LETTER

Synchronisation and stability in river metapopulation networks

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Abstract

Spatial structure in landscapes impacts population stability. Two linked components of stability have large consequences for persistence: first, statistical stability as the lack of temporal fluctuations; second, synchronisation as an aspect of dynamic stability, which erodes metapopulation rescue effects. Here, we determine the influence of river network structure on the stability of riverine metapopulations. We introduce an approach that converts river networks to metapopulation networks, and analytically show how fluctuation magnitude is influenced by interaction structure. We show that river metapopulation complexity (in terms of branching prevalence) has nonlinear dampening effects on population fluctuations, and can also buffer against synchronisation. We conclude by showing that river transects generally increase synchronisation, while the spatial scale of interaction has nonlinear effects on synchronised dynamics. Our results indicate that this dual stability – conferred by fluctuation and synchronisation dampening – emerges from interaction structure in rivers, and this may strongly influence the persistence of river metapopulations.

Keywords

Fluctuations, metapopulations, river networks, stability, synchronisation.

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INTRODUCTION

Stability is a concept central to ecology, but is subject to multiple interpretations and meanings (May 1973; Doak *et al.* 1998; Ives & Carpenter 2007). In empirical studies of population dynamics, stability is often used to describe how population sizes fluctuate over time. This can be measured with statistical approaches such as the coefficient of variation of a population trajectory (Doak *et al.* 1998; Moore *et al.* 2010; Schindler *et al.* 2010), or the spectral properties of time series (Rogers *et al.* 2013). Here and hereafter, we collectively refer to these conceptual approaches as measures of statistical stability. In contrast, theoretical studies generally employ a dynamic-systems definition of stability, which concerns whether a population trajectory is robust to perturbations (May 1973). This can be assessed by measuring the rate and direction of population trajectories after a pulse or press perturbation (Ives & Carpenter 2007) or by determining the general conditions promoting or preventing dynamic stability (Gross & Feudel 2004; Yeakel *et al.* 2011; Allesina & Tang 2012). Possible trajectories range from simple fixed points, where the population size remains constant over time, to limit cycles describing periodic oscillations, or chaotic attractors displaying complex oscillatory behaviours. We collectively refer to these dynamic-systems concepts as measures of asymptotic stability. Although we reference these conceptual frameworks separately, many seemingly disconnected definitions of stability are strongly correlated (Donohue *et al.* 2013).

Both statistical and asymptotic measures of stability are expected to be in general agreement in predicting population persistence. For example, a population that is both statistically stable (lower magnitude of fluctuations), as well as asymptotically stable (such that a population trajectory relaxes around a steady state after a perturbation) is expected to have a greater probability of persistence over time (Mangel 2006). However, in the case of non-steady-state conditions, like limit cycles or chaotic attractors, the two conceptual frameworks of stability may diverge. For example, a population trajectory that relaxes to a limit cycle with a large amplitude is asymptotically stable, but statistically unstable. Moreover, when multiple populations interact as a metapopulation, synchronisation of population trajectories can result from the convergence of populations to a coherent state (Earn *et al.* 2000). Metapopulation synchronisation is of particular interest because increased synchrony reduces the potential for neighbouring populations to rescue those nearing extinction, decreasing the probability of persistence (Heino *et al.* 1997; Holland & Hastings 2008; Moore *et al.* 2010).

Persistence is determined in part by the patterns of interactions among species within a community, or populations within a metapopulation, and different interaction structures impact persistence (Earn *et al.* 2000; Stouffer & Bascompte 2011). The importance of structure has long been recognised for food webs (Pascual & Dunne 2006), and often has large effects on the dynamics of systems with strong spatial constraints (Earn *et al.* 2000; Cuddington & Yodzis 2002; Fortuna *et al.* 2008). For example, Hanski *et al.* (1994) showed that the structure of interactions in butterfly populations has large consequences on the extinction and colonisation rates of different habitat patches. However, to what extent interaction structures

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contribute to the statistical or asymptotic stability of metapopulations is not well understood, and this is anticipated to be particularly important for populations constrained to river watersheds (Erös *et al.* 2012; Peterson *et al.* 2013).

Interactions in rivers are spatially constrained, limited by the geological forces that determine river network structure (Rodriguez-Iturbe *et al.* 1994; Rodriguez-Iturbe & Rinaldo 1997; Devauchelle *et al.* 2012), and these constraints alter population and community dynamics (Brown *et al.* 2011). For example, river network structure influences fragmentation dynamics and by extension the extinction risk of aquatic populations (Fagan 2002; Grant 2011), and impacts community diversity (Muneepeerakul *et al.* 2008; Lynch *et al.* 2011; Carrara *et al.* 2012). The structure of river metapopulations is unique compared to terrestrial systems: interactions between river populations are often asymmetrically influenced by those upstream due to directional water flow, while dendritic river structure limits transecting interactions across river branches (Grant *et al.* 2007; Erös *et al.* 2012). These watershed properties may strongly influence the statistical or asymptotic stability of river metapopulations. Whether and to what extent the structure of river metapopulation networks promotes or inhibits both synchrony and the magnitude of population fluctuations is thus of key importance for predicting extinction risks of river populations.

Here, we determine the influence of river network structure on metapopulation stability. We first introduce a method by which complex river systems are quantified as interaction networks. We then determine analytically to what extent population-level fluctuations may be expected to vary with the statistical properties of such networks. Dynamic processes of a metapopulation can be described by a series of coupled differential equations, and we show how the specialised structure of river metapopulations affects synchronisation. Our results suggest that the complexity of river metapopulation networks – in terms of the prevalence of branching subpopulations – has large, nonlinear dampening effects on fluctuations due to the integration of asynchronous population trajectories. Moreover, we show that increased branching complexity is expected to buffer against synchronisation compared to same-sized terrestrial metapopulations. We then explore whether deviations in metapopulation structure – in the form of river transects – impact synchronisation. Finally, the formalisation of spatial interaction networks is strongly dependent on spatial scaling, which is expected to vary across organisms (Erös *et al.* 2012; Grünbaum 2012). We show that our predictions of synchronisation in river networks change as a function of spatial scaling, and we conclude by discussing the potential impact that different spatial scales have on river metapopulation dynamics.

MATERIAL AND METHODS

River metapopulation network structure

River metapopulations can be depicted as branching networks (Grant *et al.* 2007; Grant 2011), where the root node corresponds to the confluence $\mathcal{C}$, and the terminal upstream nodes represent tributaries $\mathcal{T}$. In this case, nodes represent populations inhabiting *sections* of an idealised river discretised by a scale length ℓ_s, including either non-branching or branching river sections (Fig. 1). Thus, links provide structural information governing the connectance of nodes, and population processes occur exclusively within nodes, which is conceptually similar to the network description of food webs, where dynamics are constrained to species (nodes), but directed by species interactions (links). Because nodes represent river segments, they can include more than one branch (similar to the *on-network* statistical approach explored by Peterson *et al.* 2013), are not restricted to a simple bifurcation scheme where each node is linked to two upriver nodes, and thus share structural similarities with Bethe lattices (Bethe 1935). By incorporating the discretisation of space as a function of the scale length ℓ_s, we enable detailed analysis of population dynamics as a function of the organismal integration window. The organismal integration window is the spatial scale bounding local population dynamics, and is strongly dependent on the organism of interest, and may have a large influence on metapopulation dynamics (cf. Heino *et al.* 1997). Because we are quantifying the spatial network of population connections, our river network abstraction includes all linkages and is not restricted to linkages of equal size similar to that described by the Horton-Strahler stream order system.

We define three statistical properties of river metapopulation networks: (1) the maximal network order – or radius – of the river Ω, which is the river distance (in numbers of nodes) from the tributary $\mathcal{T}$ to the confluence $\mathcal{C}$, where the confluence has a value of 1. We use the lowercase ω to identify the network 'order of observation' (equivalent to shells in Bethe lattices), which identifies how far from the confluence an observation is made. Accordingly, an observation at a tributary node is given by $\omega = \Omega$, while an observation at the confluence is $\omega = 1$; (2) the probability that a node includes a branching (p) or a non-branching river section $(1 - p)$; (3) the number of river branches per river section κ, where $\kappa \geq 2$ (see Table 1).

Thus, the expected number of nodes for a river metapopulation with radius Ω is

$$\mathrm{E}\{N\} = \sum_{\omega=1}^{\Omega} [p \times \kappa + (1 - p) \times 1]^{\omega-1}, \tag{1}$$

which can be expressed as

$$\mathrm{E}\{N\} = \begin{cases} \dfrac{(p\kappa - p + 1)^{\Omega} - 1}{p\kappa - p} & \text{for } 0 < p \leq 1 \\ \Omega & \text{for } p = 0. \end{cases} \tag{2}$$

Additional complexity can be introduced by treating the branch number κ as a random variable K, such that the probability that $K = \kappa$ varies according to a truncated Poisson distribution where we consider branches ≥ 2 with a mean value of λ, and

$$\mathrm{E}\{N\}_{\mathrm{RV}} = \begin{cases} \dfrac{\Psi^{\Omega} - 1}{\Psi - 1}, \text{ where } \Psi = \dfrac{p\lambda(1 - \mathrm{e}^{-\lambda})}{1 - Q} - p + 1 & \text{for } 0 < p < 1, \\ \Omega & \text{for } p = 0, \end{cases} \tag{3}$$

where the expected value and variance of the number of branches is $\mathrm{E}\{K\} = \mathrm{Var}\{K\} = \lambda$ (see Appendix S1 for the derivation). The function Q is the regularised incomplete
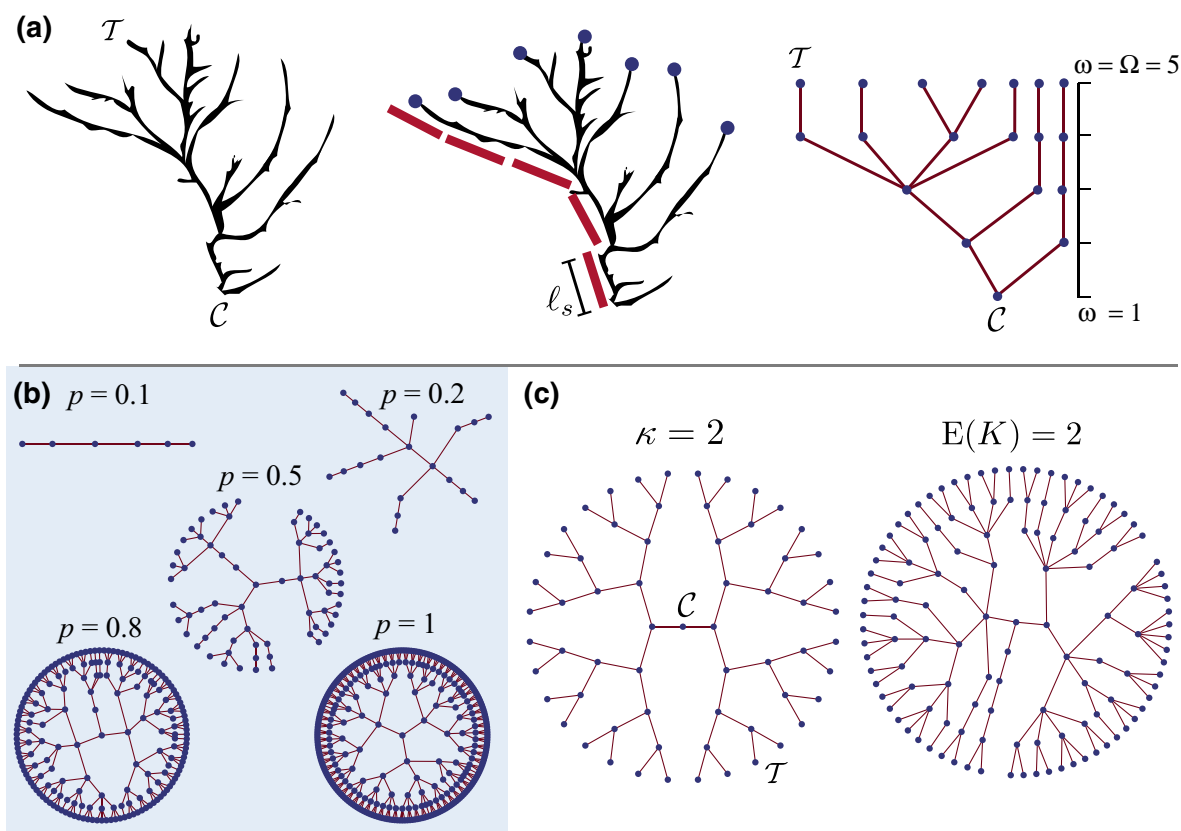
Figure 1. (a) A general framework for constructing river metapopulation networks from a watershed as a function of the scale length ℓ_s, where the tributaries and confluence are identified by $\mathcal{T}$ and $\mathcal{C}$ respectively. (b) Examples of river metapopulations with a branch number $\kappa = 3$ and with different branching probabilities p. (c) Examples of river metapopulations where $p = 1$, and where κ takes a single value or serves as a random variable. River metapopulation networks are visualised as converging on the centre of a circle; this radial visualisation simply helps display river complexity.

Table 1. Model parameters and variables used to describe and predict the statistical and asymptotic stability of river metapopulation networks

Parameter	Interpretation	Possible values or definition
p	Probability of branching	$0 \leq p \leq 1$
κ	Branch number	≥ 2
ω	Order of observation	$0 < \omega \leq \Omega$
Ω	Network radius	>1
N	Number of nodes	≥ 1
ℓ_s	Scale length	>0
CV	Coefficient of variation	≥ 0
n	Number of subpopulations	≥ 1
r	Correlation coefficient	$-(n-1)^{-1} \leq r \leq 1$
μ	Mean subpopulation size	≥ 0
σ	SD of subpopulation size	≥ 0
Ψ	Expected number of inflowing nodes	>1
$\Phi(t)$	Metapopulation trajectory	$\Phi = \bigcup_{i=1}^{N} \phi_i$
$\phi_i(t)$	Population trajectory at node i	
F	Internal dynamics function	
H	Interaction dynamics function	
ρ	Interaction strength	
$\mathbf{A}$	Network adjacency matrix	$A_{(i \text{ linked to } j)}=1$; 0 o.w.
$\mathbf{D}$	Network degree diagonal matrix	$D_{i=j} > 0$; 0 o.w.
$\mathbf{L}$	Laplacian matrix	$\mathbf{L}=\mathbf{D}-\mathbf{A}$
Λ_i	Laplacian eigenvalues	≥ 0
ε_t	Transect sensitivity	≥ 0

gamma function, simplified as $e^{-\lambda}(1 + \lambda)$, and normalises the probability distribution between 2 and ∞.

Statistical stability in river metapopulation networks

The interactions of aquatic populations in a river system are constrained by river network structure. These spatial constraints direct how changes in a population on node i – defined by the trajectory $\phi_i(t)$ – impacts connected populations, and may also influence the trajectory of the metapopulation, $\Phi(t)$ (where $\Phi = \bigcup_{i=1}^{N} \phi_i$). To determine the effect of river structure on the magnitude of fluctuating populations, we use the analytical description for the coefficient of variation (CV $= \sigma/\mu$; where μ is the mean size of a population and σ is its standard deviation) for an assembly of populations with equal mean abundances and standard deviations, such that $\phi_i(t)$ are statistically similar for all i (Doak et al. 1998). As the number of populations in an aggregate increases, the CV for the aggregate decreases if the variance (σ^2) scales to the square of the mean and populations are not perfectly correlated, such that the relative sizes of fluctuations of the aggregate decrease via statistical averaging (Doak et al. 1998), also referred to as the portfolio effect.

Upstream populations in rivers are expected to have asymmetric influence on those downstream. As an extreme

example we consider downstream population dynamics to be a function of merging upstream dynamics. In river metapopulation networks with high branching probabilities ($p \gg 0$), the number of upstream nodes increases nonlinearly with observations from the tributary to the confluence (decreasing order of observation, ω). The confluence population is thus impacted by all upstream populations, whereas tributary populations are independent. Doak *et al.* (1998) showed that the coefficient of variation for a community aggregate (CV_a) composed of n subpopulations with equivalent CVs (CV_p), and correlated as r (where r is the Pearson correlation coefficient, and all populations are correlated equally), is

$$CV_a = CV_p \left[\frac{1 + r(n-1)}{n} \right]^{1/2}. \tag{4}$$

With observations from the tributary to the confluence of a river network, the number of upstream populations contributing to the downstream aggregate increases nonlinearly. We can determine the CV_a for interacting river populations in the form of eqn (4) as a function of the properties that describe the structure of the network. Populations at the tributary nodes $\mathcal{T}$ thus have a coefficient of variation $CV_a(\omega = \Omega) = CV_\Omega$. Combining eqns (3) and (4) recursively throughout the metapopulation network (see Appendix S2) gives the expected CV for the population aggregate at the order of observation ω, such that

$$CV_a(\omega) = CV_\Omega \left[\frac{1 + r(\Psi - 1)}{\Psi} \right]^{\Omega - \omega/2}, \tag{5}$$

where the branch number is treated as a random variable with a mean value λ, and Ψ is thus interpreted as the expected number of inflowing populations to the node at the order of observation.

Dynamic and stochastic effects that promote synchronous population dynamics will result in greater correlation among subpopulations $\phi_i(t)$, such that $r \to 1$ in a perfectly synchronised system. If populations are assumed to react similarly to external forces (e.g. predation, resource limitation), it stands to reason that their correlation coefficients are similar. Here, we assume that r is the same for all populations, in comparison to ecological communities, where species may be expected to contribute differently to synchrony (Thibaut & Connolly 2013).

Asymptotic stability: synchronisation in river metapopulation networks

Network structure can influence whether the synchronisation of its interconnected components is possible (Earn *et al.* 2000; Barahona & Pecora 2002; Barrat *et al.* 2008). Synchronisation can be defined in terms of population-level correlations, or in terms of asymptotic stability. In the latter case, synchronisation is defined as the convergence of all population trajectories to a trajectory $s(t)$ (*complete synchronisation*: where $\phi_i(t) = s(t)$ for all i; Barrat *et al.* 2008). The synchronous trajectory $s(t)$ is thus considered dynamically stable if trajectories under a small perturbation return to $s(t)$. Here, we consider under what conditions the dendritic structure of river networks can

diminish or amplify the potential for complete synchronisation of a metapopulation.

The mathematical description of metapopulation network structure is summarised by the adjacency matrix **A**, which is an $N \times N$ matrix (where N is the number of nodes in the network). The elements of the matrix $A_{i \neq j} = 1$, if a link exists between node i and node j, and 0 otherwise. If each node represents a discrete river segment, we can assume that each node has both internal dynamics (driven by processes that occur in a given node i) and external dynamics (driven by nodes that are connected to node i). We describe the internal dynamics of node i as

$$\frac{d}{dt} \phi_i = F(\phi_i) \quad \text{for } i = 1, \ldots, N,$$

where the function $F(\phi_i)$ describes the internal population-level processes that determine the temporal change of a population ϕ inhabiting node i within the metapopulation Φ. Because $d\phi_i/dt$ should depend on internal and external effects, we must include the influence of node i's neighbours and the interaction strength ρ, such that

$$\frac{d}{dt} \phi_i = F(\phi_i) + \rho \sum_{j=1}^{N} L_{ij} H(\phi_j) \quad \text{for } i = 1, \ldots, N, \tag{6}$$

where the function $H(\phi_j)$ describes the interaction between ϕ_i and ϕ_j, and L_{ij} is an element of the Laplacian matrix **L**, which introduces the structure of the metapopulation. Here, we assume that the strength of interactions between nodes is equivalent across the metapopulation Φ. Unlike our analysis of statistical stability, we assume that interactions are symmetric such that upstream and downstream populations are treated equally. This simplification stipulates that neighbouring upstream and downstream populations have similar influence, such that movement between nearest-neighbouring habitats is not affected by water flow.

The Laplacian matrix is $\mathbf{L} = \mathbf{D} - \mathbf{A}$ where **D** is the diagonal matrix with each on-diagonal element representing the degree of the nodes in the network (and 0 otherwise). Thus, the elements of the Laplacian matrix $L_{i \neq j} = -1$ if a link exists between node i and node j, while $L_{i=j}$ is the degree of node i. All matrices can be described by a spectrum of eigenvalues (Λ; the number of eigenvalues is equal to the number of nodes N), and that of the Laplacian matrix can be used to determine whether a network is prone to synchronous dynamics, even when the functions that describe the internal and external dynamics of the system are unknown (Barahona & Pecora 2002; Motter *et al.* 2005; Barrat *et al.* 2008). Written sequentially, we identify the eigenvalues as $0 = \Lambda_1 \leq \Lambda_2 \leq \ldots \leq \Lambda_{max}$.

The eigenratio Λ_{max}/Λ_2 measures the potential that dynamics on a network converge to the stable synchronised trajectory $s(t)$ (Barahona & Pecora 2002; Motter *et al.* 2005; Barrat *et al.* 2008). To show this, if a small deviation ξ is introduced to the proposed synchronous trajectory of the dynamic system (eqn 6), such that $\phi_i(t) = s(t) + \xi_i$, the trajectory is stable if the deviation decays over time and unstable if it does not. The change in ξ_i over time is decoupled along the eigenvectors of the Laplacian, ζ_i, as the eigenvectors represent linear com-

binations of the perturbation ξ. By Taylor expansion, $\zeta_i(t) = \zeta_i^0 \exp\{[F'(s) + \rho\Lambda_i H'(s)]t\}$, where ζ_i^0 is the initial perturbation, and $F'(s)$ and $H'(s)$ are the derivatives of the functions describing internal and external dynamics with respect to s (Barahona & Pecora 2002; Motter *et al.* 2005; Barrat *et al.* 2008).

The trajectory $s(t)$ is stable if, across the trajectory and for each Laplacian eigenvalue, the exponential term $F'(s) + \rho\Lambda_i H'(s)$ is negative, such that the deviance ξ_i decays over time. Thus, we identify the master stability function

$$\Gamma(\rho\Lambda_i) = \max_s[F'(s) + \rho\Lambda_i H'(s)]. \tag{7}$$

If $\Gamma > 0$, the deviation is magnified over time, and the synchronous trajectory is unstable, while if $\Gamma < 0$ the deviation decays to the stable synchronous trajectory (Motter *et al.* 2005). The conditions that result in synchrony can be defined if the region where $\Gamma < 0$ is identified. We define the boundaries of this stable region as α_1 and α_2 such that $\Gamma(\rho\Lambda_i) < 0$ if $\alpha_1 < \rho\Lambda_i < \alpha_2$. The identities of α_1 and α_2 are thus determined by the functions F and H, while the maximum and minimum extent of these bounds are found by substituting Λ_2 (the lowest non-zero Laplacian eigenvalue) and Λ_{max} (the highest Laplacian eigenvalue) for Λ_i. The condition under which synchrony occurs is thus given by

$$\frac{\Lambda_{max}}{\Lambda_2} < \frac{\alpha_2}{\alpha_1}. \tag{8}$$

This is an oft-used relationship in spectral theory (Barahona & Pecora 2002; Motter *et al.* 2005; Barrat *et al.* 2008), and is remarkable because the structural determinants of the system (the Laplacian eigenvalues) are separated from the dynamical determinants of the system (α_1 and α_2). Synchrony is thus more likely to occur if the eigenratio is relatively small even if α_1 and α_2 are unknown, and this can be determined directly from metapopulation structure. In fact, the spectral properties of tree-like networks have been investigated (Fan *et al.* 2008) – particularly in systems with a star structure (and therefore no branches beyond the confluence node). Although star structured networks have been shown to have the largest difference between Λ_{max} and Λ_2, it is unknown to what extent branching influences the potential for synchronisation in the context of river metapopulation networks.

To examine under what conditions river metapopulations are more or less likely to synchronise, we compared the eigenratio of river metapopulation networks to those of corresponding random metapopulation networks. Random metapopulations are generally representative of those occupying terrestrial habitats, as multiple interaction pathways can exist between populations, although we acknowledge that terrestrial metapopulations have unique spatial constraints that we do not explore (e.g. see Hanski *et al.* 1994). For an ensemble of constructed river metapopulation networks, each river metapopulation is paired with a corresponding random metapopulation that has (1) the same number of nodes, (2) 2× the number of links (a random network with the same number of links as a river metapopulation is always constrained to a tree-like branching structure) and (3) a single component, such that the metapopulation is not disconnected. Accord-

ingly, as a river metapopulation becomes more branched, the number of nodes and links in the random metapopulation grow in proportion to its riverine counterpart.

To determine whether and to what extent the strict branching structure of river metapopulation networks influences synchronisation, we introduced transecting links between otherwise separated nodes. Transects are links that connect populations in different branches, effectively short-circuiting the dendritic structure of river network metapopulations. To determine the effect of transects on the dynamic synchronisation of river metapopulation networks, we define the transect sensitivity metric, ε_t, as the eigenratio of a transected river metapopulation divided by the eigenratio of a metapopulation with equivalent structure but without transecting links. If $\varepsilon_t < 1$ the transected metapopulation is more likely to synchronise while if $\varepsilon_t > 1$ the transected metapopulation is less likely to synchronise. This analysis thus quantifies the importance of branching structures on synchronisation dampening and also lends insight into how anthropogenic alterations of river metapopulation structure can change the expected dynamics.

RESULTS

Statistical stability

As the complexity of river metapopulation networks increases (in terms of the prevalence of branching nodes), the statistical stability of downstream populations increases nonlinearly. For nodes at an order of observation $\omega < \Omega$, the number of populations in the aggregate increases, leading to lower values of CV_a in accordance with Doak *et al.* (1998). However, the magnitude of this decrease is strongly contingent on network structure. Our framework predicts that increased river branching complexity dampens the fluctuations of downstream populations. The probability of branching strongly decreases CV_a, while increasing the mean branch number does not significantly impact CV_a if p is low. As p increases, the influence of the mean branch number is amplified. Comparatively, the aggregating effects of populations moving towards the confluence (with decreasing ω) result in the largest changes in CV_a (Fig. 2a). Predicted changes in the magnitude of CV_a thus represent baseline expectations of the portfolio effect acting on populations that aggregate from the tributaries to the confluence, given river metapopulation structure.

As the population trajectories $\phi_i(t)$ become synchronised such that the correlation coefficient r is increased, the role of river metapopulation structure in lowering CV_a is diminished (Fig. 2b). Importantly, the effect of increased correlation is strongly dependent on the branching probability; as the river network metapopulation becomes more branched, the potential impact of population-level correlations increases, particularly near the tributary nodes. Near the confluence, population-level correlations always have a strong impact on CV_a. Thus, our findings suggest that river network complexity can counter, but not eliminate, the variance-magnifying effects of strong correlations between populations, and this effect is emphasised in populations close to the confluence.
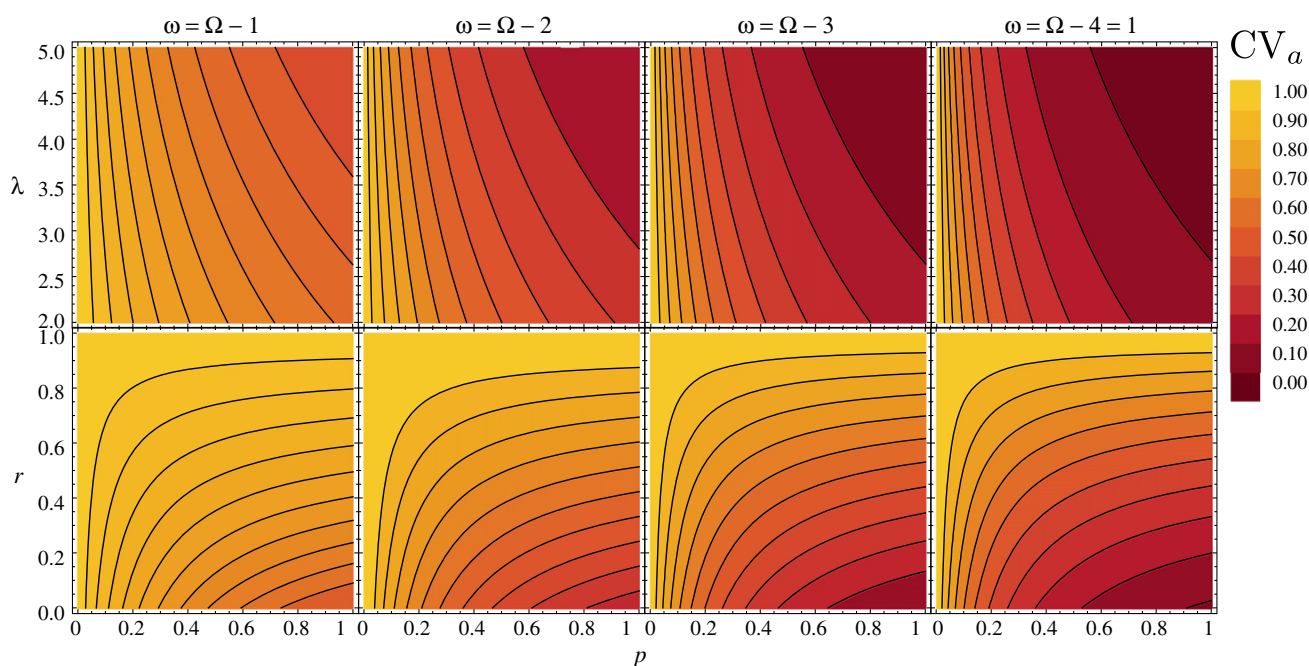
Figure 2. The coefficient of variation for a population aggregate on a river metapopulation (CV_a) with a radius $\Omega = 5$ as a function of the branching probability p, branch number $E\{K\} = \lambda$, and correlation coefficient r. For the top row, $r = 0$; for the bottom row, $\lambda = 3$. Darker colours represent greater statistical stability (lower CV). Each contour plot is shown at different orders of observation from the node directly downstream from the tributary $\omega = \Omega - 1$ to the confluence $\omega = \Omega - 4 = 1$. Populations closer to the confluence and that are less correlated have greater statistical stability.

Asymptotic stability

To evaluate the role of watershed metapopulation structure on synchronisation, we compared the eigenratios (Λ_{max}/Λ_2) of 2×10^4 river metapopulations to those with randomly assigned links. We found that metapopulation structure had large, but opposing, effects on the potential for synchronised dynamics for both river and their corresponding random metapopulations. Random, or terrestrial, metapopulations have many interconnected nodes, and the likelihood of dynamic synchronisation remains relatively unchanged as p increases (Fig. 3). By comparison, an increase in the branching of river metapopulations results in higher eigenratio values, which decreases the potential for synchronisation.

To measure the impact of the eigenratio to changes in network structure, we determined the transect sensitivity ε_t for 5×10^5 randomly drawn river metapopulation networks with a radius $\Omega = 12$, a branching probability $p = 0.5$, and a branch number $\kappa = 2$. For each river metapopulation, a single transecting link was added randomly at orders of observation $\omega = 2,\ldots,\Omega$. If the measurements for all transected river metapopulations are taken together, our results show that the distribution of ε_t values is bimodal and skewed towards values less than 1 (overall median: 0.94, low mode: 0.84, high mode: 1.05; Fig. 4a). The bimodality of ε_t values suggests that transects added between different nodes have variable effects on synchronisation: some decrease the potential for synchronisation, while most tend to increase the potential for synchronisation. Specifically, we find that transects introduced near the confluence tend to decrease ε_t (increasing the potential for

synchronised dynamics), while those introduced at intermediate distances from the confluence to the tributaries have more variable effects and can sometimes restrict synchronisation (Fig. 4b,c). Transects introduced among tributary nodes ($\omega = \Omega$) have effects similar to those introduced near the confluence, and always increase the potential for synchronised dynamics.

The addition of a single transecting link has generally weak – but occasionally large – impacts on the eigenratios of river metapopulation networks, while increasing the proportion of transected nodes in a river metapopulation has strongly nonlinear effects on ε_t. We find that ε_t is extremely sensitive to the proportion of transected tributary nodes, decreasing to a median value of $\varepsilon_t = 0.38$ if the proportion of transected nodes is increased to 20%, and to $\varepsilon_t = 0.06$ if the proportion is increased to 100% (Fig. 4d). Therefore, short-circuiting the river metapopulation, such as through water engineering projects that link tributaries, will increase the potential for synchronised dynamics within the river network.

DISCUSSION

Structure and stability

Our mathematical treatment reveals two principle findings regarding the predicted statistical and asymptotic stability of watershed metapopulations. First, river metapopulation structure buffers variance through statistical averaging. River metapopulations with more complex branching structures decrease the magnitude of fluctuations for downstream populations, but this effect is inhibited as population trajec-
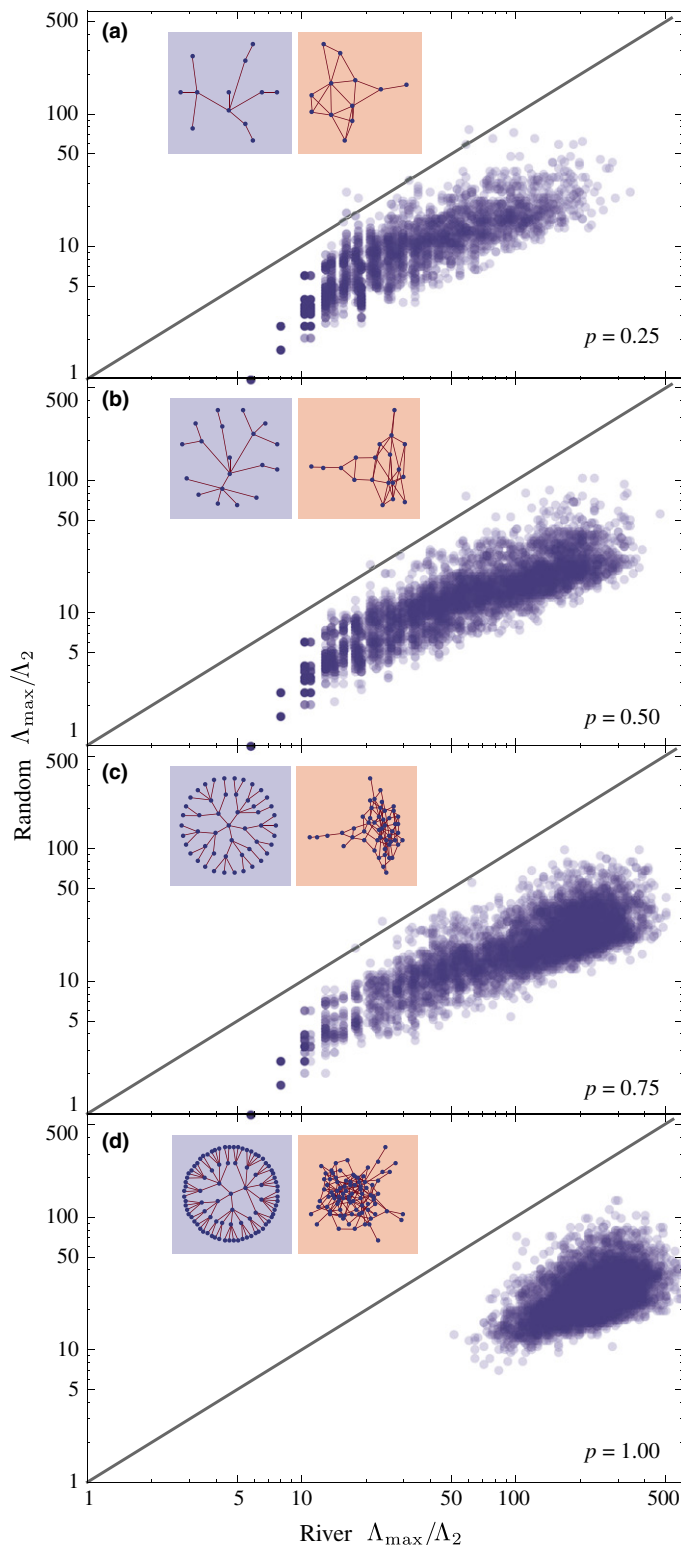
Figure 3. (a–d) Frequency distributions for the eigenratio Λ_{max}/Λ_2 for 5×10^3 river metapopulations (left inset) vs. the eigenratio for corresponding random metapopulations (right inset) across different values of the branching probability p, where $E\{K\} = 3$, $\Omega = 4$. Lower eigenratio values describe networks that are more prone to synchrony (random metapopulations) vs. those that are less likely to develop synchronised dynamics (river metapopulations).

tories become more correlated, or synchronised (Fig. 2). Second, river metapopulations are naturally buffered against synchronised dynamics as a consequence of structure alone (Fig. 3), and this contrasts with expectations for terrestrial metapopulations. These complementary findings indicate that the branching structure of river metapopulation networks has large, nonlinear dampening effects on population fluctuations due to the integration of asynchronous population trajectories, while an increase in the number of branches intrinsically buffers the system against synchronisation.

Our statistical and asymptotic analyses incorporate important assumptions regarding interaction structure as well as population equivalence across watersheds. Our river metapopulation networks necessarily simplify the complex structure of real-world river networks, in particular by ignoring smaller tributaries that enter disproportionately larger tributaries. Because including smaller tributaries increases the number of subpopulations at every order of observation ω, and because this does not change the scaling relationship between metapopulation eigenratios and the number of tributaries (Fig. S1), we submit that our simplification leads to conservative estimates of the effects of metapopulation structure on aggregation and synchronisation dynamics.

Both statistical and asymptotic approaches assume that each population, and all interpopulation interactions, is equivalent across the river network, while the eigenratio analysis makes the simplifying assumption of symmetric flow between upstream and downstream populations. Although abiotic variables are expected to be principally influenced by downstream water flow (e.g. sediment transport; Benda *et al.* 2004), populations of many aquatic organisms, such as salmon, may interact symmetrically with both up- and downstream populations, but are generally constrained to river branches (Grant *et al.* 2007). The inclusion of down-to-upstream interactions serves to increase the fluctuation-dampening effects of aggregation by increasing the number of populations that influence the aggregate at ω. If it is assumed that a population one node downstream from the order of observation (such that $d = \omega - 1$) aggregates into the node at ω, the CV of the aggregate at the downstream node is $CV_a(d) = CV_a(\omega - 1)$, assuming bidirectional flow from the node at d and the node at ω. Given bidirectional flow, we can assume that the mean population size at the downstream node approximates that at ω, and in this case, the CV for the aggregate of both scales as $CV_a(\omega,d) \propto \Psi^{-1} CV_a(\omega)$.

Interaction strengths influence both the structure (Yeakel *et al.* 2012) and dynamics (Estes *et al.* 2011) of food webs, and it is likely that they have a similarly important role between populations in river networks (*sensu* Schick & Lindley 2007). Although our asymptotic analysis assumes equivalent interaction strengths between all populations, there is precedence for using the eigenratio method to investigate synchronisation on networks with interaction strengths scaled to node degree (Motter *et al.* 2005). Analysis of synchronisation in metapopulations where interaction strengths scale to the order of observation ω, may thus have particular relevance to river systems.
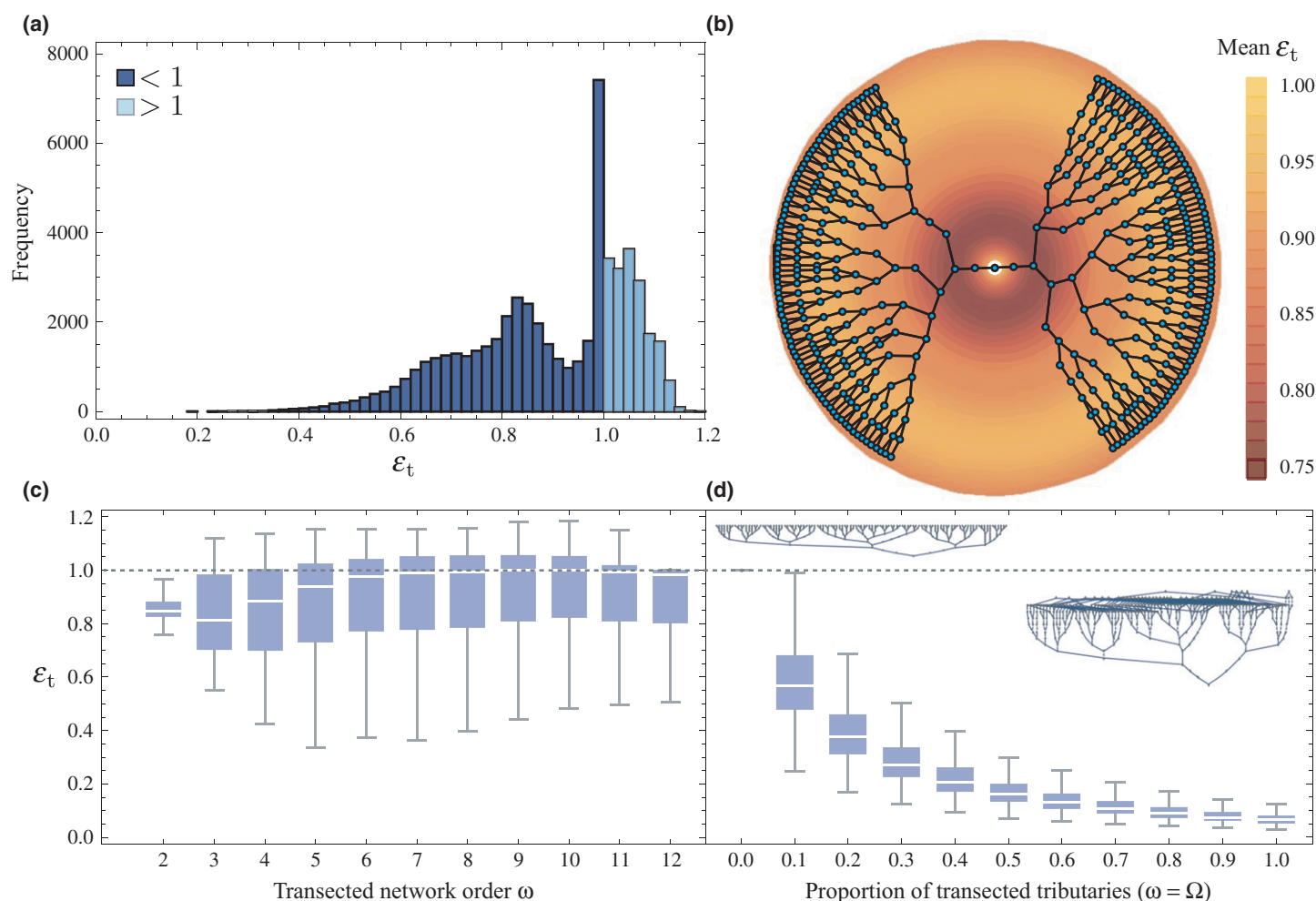
Figure 4. The influence of transects on synchronisation in river metapopulations ($p = 0.5$, $\kappa = 2$, and $\Omega = 12$). (a) Frequency distribution of the transect sensitivity metric (ε_t, where values < 1 correspond to increased potential for synchronisation on transected networks), for 5×10^5 simulated river metapopulation networks with and without a single transecting link. Mean values (b) and frequency distributions (c) of ε_t as a function of the transecting link being placed among nodes at the order of observation ω. Transects placed among nodes near the confluence and tributaries are more likely to increase the potential for synchronisation. (d) Frequency distributions for ε_t as a function of the proportion of transected tributary nodes.

Synchronisation and deviation of river metapopulation structure

Synchronisation can be explored further by altering the principle characteristics of river metapopulation structure and observing the effects on $\Lambda_{\max}/\Lambda_2$. When transects between river branches are prohibited, node dynamics are naturally more isolated in river networks with complex branching structures, generally decreasing the potential for synchronised dynamics. Short-circuiting the dendritic structure of river metapopulations may result from water engineering projects such as canals that link tributaries (Cowley *et al.* 2007), migrations of animals that are not exclusively aquatic such as amphibians or stream insects (Finn *et al.* 2007), or active anthropogenic translocation or movement of fish within and across watersheds (Simon & Townsend 2003). In our analyses, these connections effectively link tributaries that would otherwise be separate, such that distant populations can influence each other, increasing the potential for synchronisation. In contrast, transects that decrease the potential for synchronisation linked more closely connected nodes (Fig. S2).

The inclusion of river transects can greatly lower the capacity of the metapopulation network to buffer against synchronisation, and single transects can dramatically lower network eigenratios (Fig. 4a). Importantly, the spatial location of such transects has nonlinear effects on synchronisation. The lower ε_t distributions of nodes either close to the confluence or linking tributaries (Fig. 4b,c) highlight their importance in determining the dynamics of river metapopulations. Our framework predicts that interactions transecting river branches at these locations strongly increase the potential for synchronisation, and that this effect can be realised by a small number of connected river branches (Fig. 4d). This may be of particular consequence for systems with large numbers of transecting irrigation canals, such as those in arid environments (Cowley *et al.* 2007). Moreover, many stream invertebrates have a terrestrial (flying) life stage, where populations cross between river branches (Finn *et al.* 2007). Thus, the behaviour and mobility of stream organisms will modulate the impacts of river metapopulation structure. Our research also adds to an understanding of how river structure influences the

resilience and recovery of species following disturbances. While river networks can be easily fragmented (Fagan 2002), tributary populations can serve as sources of species diversity, aiding recolonisation after downstream disturbances (Raven & George 1989). Our results indicate that the branching structure conferred by river networks decreases the potential for synchronisation, facilitating such recolonisation.

Scales of interaction

Metapopulation structure depends on the scale over which an organism's dynamics are integrated across space (Olden 2007; Erös et al. 2012). This spatial scale determines the discretisation of the network, which we specify as the scale length ℓ_s. The scale length is similar to the 'grain at which [organisms] perceive their environment' (Erös et al. 2012), but can be refined further to define the area over which local population-level processes occur, and this can be used to establish the *effective network* for a given organism. The statistical properties of the effective network may be expected to differ for organisms with different scale lengths. For instance, due to differences in movement and body size, salmon metapopulation networks will differ from snail metapopulations in the same river network, potentially influencing synchronisation.

As the integration window for an organism decreases, the effective size of the river metapopulation increases, proportionately increasing the radius Ω. The river metapopulation would thus conserve the number of branching nodes, but have an increased number of nodes separating branches as ℓ_s decreases, and this alters the probability of branching p. Thus,

$p \propto \Omega^{-1}$, such that as ℓ_s decreases, there is a corresponding nonlinear decrease in p (Fig. 5a). We find that the eigenratios of river metapopulation networks saturate as ℓ_s decreases, which we simulate by increasing Ω (Fig. 5b). Thus, if the integration window of an organism is small, and the metapopulation network retains the same branching structure, there is an increasing resistance to synchronised dynamics. This result is in accordance with theoretical experiments showing that synchronisation is more likely to occur if the distance between spatial patches is decreased in metapopulations (similar to increasing ℓ_s; Heino et al. 1997). This would suggest that organisms with smaller integration windows are predicted to have greater persistence over time.

As the integration window decreases, the statistical properties of the metapopulation should change. For instance, smaller organisms have access to river branches that larger animals cannot use, altering the effective network structure. If p decreases linearly with ℓ_s, there is greater-than-expected branching for smaller scale lengths (Fig. 5c), accounting for increased access to smaller river branches inaccessible to larger bodied organisms. This modified relationship has a large influence on network eigenratios, such that both large and small scale lengths increase the potential for synchronised dynamics. This suggests that organisms with intermediate integration windows are more buffered against synchronisation in river networks, enabling a greater capacity for ecological rescue, and reducing extinction risk. In fact, a unique bimodal size-based extinction risk has been observed for freshwater fish populations (Olden et al. 2007), and although we acknowledge that many factors contribute to this rela-
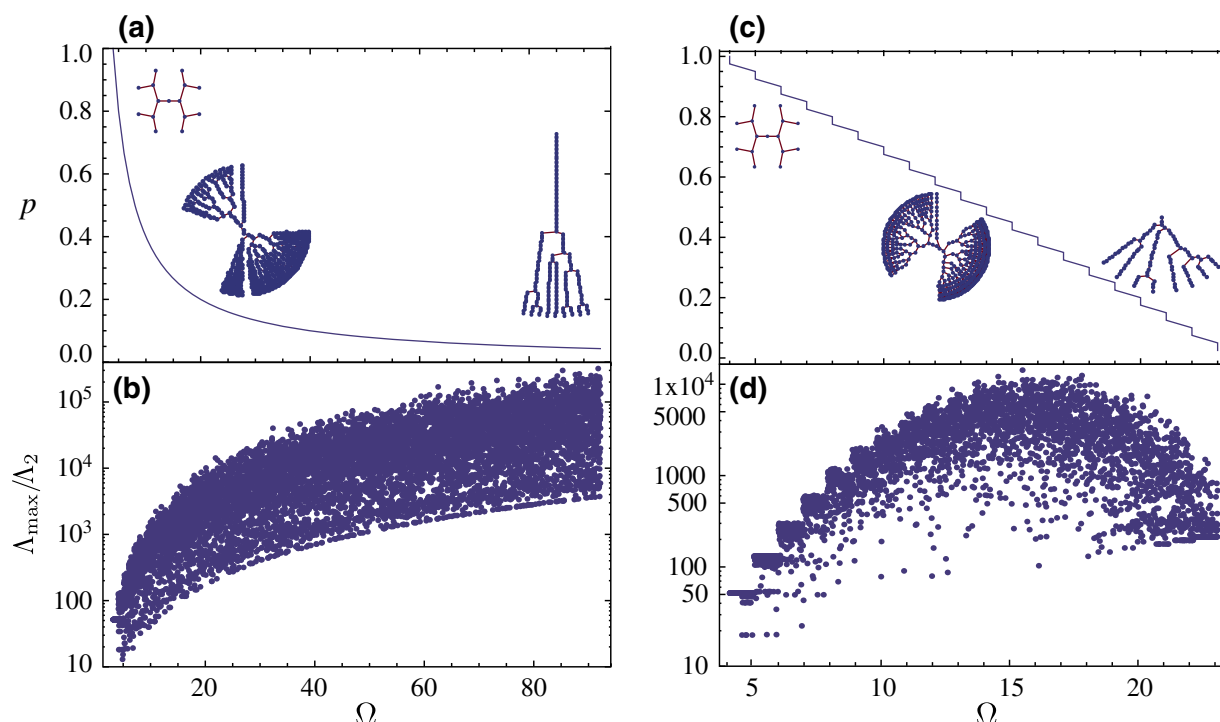

Figure 5. The relationship between river metapopulation eigenratios across decreasing scale lengths ℓ_s, simulated by increasing Ω. Lower eigenratio values describe networks that are more prone to synchrony. (a,b) Eigenratios for river networks as p changes nonlinearly with increasing Ω, simulating river metapopulation structure that remains constant as the scale length decreases. (c,d) Eigenratios for river metapopulations as p decreases linearly with increasing Ω, simulating river metapopulation structure that becomes increasingly branched as the scale length decreases.

tionship, it is worthwhile to consider the role of synchronisation and extinction risk as a function of organismal scale length.

Our results show that the structure of river metapopulations confers dual stability by dampening fluctuations and maintaining the asynchrony that attenuates variability. Thus, river network structure should influence the long-term dynamics and extinction risk of metapopulations. However, populations are not isolated, and the dynamical consequences of interactions in metacommunities can themselves be spatially structured (Holland & Hastings 2008). For example, consumer-resource interactions in networks can give rise to Turing patterns, or self-organised spatial arrangements of species abundances (Nakao & Mikhailov 2010; Fernandes & de Aguiar 2012), and whether this is possible in river networks may influence community persistence. We have shown that river metapopulation structure strongly impacts the potential for synchronisation. We anticipate that this general theory will inspire examination of the mechanistic underpinnings that promote or impede synchronisation. Understanding how the structural properties of river networks influence the dynamics and potential extinction risk of river metapopulations is essential for effective management of river ecosystems.

AUTHORSHIP

JDY and JWM designed the analyses. JDY, PRG, and MA derived and implemented analytical results and numerical simulations. JDY and JWM wrote the manuscript. All authors participated in conception, discussion of the results, and manuscript preparation.

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