Optimal Channel Networks accurately model ecologically-relevant geomorphological features of branching river networks

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River networks’ universal fractal structure not only defines their hydrology and connectivity, but also has profound biological consequences, especially regarding stability and persistence of organismal populations. While rivers’ scaling features are captured by Optimal Channel Networks, knowledge on adequate network topologies has hitherto been only partially transferred across geo- and biosciences. Consequently, ecologists have often studied riverine populations via random networks not respecting real rivers’ scaling character. Here we show that an alleged property of such random networks (branching probability) is a scale-dependent quantity that does not reflect any recognized metric of rivers’ fractal character, and hence cannot be a driver of ecological dynamics. Moreover, we show that random networks lead to biased estimates of population stability and persistence, while only Optimal Channel Networks yield estimates comparable to real rivers. We hence advocate Optimal Channel Networks as model landscapes for realistic and generalizable projections of eco-hydrological dynamics in riverine networks.
River networks are endowed with a ubiquitous fractal signature, that is, the similarity between the parts and the whole. The shape of river networks observed in Nature results from the interplay between chance (precipitation events, landslides and tectonic activity engendering local changes in landscape morphology) and necessity (the action of gravity and erosion driving network configurations towards optimal states). Indeed, the most probable river network configurations are those corresponding to a local minimum of energy dissipation. The fractal character of river networks is subsumed by Horton’s laws on bifurcation, length and area ratios, and by the power-law scaling of distributions of drainage areas and lengths. These distinguishing features of river networks are relevant from a hydrological and geomorphological perspective as they control the hydrological response of a basin, its hydraulic geometry attributes and its sediment transport rates.

Equally important, but hitherto often neglected, is the relevance of these river network properties from a biological perspective, and thus the adequate understanding of biological processes in river networks, such as biogeochemical cycling and the distribution of populations, species and pathogens. Understanding how the spatial structure of landscapes influences community and ecosystem dynamics is a classic theme in ecology. While some studies acknowledged the uncertainty thereof) irrespective of the shape of a given river network, which permits a proper assessment of ecological dynamics (and hence the upstream area spanning the river network), the first observational scale required is thus the pixel length \( l \) of the DEM, which defines the extent of a network node. A second scale is then needed to distinguish the portion of the drainage network effectively belonging to the channel network. The simplest but still widely used method defines channels as those pixels whose drainage area exceeds a threshold value \( A_T \). Hydrologically based criteria to determine the appropriate value for \( A_T \) exist; however, for the sake of simplicity, we here consider \( A_T \) as a free parameter.

BBTs and RBNs are random constructs, and as such they do not satisfy the optimality criterion of minimizing total energy expenditure, which is the fundamental physical process shaping fluvial landscapes. Furthermore, neither of these networks is a spanning tree, which is a key attribute of real fluvial landforms, in fact, in both BBTs and RBNs, the extent of the drained domain is not defined. As a result, the drainage area at an arbitrary network node cannot in principle be attributed, unless by using the number of upstream nodes as a proxy. This has practical implications from an ecological viewpoint because drainage area is the master variable controlling several attributes of a river, such as width, depth, discharge, or slope, which in turn impact habitat characteristics and the ecology of organisms therein.

In BBTs and RBNs, branching probability \( p \) has been defined as the probability that a network node is branching, i.e. connected to two upstream nodes. As such, the branching probability of a realized river network (be it a real river or a synthetic construct) could be evaluated as the ratio between the number of links \( N_L \) constituting a network and the total number of network nodes \( N \); if a unit distance between two adjacent nodes is assumed, the denominator equals the total network length. We note that the former definition of branching...
probability only holds in the context of the generation of a synthetic random network; it is in fact improper to refer to a “probability” when analyzing the properties of a realized river network. We clarify this aspect by introducing the concept of branching probability only holds in the context of generating a synthetic random network; it is in fact improper to refer to a “probability” when analyzing the properties of a realized river network. We clarify this aspect by introducing the concept of branching probability when analyzing the properties of a realized river network. We clarify this aspect by introducing the concept of branching probability.
To this regard, we note that the networks analyzed by statistical inevitability of such laws for any network argued by analysis. normalized branching ratios (i.e., for each BBTs of comparable size (see Methods).

Fig. 3 Values of branching ratio as a function of threshold area $A_T$ for the 50 real river networks analyzed in this study. a Natural values of $p_r$ in logarithmic scale. b z-normalized branching ratios (i.e., for each $A_T$ value, values of $p_r$ are normalized so that they have null mean and unit standard deviation), which better shows how rivers rank differently in terms of $p_r$ for different observation scales (i.e., $A_T$). Lines connect dots relative to the same river. For visual purposes, rivers that rank first, second, second-to-last or last in at least one of the $A_T$ groups are displayed in colors; the other rivers are displayed in grey.

Topological and scaling of river networks and random analogues. To verify the topological (i.e., Horton’s laws on bifurcation and length ratios) and scaling (i.e., probability distribution of drainage areas) relationships of the different network types, we extracted from DEMs 50 real river networks encompassing a wide range of drainage areas (Fig. 4), and we generated 50 OCNs, 50 RBNs and 50 BBTs of comparable size (see Methods).

While the power-law scaling of areas in OCNs (Fig. 5c) has an exponent $\beta = 0.45$ that closely resembles the one found for the real rivers ($\beta = 0.46$) and within the typically observed range $0.40 \pm 0.02$, drainage areas of RBNs scale as a power law with an exponent $\beta = 0.51$, which departs from the observed range. Conversely, BBTs do not show any power-law scaling of areas. Scaling exponents of drainage areas fitted separately for each real river network yielded values in the range $0.36 \pm 0.57$ (Supplementary Table 1). In particular, we observed that these values tend to the expected range $\beta = 0.43 \pm 0.02$ for increasing values of $A$, expressed in number of pixels (Supplementary Fig. 3), hence implying that highly resolved catchments are required in order to properly estimate $\beta$. Interestingly, the observed values of Horton ratios and scaling exponent $\beta$ for RBNs are compatible with the values $R_B = 4$, $R_I = 2$, $\beta = 0.5$ predicted for Shreve’s random topology model $^{13,60,62}$, which is actually equivalent to a RBN with infinite links.

Ecological implications. We compared the different network types via two metrics that express the ecological value of a landscape for a metapopulation: the coefficient of variation of a metapopulation $CV_M$ and the metapopulation capacity $\lambda_M$. The coefficient of variation of a metapopulation $^{63}$ is a measure of metapopulation stability (a metapopulation being more stable the lower $CV_M$ is), while the metapopulation capacity $^{42,64}$ expresses the potential for a metapopulation to persist in the long run (persistence being more likely the higher $\lambda_M$ is). Both measures are among the most universal metrics describing dynamics of spatially fragmented populations $^{24,40}$.

In order to assess the impact of the two landscape features mostly affecting metapopulation dynamics, i.e. spatial connectivity and spatial distribution of habitat patches, we calculated these metrics for the four...
network types under two different scenarios: uniform \((CV_{MU}, \lambda_{MU})\) and non-uniform \((CV_{M,H}, \lambda_{M,H})\) spatial distribution of habitat patch sizes. In the first scenario, \(CV_{MU}\) and \(\lambda_{MU}\) assess stability and persistence (respectively) of a metapopulation solely based on pairwise distances between network nodes; in the second scenario, \(CV_{M,H}\) and \(\lambda_{M,H}\) depend on the interplay between pairwise distances and spatially heterogeneous habitat availability (namely, downstream nodes being larger than upstream ones).

We found that the values of \(CV_{M}\) (be it derived with uniform \((CV_{MU})\) or nonuniform \((CV_{M,H}, \lambda_{M,H})\) distributions of patch sizes) obtained for OCNs match strikingly well those of real rivers (Fig. 6). These \(CV_{M}\) values are consistently lower than those found for RBNs, while values of \(CV_{M}\) for BBTs are even higher. Notably, this result holds for different values of \(A_T\) (and hence different \(p_i\) values) at which real rivers and OCNs are extracted (Fig. 6a–c; g–i), and for values of mean dispersal distance \(\alpha\) (see Methods) spanning multiple orders of magnitude (Supplementary Figs. 4–7).

For a constant \(\alpha\) value, the \(CV_M\) of real rivers, OCNs and RBNs decreases as the resolution at which the network is extracted increases (i.e., \(A_T\) decreases; see Fig. 6 and Supplementary Figs. 4–7). This is expected\(^{63}\), since a decrease in \(A_T\) corresponds to an increase in \(N\) (Fig. 2a), leading to a decrease in \(CV_M\). Indeed, a larger ecosystem, constituted of more patches, has the potential to include a larger (and more diverse) number of subpopulations, which increases stability at a metapopulation level through statistical averaging—a phenomenon widely known as the portfolio effect\(^{65}\). We also found that BBT networks do not generally follow the above-described pattern of decreasing \(CV_M\) with increasing \(N\); rather, the \(CV_M\) of BBTs increases with \(N\) when the mean dispersal distance \(\alpha\) is set to intermediate to high values (Fig. 6 and Supplementary Figs. 5–7), and only when \(\alpha\) is very low (e.g., \(\alpha = 10^{-1}\) as in Supplementary Fig. 4) and a uniform patch-size distribution is assumed does \(CV_{MU}\) follow the expected decreasing trend with increasing \(N\).
However, we need to warn against the conclusion that river networks with higher values of \( p_r \) (and hence lower \( A_T \), see Fig. 2b) are inherently associated with higher metapopulation stability. Indeed, our result was obtained by changing the scale at which we observed the same river networks, and not by increasing the river networks’ size. If the number of network nodes (and, consequently, the branching ratio \( p_r \)) is determined by the scale at which the landscape is observed, one cannot directly assume that any of such nodes is a node (or patch) in the ecological sense, i.e. the geographical span of a local population: the extent of such patches should be determined based on the mobility characteristics of the focus species, and should be independent of the scale at which the river network is observed. In contrast, we note that, if different river networks spanning different catchment areas (say, in km²) are compared, all of them extracted from the same DEM (same \( l \) and same \( A_T \) in km²), then the larger river network will appear more branching (i.e., have larger \( p_r \)). Indeed, by selecting catchments with larger \( A_T \) (in km²) for fixed \( l \) and \( A_T \) (in km²), one moves towards the top-left corner of Fig. 2a, b (i.e., perpendicular to the level curves \( A_T/A \)). The apparent higher “branchiness” of the river network with larger \( A_T \) will result in lower values of \( CV_M \); however, the higher metapopulation stability of the larger network will not be due to its (alleged) inherent more branching character, but only dictated by its larger habitat availability.

We observed that metapopulation capacity \( \lambda_M \) values of OCNs (be it evaluated under uniform (\( \lambda_M, U \)) or non-uniform (\( \lambda_M, H \)) patch-size distribution assumption) are the closest to those of real rivers, while RBNs (and even more so BBTs) generally overestimate \( \lambda_M \) with respect to real rivers and OCNs (Fig. 6d–f; j–l). This result holds irrespective of the choice of \( A_T \) and for intermediate to high values of \( \alpha \) (Supplementary Figs. 5–7). When

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**Fig. 6** Comparison of values of metapopulation metrics across river network types and observational scales (\( A_T \)). a–c \( CV_M, U \). d–f \( \lambda_M, U \). g–i \( CV_M, H \). j–l \( \lambda_M, H \). Boxplot elements are as follows: center line, median; notches, \( \pm 1.58 \cdot \text{IQR}/\sqrt{\text{IQR}} \), where IQR is the interquartile range; box limits, upper and lower quartiles; whiskers, extending up to the most extreme data points that are within \( \pm 1.5 \cdot \text{IQR} \); circles, outliers. Metapopulation metric values were obtained by setting \( \alpha = 100 \). Note that in Eq. (1), given \( A = 40,000 \), \( A_T = 20 \) results in \( E[N] \approx 4574, E[p_r] \approx 0.228 \); \( A_T = 100 \) yields \( E[N] \approx 2231, E[p_r] \approx 0.098 \); \( A_T = 500 \) results in \( E[N] \approx 1088, E[p_r] \approx 0.042 \).
the mean dispersal distance is instead set to very low values ($\alpha = 10 \text{ km}$ — Supplementary Fig. 4) and the river network is extracted at a high resolution (i.e., low $A_T$), the metapopulation capacity of OCNs under assumption of uniform patch-size distribution ($\lambda_{M,U}$) is underestimated with respect to that of real rivers. A likely explanation for this apparent mismatch is that, for low values of $A_T$, the number of nodes $N$ tends to be somewhat higher for the extracted river networks used in this analysis than for OCNs (Supplementary Fig. 8), and the effect of the different dimensionality of real rivers and OCNs in the metapopulation capacity estimation tends to be more evident as the mean dispersal distance decreases. Interestingly, such mismatch is absent when a non-uniform patch size distribution is assumed, as $\lambda_{M,H}$ values for OCNs match those for real rivers regardless of the mean dispersal distance value and the river network resolution (Fig. 6; Supplementary Figs. 4–7).

The OCN construct encapsulates both random and deterministic processes, the former related to the stochastic nature of the OCN generation algorithm, and the latter pertaining to the minimization of total energy expenditure that characterizes OCN configurations. As such, OCNs reproduce the interplay of differences in distance matrices and patch size across network types (Supplementary Fig. 9a–c). Our analysis shows that the connectivity structure of these random networks (subsumed by the matrix of pairwise distances) is too compact with respect to that of real rivers, which leads to an overestimation of the role of dispersal in increasing the ability of a metapopulation to persist in the long run, but also an increased likelihood of synchrony among the different local populations, which results in higher instability.

Comparison of patch size distributions among the network types expressed in terms of $\text{CV}_{M,U}$ (i.e., the portion of $\text{CV}_{M,H}$ that uniquely depends on the distribution of patch sizes and not on pairwise distances) shows that, while for coarsely resolved networks ($A_T = 500$) no clear differences in $\text{CV}_{M,U}$ emerged, for highly resolved networks ($A_T = 20$) BBTs heavily underestimate the $\text{CV}_{M,U}$ of real rivers and OCNs, while RBNs slightly overestimate it (Supplementary Fig. 9d–f). As a result of the interplay of differences in distance matrices and patch size distributions, BBTs and (to a lesser extent) RBNs tend to underestimate pairwise distances with respect to real rivers and OCNs, as documented by a comparison of mean pairwise distances across network types (Supplementary Fig. 9a–c). Our analysis shows that the connectivity structure of these random networks (subsumed by the matrix of pairwise distances) is too compact with respect to that of real rivers, which leads to an overestimation of the role of dispersal in increasing the ability of a metapopulation to persist in the long run, but also an increased likelihood of synchrony among the different local populations, which results in higher instability.

Methods

**Generation of synthetic river networks.** We generated 50 OCNs via the R-package OCNet \(^{46}\) on lattices of size 200 x 200 with a random positioning of the outlet pixel. All OCNs hence spanned an area $A = 40,000$ pixels. Each of the 50 OCNs was extracted by imposing a threshold area $A_T$ equal to 20, 100 and 500 pixels. The threshold area value $A_T = 1$ pixel was also applied in order to assess the scaling of drainage areas shown in Fig. 5c. For each OCN and each $A_T$ value, we computed the respective number of nodes $N$ and branching ratio $p_l = N_l/N$, and generated a corresponding random branching network (RBN) and balanced binary tree (BBT). Following ref. \(^{45}\), BBNs were generated by randomly sampling network links with length following a geometric distribution with mean $1/b_0$, and such that the total network length be equal to $N$. The geometric distribution is the discrete equivalent of the exponential distribution, which approximates well the distribution of link lengths \(^{44}\). The network was then randomly assembled by imposing each link to have an outdegree (see Supplementary Note 1) of 1 (except possibly one link–the most downstream one) and an indegree (see Supplementary Note 1) of either 0 (source links) or 2 (links downstream of a confluence); moreover the network configuration had to be loopless. Details are provided in the Supplementary Methods.

BBTs were generated following ref. \(^{45}\): the network was initialized with one node (the root), which was attributed to order 1. For all nodes thus generated to a given order $i$, one or two upstream nodes were randomly assigned, the latter event occurring with probability $p$; all nodes thus generated belonged to order $i + 1$. The
Extraction of real river networks. We extracted 50 real river networks from open-source digital elevation models retrieved via the R-package *elevatr*. We selected catchments from different geographical areas: 25 in Europe and 25 in North America (Fig. 4). To guarantee a high similarity between extracted and actual river networks, catchments were essentially selected from regions with marked elevation gradients (i.e., the Alps, the North American Cordillera and the Appalachian Mountains). We chose catchments spanning a wide range (367 km² - 57,949 km²) of drained areas (Supplementary Fig. 10a). To enable comparison between the extracted real rivers and the synthetic networks, we limited our search to catchments made up of 40,000 pixels ± 20% (Supplementary Fig. 10b). To do so, we used DEMs of different resolutions, by appropriately tuning the zoom option in the function *get_elev raster* of *elevatr*. Note that the value in meters of the pixel size l varies both as a function of the zoom level and of latitude (Supplementary Table 2). Flow directions were derived via the D8 algorithm in a TauDEM routine. The networks were finally extracted by imposing A2 = 20, 100 or 500 pixels.

Relationships between the networks’ parameters. Ref. 69 evaluated how N and Nl were scale as a function of the two observational scales A2 and A for four large OCNs. By rearranging those relationships, the expected values of N and p, for OCNs (and, in turn, real rivers) read, respectively:

\[
E[N] = 0.435 A^{0.464}\gamma; \quad E[p_{A}] = 1.531 A^{0.0522} A^{-0.0522}
\]

where A, A2 and N are expressed in the number of pixels, and p, is dimensionless.

Note that the approximately equal sign in Eq. (1) highlights the fact that these relationships, being derived from a limited number of OCNs without exploring the full range of parameters involved in the OCN generation,68 are to be intended as a first approximation. A graphical representation of these expressions is provided in Fig. 2a, b. Note that Eqs. (1) are valid as long as A2 lies in the range of drainage area values for which the power-law scaling of the drainage area is verified68; for example, in the limiting case A2 = 1, every pixel of the drainage domain belongs to the channel network, hence A = N and p, approaches 1.

Coefficient of variation of a metapopulation. In the general case, the coefficient of variation of a metapopulation made up of N nodes read:

\[
CV_{M} = \sqrt{\frac{\sum_{i=1}^{N} \sigma_{i}^{2} + \sum_{i=1}^{N} \sum_{j \neq i} \sigma_{ij} C_{ij}}{\sum_{i=1}^{N} \mu_{i}}}
\]

where \(\mu_{i}\) and \(\sigma_{i}\) are the mean and standard deviation of the local population abundance at node i, respectively, while \(C_{ij}\) is the covariance between nodes i and j. We hypothesized that both mean and standard deviation of local population abundance scales linearly with the local habitat size \(H_{i}\), \(\mu_{i} = \mu H_{i}\), \(\sigma_{i} = \sigma H_{i}\) without any loss of generality, we further assumed \(\sigma = \mu\). The covariance \(C_{ij}\) was expressed via an exponential kernel: \(C_{ij} = \sigma_{i} \sigma_{j} \exp(-d_{ij}/a)\), where \(d_{ij}\) is the along-stream distance between i and j, and \(a\) a parameter expressing the distance dependence of local population covariance. Note that \(d_{ij} > 0\) also for pairs of nodes that are not flow-connected, as in a so-called tail-down exponential covariance model80, which has been used to describe the spatial covariance of any variable measured in streams, including ecological population counts80. Note also that dependence of population synchrony along downstream distance has been widely observed in long-term fish population time series in European basins80. In the case of uniform patch size distribution, \(H_{i} = \text{H}\) does not depend on i, and Eq. (2) becomes:

\[
CV_{M} = \sqrt{\frac{1 + \frac{\sum_{i=1}^{N} \sum_{j \neq i} \exp(-d_{ij}/a)}{N}}{N}}
\]

In the non-uniform patch-size distribution scenario, we assumed that local habitat size \(H_{i}\) is proportional to the river width, which is known to scale along a river as the square root of drainage area55. Given that drainage areas are not defined in BFTs and RBNs, to enable a fair comparison between the different network types we used the number \(U_{i}\) of nodes upstream of a node i as a proxy for drainage area; moreover, we normalized the local habitat size so that each network has a regional habitat availability of 1:

\[
H_{i} = U_{i}^{0.5} \text{Drains}
\]

In this case, Eq. (2) becomes:

\[
CV_{M} = \sqrt{\frac{\sum_{i=1}^{N} H_{i}^{2} + \sum_{i=1}^{N} \sum_{j \neq i} \mu_{i} H_{i} H_{j} \exp(-d_{ij}/a)}}{N}
\]

To assess the sensitivity of our results to variation of the mean dispersal length, we evaluated \(CV_{M,\text{LL}}\) and \(CV_{M,\text{HL}}\) for a equal to 10, 20, 100, 200 and 1000 pixel sizes l. Moreover, we evaluated \(CV_{M,\text{LL}}\) in the limit \(a \rightarrow 0\), which is equal to:

\[
CV_{M} = \sqrt{\sum_{i=1}^{N} H_{i}^{2}},\text{ as a measure of the role of patch size distribution on metapopulation stability.}
\]

Metapopulation capacity. We evaluated the metapopulation capacity64 as the maximum eigenvalue of a matrix M of order N with entries \(m_{ij} = H_{i} H_{j} \exp(-d_{ij}/a)\) if \(i \neq j\) and \(m_{ij} = 0\). In particular, in the uniform patch-size distribution scenario, \(\lambda_{M,\text{LL}}\) was evaluated by assuming \(H_{i} = 1\); in the non-uniform scenario, \(\lambda_{M,\text{HL}}\) was calculated with \(H_{i}\) given by Eq. (4). As stated previously, a represents the mean dispersal distance (assuming an exponential kernel for the dispersal process). To assess the sensitivity of our results to variation of such parameter, we evaluated \(\lambda_{M,\text{LL}}\) and \(\lambda_{M,\text{HL}}\) for a equal to 10, 20, 100, 200 and 1000 pixel sizes l.

Data availability

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

Code availability

R scripts reproducing the results shown in this manuscript are available on Zenodo.71

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Author contributions

L.C. ensured funding, conceived the presented ideas, developed the methods, performed analyses and computations, and led the writing of the manuscript. F.A. ensured funding, and contributed to the conceptualization and to the writing of the manuscript.

Competing interests

The authors declare no competing interests.
