriguez-Iturbe & Rinaldo, 2001). We might therefore find significant similarities between the metapopulation capacity of a retracting network and that of a static network observed at increasingly smaller spatial scales. In general, pixels with high contributing area show a relatively high contribution to metapopulation capacity, while pixels with very small area are prone to noise and may or may not contribute significantly to the metapopulation capacity.

Other features will need deeper scrutiny because they may be affected by the assumptions built in the present study. For example, within the contraction phase, the relative number of pixels suitable to the persistence of the focus species is suggested to generally increase, suggesting that the dispersal of the species outside of suitable areas to maintain the species' presence is increasing in importance when the network contracts. This echoes previous exact theoretical results on species' persistence in view of the dispersal of the focus species outside of suitable areas to maintain the species' presence (Mari et al., 2014b). This is suggested by the results shown in Figure 5a. While they may still be an artifact of our simplifying assumption, further inquiry is warranted, in particular directed at limits and validity of the scaling framework we have found, which in turn retains its intrinsic predictive power stemming from the universal characters of river network aggregation epitomized by the distribution of total contributing area at any point of a fluvial domain (Rinaldo et al., 2014; Rodriguez-Iturbe & Rinaldo, 2001). Moreover, the results in Figure 4 suggest that other scaling processes may be further investigated. In particular, one wonders about the meaning of the pseudo-collapse that may be obtained for every time step if one also rescales the contributing area (not shown). In analogy, Figure 5a also suggests that, as the active network contracts, a larger fraction of the active network contributes to the metapopulation capacity. In turn, this suggests that the variability in the area of suitable habitat is smaller than the variability of the active network, that is, habitat area bears a somewhat dampened sensitivity to network dynamics. This becomes evident by an analogous plot with the total number of viable pixels on the y -axis (not shown).

A note of caution is in order at this point. Computing the metapopulation capacity $\lambda_{k,t}$ of the k th OCN realization at step t of the cyclic flowing network configuration, as described above, implicitly assumes that the fluvial ecosystem is allowed enough relaxation time to attain approximately steady state between changes, and therefore that ecological processes operate faster than seasonal hydrological change dynamics. The driving process is roughly the monthly effective precipitation ($P - ET$; Durighetto et al., 2020). In dry climates the complete network shrinking can be observed in roughly 2.5 months (Senatore et al., 2021). This sets the time scale for dispersal to no more than 1–2 weeks.

The assumption of fast ecological process is hardly valid in general, in particular for several fish species in the light of observations related to time-varying lateral hydrologic connections in river-floodplain ecosystems. The immigration functions studied by Stoffels et al. (2016) underpin the limited number of species meeting the above limits and only appropriate for those species that exhibit the highest immigration rates for connections lasting less than 20 days. Dispersal magnitudes among floodplain waterbodies are not necessarily a reflection of the processes described here, nor of local species abundance. Rather, dispersal magnitudes depend on the focus species' behavioral and life-history traits (Stoffels et al., 2016), and this has consequences because many metapopulation models of animal movement within patchy environments assume that colonization rates are proportional to local abundance and that dispersal rates are a function of specific physiological, behavioral, and life-history traits of the focus species.

Therefore, the approximate steady state of the adaptation to each retraction/advancement step (or the much slower time scale of drainage density with respect to the dispersal ability of the focus species) is a significant weakness of our analysis. It remains to be seen whether the scaling properties identified in this manner are robust with respect to selective relaxations of the simplifying assumptions. On this, further research is ongoing.

For specific focus species whose life-history attributes violate such conditions, Floquet or Lyapunov theories would need to be employed (Mari et al., 2014a, 2014b, 2017; Rinaldo et al., 2020). In a few studies of this kind, differences in the overall assessment of species viability proved relatively small, however, especially when nonlocal controls, like contributing area at any point, are relevant (Mari et al., 2014b; Rinaldo et al., 2020). Therefore, some relevance is likely for the present theoretical assessment of the ecological impacts of time-varying connectivity and habitat as a consequence of dynamic drainage densities in the fluvial basin.

The metapopulation framework within dynamically fluctuating fluvial substrates for ecological interactions presented in this study is idealized and therefore aimed at purportedly general behavior. Obviously, it could be made more realistic. For example, the current formulation accounts for disparate time scales for the ecological and geomorphological dynamics. Adding seasonal variability where ecological dynamics have comparable time scales would demand a more elaborated mathematical treatment, possibly relying on Floquet (Klausmeier, 2008; Mari et al., 2014a) or Lyapunov (Ferrière & Gatto, 1995) approaches. Specifically, for specific focus species whose life-history attributes are fully defined, the assumptions underlying our quasi steady scheme may prove unsuitable, and Floquet or Lyapunov theories would need to be employed (Mari et al., 2014a, 2014b, 2017; Rinaldo et al., 2020). Differences in the overall assessment of species viability in many cases of interest prove relatively small, however (Mari et al., 2014b; Rinaldo et al., 2020). We thus stand by the interest in the current theoretical assessment of the ecological impacts of dynamic drainage densities in the fluvial basin.

From a hydrological perspective, the temporal evolution of dynamic networks could be much more complex than a simple, continuous retraction from the sources to the outlet, owing to the presence of seasonal climatic cycles superimposed to event-based variability of the active length (e.g., Durigetto et al., 2020), often leading to discontinuous flow patterns in space and time. Another aspect that will deserve future attention concerns demographic stochasticity that plays an important role in metapopulations dynamics close to the extinction threshold (Casagrandi & Gatto, 1999, 2006).

One must also note that the scenarios considered in this study are reasonable for most fluvial landscapes in runoff-producing areas (Rodríguez-Iturbe & Rinaldo, 2001), and in particular for those exposed to humid climates. However, other types of transient connectivity windows exist in nature for fluvial domains. For example, in dryland or spring-fed systems, retraction occurs toward the branch tips as the water flow becomes insufficient to sustain downstream flow (Zhou & Fagan, 2017). Interestingly, in that case spatial refugia prove opposite from those identifiable in the cases dealt with here. Similar issues arise when extinction risk in dynamic landscapes is exacerbated by refractory periods (Ellner & Fussmann, 2003) or autocorrelation in disturbance timing owing to the implied reduction of the amount of habitat available in the dynamic fluvial landscape (Zeigler & Fagan, 2014). To address a broader class of problems of transient windows for connectivity in fluvial systems, one should also consider to divert attention from river networks in runoff-generating areas (where a treelike dendritic drainage structure is inevitably selected for dynamic reasons Banavar et al., 2001) and look after looping distributary systems where connections between different sites are multiple. The inland Okavango Delta in Botswana comes to mind as an example of paramount importance for the dramatic extent of the seasonal variations of the flowing deltaic branches (Bauer et al., 2006). Ecological consequences are major. Clearly, these are interesting but rather different problems which this study does not address.

We also suggest that the metapopulation framework used here to derive species survival in dynamic river networks as their ecological substrate, its limitations notwithstanding, may be applied to study other ecological problems. One possible extension that naturally comes to mind concerns the persistence of a metapopulation of stream salamanders in a river network (Mari et al., 2014b). This is particularly relevant for the metapopulation model, because it must be comprising two life stages, the juvenile and adult stages,

endowed with different abilities to survive outside the permanently channeled portion of the river network, as a function of demographic and dispersal data. Specifically, the juvenile stage (indeed for a number of amphibian species) can move in unchanneled terrain equally well as in streams, whereas their larvae and adult stages are sessile. Juveniles' dispersal in streams is known to be biased toward the upstream sites (Mari et al., 2014b; Rinaldo et al., 2020), and the direct relevance to metapopulation persistence derives from the "cost of dispersal" (e.g., the fraction of individuals that may disperse outside their suitable habitat sensu Mari et al., 2014b). If this cost may be considered negligible, along stream as well as overland, the metapopulation is predicted to persist (strongly). However, at increasing costs of dispersal, the metapopulation will eventually violate the persistence threshold and thus be doomed to extinction, due to demographic shifts caused by habitat alterations induced by the seasonal regressions/transgressions of the flowing river (e.g., Botter & Durighetto, 2020; Rinaldo et al., 2020; van Meerveld et al., 2019). Interestingly, survival capabilities are known (Mari et al., 2014b) to peak at intermediate values of overland dispersal rates, echoing the intermediate dispersal principle of metapopulation ecology (Casagrandi & Gatto, 1999, 2006).

In general, metapopulation persistence can be established by studying the conditions under which the persistent equilibria become unstable (Rinaldo et al., 2020). The extension of the framework presented here to interacting functional groups should allow to study persistence in a broader context, open to many types of aquatic metacommunities possibly endowed with complex life cycles for example (Rinaldo et al., 2020), and affected by noise-induced phenomena (e.g., Ridolfi et al., 2011).

Finally, it is worth discussing why OCNs matter so much. Aggregation structures define the properties responsible for a network's overall connectivity and local habitat quality—jointly with life-history attributes of the focus species, the determinants of metapopulation survival. It is therefore necessary to study ensemble averages of fluvial structures draining a given terrain with coherent aggregations to sort out geomorphic inferences. To that end, one must remark that topological measures are unsuitable to compare network structures for they are lenient comparative tools. In fact, almost inevitably the topology of spanning trees is akin to statistics that reproduce those of real rivers even when aggregations are unsuitable. One conclusive example is Peano's network (Mandelbrot, 1982), a spanning tree whose exactly computed topologic measures are indistinguishable from those of real rivers (Marani et al., 1991; Rodriguez-Iturbe & Rinaldo, 2001) although its aggregation is exactly known to be radically different from empirical evidence (Marani et al., 1991). OCNs are synthetic constructions of stochastic spanning trees that reproduce systematically all aggregation and metric measures of real rivers over an assigned domain (Rinaldo et al., 1999) and are therefore suited to generate independent realizations of river network replicas for the scopes of this work.

5. Conclusion

The following conclusions are worth mentioning:

1. Ecologists are challenged to construct models of the biological consequences of environmental change, be it reflected in habitat loss or fragmentation or simply in temporal variations of features like connectivity or local site quality. This work investigates whether general rules exist in species viability in a river network when seasonal variations occur in its flowing extent, the subject of much recent scrutiny in the hydrological (but not ecological) literature.
2. Dynamic fluctuations of drainage density of fluvial networks in runoff-producing areas, reflected in seasonal contractions and expansions of the flowing river domain, affect a species' metapopulation dynamics owing to related, predictable changes on connectivity and local habitat size and suitability.
3. The general viability of a focus species is determined by the value of the maximum eigenvalue of a suitable landscape matrix which is functionally related to the dynamic drainage density under the simplifying assumptions of this study. Here, we have explored emerging properties of the ensemble of several replicas of OCNs statistically indistinguishable from real rivers. In this manner, a coherent statistical ensemble has been created.
4. We addressed the range of metapopulation capacities (a property of the landscape that relates to the probability of extinction of the focus metapopulation sensu Hanski) obtained for the statistical ensemble of substrates we have created. We found that the range of metapopulation capacities of a dynamically changing flowing river network is proportional to total contributing area at a point, whose properties—based on recursive aggregation structures found in nature—thus imply average ecological connectivity.

5. The theoretical approach employed here is not devoid of major assumptions. Whether the scaling properties found under the current set of simplifying assumptions will prove robust under progressive relaxation of the variety of simplifications adopted remains to be seen. On this further research is forthcoming.

Data Availability Statement

This is a theoretical study and no data availability statement is applicable. The model implementation can be found on <https://github.com/GieziJo/FluvialMetapopPersistence>.

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