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The effects of dispersal and river spatial structure on asynchrony in consumer–resource metacommunities

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Abstract

1. River network structure influences many important population and community processes. Previous work examining ecological dynamics in river networks has focused on within-trophic-level dynamics, with less emphasis on food-web interactions. Yet, trophic interactions in rivers are influenced by processes that may interact with network structure and position.

2. Using a spatially explicit consumer–resource model, we explore how trophic dynamics are influenced by the branching nature of river networks. We focus on cases where the consumer–resource interaction is prone to temporal oscillations and periodic low population sizes. In these cases, we find that the influence of network structure and dispersal can reduce temporal variability and increase persistence of consumers and resources at the metacommunity scale.

3. The effects of network structure and dispersal on our observed metacommunity dynamics result from asynchrony among dynamics of local communities: when asynchronous local fluctuations are averaged, consumer–resource dynamics become less variable and bounded higher above zero at regional spatial scales. Fluctuations synchronise across clusters of linked local communities.

4. Communities that connect to only one other downstream community typically vary independently of other patches and show high variability, while communities that are linked to multiple upstream and downstream habitats show greater clustering and less variability. These patterns suggest that headwater versus mainstem locations in river networks may show different levels of population variability and thus differential responses to management and restoration efforts.

KEYWORDS
asynchrony, consumer–resource interactions, dispersal, metacommunities, networks

1 | INTRODUCTION

Ecological communities are dynamic and exist in spatially complex environments. Increasingly, studies of natural communities have used metacommunity theory to ask how communities are influenced by spatial processes (Holyoak, Leibold, & Holt, 2005). Theoretical (Loreau, 2010; Mouquet & Loreau, 2003) and empirical (Howeth & Leibold, 2010; Kneitel & Miller, 2003; Vanschoenwinkel, De Vries,

Seaman, & Brendonck, 2007) research suggests that dispersal can have a positive effect on species richness, either locally or regionally, through a variety of mechanisms such as rescue effects, spatial refuges and source–sink dynamics (Holyoak et al., 2005). Because these multitude of mechanisms have been long predicted to operate most strongly at intermediate levels of dispersal, empirical studies have largely focused on manipulating dispersal rates and scales (Cadotte, 2006; Kneitel & Miller, 2003; Steiner, Stockwell, Kalaimani,

& Aqel, 2011) and typically alter only the presence of connections among local communities (Ellner et al., 2001; Holyoak & Lawler, 1996; Vasseur & Fox, 2009). More recently, however, research has shown that altering patterns of connectivity can have a considerable effect on diversity and species variability in metacommunities independent of dispersal rate (Chisholm, Lindo, & Gonzalez, 2011; Holland & Hastings, 2008), suggesting that community assembly and dynamics may vary across ecosystem types owing to differences in the spatial configuration of underlying habitat.

Much research on the ecological effects of connectivity patterns has been advanced in the context of river ecology. The distribution of habitat in most rivers has a branching, or dendritic, structure. This branching structure of river networks differs from other natural and human networks, which are typically more regular or random in topology, due to constraints from nearest neighbour dispersal and underlying geomorphology (Rodriguez-Iturbe & Rinaldo, 1997; Urban, Minor, Treml, & Schick, 2009).

For organisms whose dispersal is constrained by river geometry, ecological dynamics may be strongly altered relative to other ecological systems. Single-species (metapopulation) models demonstrate that branching connectivity patterns can increase metapopulation persistence relative to linearly (Fagan, 2002; Labonne, Ravigne, Parisi, & Gaucherel, 2008; Sarhad, Carlson, & Anderson, 2014) and randomly connected (Yeakel, Moore, Guimaraes, & De Aguiar, 2014) metapopulations, depending on the mechanism of dispersal. Furthermore, an increased variance in connectivity associated with greater structural complexity in dendritic networks has been associated with greater spatial variability in population density (Labonne et al., 2008; Padgham & Webb, 2010; Sarhad & Anderson, 2015; Sarhad, Manifold, & Anderson, 2017). Predicted patterns of population variability in dendritic metapopulations have been observed in microcosm (Altermatt & Fronhofer, 2018) and field studies (Moore et al., 2015). At the level of the metacommunity, patterns of α-, β- and γ-diversity can all be strongly influenced by dendritic spatial structure relative to regular spatial structure (Auerbach & Poff, 2011; Carrara, Altermatt, Rodriguez-Iturbe, & Rinaldo, 2012; Carrara, Rinaldo, Giometto, & Altermatt, 2014; Muneepeerakul, Weitz, Levin, Rinaldo, & Rodriguez-Iturbe, 2007; Seymour, Fronhofer, & Altermatt, 2015), with the magnitude and direction of effects often being sensitive to the particulars of dispersal rate and directional bias. Yet, a full mechanistic understanding of the linkages between dendritic spatial structure and ecological dynamics, especially at the level of the metacommunity, is still lacking. Determining the role of dendritic spatial connectivity on community structure and dynamics remains a primary ecological challenge for freshwater ecologists with significant conservation implications due to widespread fragmentation and flow alteration in rivers (McCluney et al., 2014).

A primary factor underlying differences between metapopulations/metacommunities and non-spatial (i.e. well-mixed) systems is asynchrony in the dynamics of local patches from one another. When patches vary asynchronously, populations can be buffered from local extinctions through rescue effects and dispersal (Brown & Kodric-Brown, 1977; Leibold et al., 2004; Murdoch, 1994); averaging

of asynchronous local dynamics can in turn lead to an overall reduction in the amplitude of fluctuations at the regional scale (Maser, Guichard, & McCann, 2007). Thus, understanding conditions responsible for generating asynchrony is a fundamental goal of metacommunity ecology (Gouhier, Guichard, & Gonzalez, 2010; Steiner, Stockwell, Kalaimani, & Aqel, 2013). Increasing the number of dispersal connections, or "connectivity," tends to increase persistence and therefore richness (Holyoak & Lawler, 1996; Liebhold, Koenig, & Bjornstad, 2004; Paradis, Baillie, Sutherland, & Gregory, 1999), yet dispersal rates that are too high tend to synchronise fluctuations and homogenise metacommunities (Hastings, 1993; Koelle & Vandermeer, 2005). More recent work has shown that patterns of connectivity—the distribution of dispersal links among patches—can also strongly alter asynchrony potential across wide ranges of baseline connectivity and dispersal (Gilarranz & Bascompte, 2012; Holland & Hastings, 2008; Strogatz, 2001). River networks possess irregular patterns of connectivity that favour the formation of asynchronous ecological dynamics (Marleau, Guichard, & Loreau, 2014; Yeakel et al., 2014), potentially accounting for differences in diversity patterns among regular networks and those characteristic of river drainages (Cadotte, 2006; Carrara et al., 2012).

A large proportion of metacommunity theory in river networks such as that cited above has been generated around competitive metacommunities, where most species are similar in trophic role or position, without much focus on consumer–resource communities. Yet appreciation of the role of space in community dynamics in ecology more broadly has been greatly advanced by studies of consumer–resource interactions (Briggs & Hoopes, 2004; Holyoak et al., 2005; Murdoch, Briggs, & Nisbet, 2003). More recent work in this vein has explored the role of network structure on both pairwise (Holland & Hastings, 2008) and multispecies consumer–resource interactions (Pillai, Gonzalez, & Loreau, 2011). In river networks, branching structure may reduce fluctuations among consumers and resources (Cuddington & Yodzis, 2002) and affect many aspects of food-web structure and dynamics (Grant, Lowe, & Fagan, 2007; Power & Dietrich, 2002), although our understanding of the range of these impacts, and the mechanisms behind them, is still developing. In particular, the role of spatial structure on asynchrony and, in turn, persistence and population variability at both the local community and metacommunity level in river consumer–resource systems is unclear. Given the importance of trophic relationships in diversity maintenance (Chase et al., 2002), energy transfer (Hairston & Hairston, 1993) and material cycling (Bassar et al., 2010; McIntyre, Jones, Flecker, & Vanni, 2007), further exploration of how asynchrony of consumer–resource interactions is influenced by river network structure could provide important insights into a wide range of community and ecosystem processes in rivers.

Here, we use a spatially explicit consumer–resource model to explore how dynamics of trophically interacting species are influenced by the branching nature of river networks. We assume that both the consumer and resource are able to disperse among habitat patches that are arranged in a branching structure and that dispersal is largely constrained to the river network, such as would be

exhibited by fishes or insects that disperse aquatically or along riparian corridors. Consumer–resource dynamics are also simulated on regular and random networks for comparison.

By simulating consumer–resource dynamics over a range of metacommunity sizes, dispersal rates and spatial network structures, we aim to address the following questions: (1) How much do the relative amounts of asynchrony in consumer–resource oscillations in different spatial network types differ across gradients in dispersal and metacommunity size? (2) How prone are river metacommunities to asynchrony, particularly in comparison with other network structures? (3) To what extent does asynchrony reduce the amplitude of regional oscillations and bound consumers and resources from zero, increasing persistence potential? and (4) What spatial patterns of asynchrony emerge in dendritic river networks, and how do these differ from other network configurations?

Our simulation results highlight spatial patterns of asynchrony that emerge in the dynamics of consumer–resource systems that are driven by network size and structure. Furthermore, compared with regular and randomly connected habitats, we show how consumer–resource systems in river networks can exhibit unique patterns of asynchrony that reflect different dynamics in headwater communities that connect to only one other downstream community versus mainstem communities that are linked to multiple upstream and downstream habitats.

2 | METHODS

2.1 | Consumer–resource model

We simulated consumer–resource interactions in metacommunities using the well-studied Rosenzweig–MacArthur model (Rosenzweig & Macarthur, 1963) with the addition of dispersal,

$$
\frac{dR_i}{dt} = \underbrace{rR_i\left(1 - \frac{R_i}{K}\right)}_{\substack{\text{resource} \\ \text{production}}} - \underbrace{\frac{aC_iR_i}{b + R_i}}_{\substack{\text{resource} \\ \text{consumption}}} + \underbrace{D\sum_{j=1}^{n} A_{ij}R_j}_{\substack{\text{resource} \\ \text{dispersal}}}
$$

$$
\frac{dC_i}{dt} = \underbrace{\frac{caC_iR_i}{b + R_i}}_{\substack{\text{consumer} \\ \text{production}}} - \underbrace{mC_i}_{\substack{\text{consumer} \\ \text{mortality}}} + \underbrace{D\sum_{j=1}^{n} A_{ij}C_j}_{\substack{\text{consumer} \\ \text{dispersal}}}
$$

(1)

Here, R_i and C_i are the amount of resources and consumers, respectively, in local community i at time t. Resource production is modelled by logistic growth where r is the intrinsic population growth rate and K is the resource carrying capacity. Resources are lost to consumption according to a type II functional response with a being the consumer attack rate and b being the half-saturation coefficient. Consumed resources are converted into new consumer biomass at rate c, and consumer biomass is lost with constant per capita rate m.

The final terms in each equation in Equation (1) represent dispersal among communities in the spatial network; each local community is a "patch" or "node" and dispersal connections are "edges" in the network sense. Spatial structure of the metacommunity is introduced

through the matrix A, which encodes in the off-diagonal elements whether communities i and j are connected by dispersal. For A_{ij} ($i \neq j$), a value of "1" denotes that local communities i and j are connected by dispersal, whereas a "0" means there is no such connection. Although downstream flow can introduce directional biases in the movement of organisms and material, we assume that dispersal is always bidirectional for simplicity, that is $A_{ij} = A_{ji}$. The diagonal elements A_{ii} are the negative sum of off-diagonal elements for rows i, reflecting the total amount of emigration from the community i. The dispersal rate D scales the amount of dispersal across each connection in the metacommunity.

We recast Equation (1) into a non-dimensional form that retains the same dynamics but possesses fewer parameters. The fact that Equation (1) possesses many parameters can lead to a large number of simulations that can obscure important mechanisms led us to rescale the model using ratios of the original parameters and state variables. We chose the resource instantaneous per capita growth rate as the base unit of time such that $\hat{t} = rt$ and recast the resources and consumers, respectively, as. $\hat{R} = R/b$ and $\hat{C} = aC/rb$. Following these substitutions, model dynamics are now determined exclusively by the consumer–resource conversion rate relative to the resource instantaneous per capita growth rate ($\phi = ca/r$), resource self-regulation ($\theta = b/K$), the consumer per capita mortality rate relative to the resource instantaneous per capita growth rate ($\eta = m/r$), dispersal relative to the resource instantaneous per capita growth rate ($\hat{D} = D/r$) and the metacommunity dispersal network's spatial structure (A). Dropping the hats for convenience, the non-dimensional form of Equation (1) thus becomes

$$
\frac{dR}{dt} = R(1 - \theta R) - \frac{RC}{1 + R} + D\sum_{j=1}^{n} A_{ij}R_j
$$

$$
\frac{dC}{dt} = \frac{\phi RC}{1 + R} - \eta C + D\sum_{j=1}^{n} A_{ij}C_j
$$

(2)

For simplicity, we assume that there is no spatial heterogeneity in parameter values, meaning that local communities do not differ in underlying parameter values, only spatial position. Furthermore, dispersal rates are assumed to be the same for both consumer and resource. We revisit these and other assumptions in the Discussion section.

To focus on the effects of changing spatial structure, we limited our simulations to parameter values corresponding to high-amplitude oscillations ($\phi = 5$, $\theta = 0.3$, $\eta = 1$) used in previous studies of consumer–resource dynamics on spatial networks (Holland & Hastings, 2008). Equation (2) is capable of generating a wide array of dynamics, including stable fixed points, damped oscillations and limit cycles. The parameter values we chose reflect the case of limit cycles generated by strong consumption, strong resource self-regulation and relatively high predator mortality. In nature, these dynamics would correspond to a consumer–resource system that shows high oscillatory variability in consumers and resources and periodic low population sizes, both of which make the system susceptible to extinctions. Therefore, the parameter range we chose is ideal for evaluating the

influence of spatial asynchrony on consumer–resource variability and regional persistence.

## 2.2 | Spatial network structure

To explore the effects of dendritic spatial structure on consumer–resource asynchrony in a maximally simple and manageable context, we first compared dynamics on a range of deterministically generated networks (Figure 1). River metacommunities were constructed as simple branching trees. Each local community was connected to two upstream communities and one downstream one, except for the basal community at the river network outflow (the "root" in network terminology) and the terminal upstream headwater communities (the "leaves"). The communities in each branching level can be interpreted as reaches of similar Strahler stream order; in the deterministic configuration, each community at a given order is the same distance from the community at the outflow.

To assist in determining properties potentially unique to dendritic river networks, we compared river metacommunities with (1) linear metacommunities, where communities arranged in a single line, and (2) ring-lattice metacommunities, where communities are arranged in

a circle and each is connected to the two closest patches on either side (Figure 1). The number of local communities in a river metacommunity is $2l - 1$, where l is the number of levels. We simulated dynamics on metacommunities of different sizes; those reported here include metacommunities with 7, 15, 31 and 63 local communities, which in turn generates metacommunities with three, four, five and six branching levels, respectively. Linear and ring-lattice metacommunities were compared with river metacommunities of equivalent local community number.

To confirm results in a slightly more realistic context, we additionally examined the dynamics of Equation (2) on sets of river metacommunities with stochastically generated spatial structure. Multiple replicate stochastic river metacommunities were generated using an algorithm which begins with a single basal community at the outflow and iteratively "grows" the network by adding upstream communities to randomly selected downstream ones. We imposed the limitation that each local community may only be linked to two upstream ones. Branching events were determined by comparing draws from a standard uniform distribution to a given branching probability. We generated 50 replicates of each of three sets of river metacommunities with branching probabilities of 0.15, 0.5 and 0.85 (Figure 1). These networks occupy a gradient between in network shape between the deterministic linear and river graphs: the linear deterministic metacommunity is one with a branching probability of 0, while the deterministic metacommunity has a branching probability of 1. Such structures respectively could serve as first approximations of more dendritic- to more trellis-shaped drainage networks (Pidwirny, 2006).

The dynamics of stochastically generated river metacommunities were then compared to a set of non-dendritic random networks with the same number (50) of communities produced by the Erdös–Rényi (ER) random graph model, constructed with the Boost Graph Library in C++ (http://www.boost.org/doc/libs/1_63_0/libs/graph/doc/). These metacommunities could be considered as terrestrial systems or the network of dispersal exhibited by aquatic organisms whose movements are not confined to the wetted channel, such as salamanders or insects with a flying adult stage. We set the probability of a dispersal link between any two communities for non-dendritic random metacommunities to be that which yields the same number of connections as a similarly sized river metacommunity; this value is simply one less than the metacommunity size. Any ER random metacommunities that were generated with unconnected communities were discarded. Fifty networks were generated for each level of branching probability in river metacommunities as well as for the ER random networks.
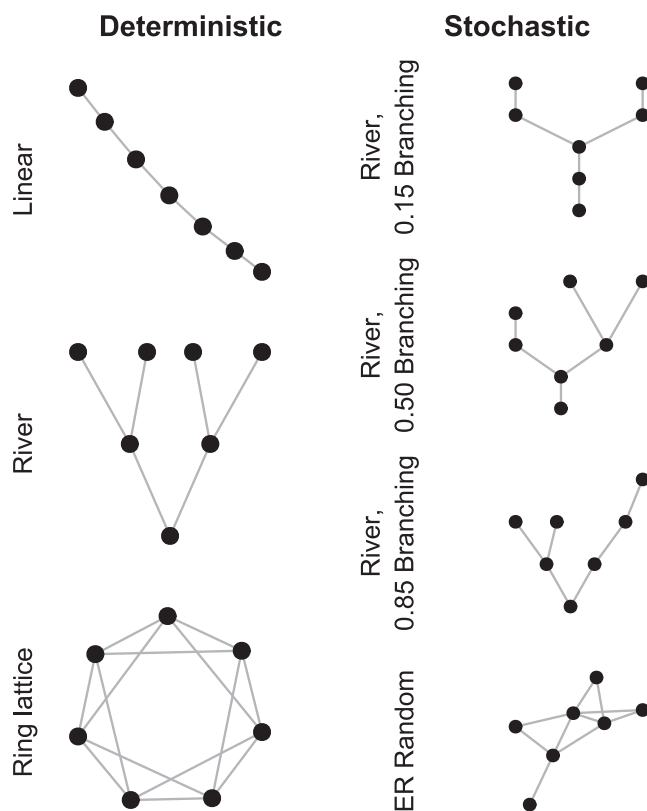
FIGURE 1 Examples of metacommunity spatial configurations used in this study. Dark circles represent local communities, while lines represent dispersal connections. Shown are metacommunities with seven local communities; systems with 7, 15, 31 and 63 were examined in this study. For stochastic networks, single examples are shown, although multiple networks were created for each branching probability used

2.3 | Simulation methods and analyses

The dynamics of Equation (2) were simulated on the different metacommunity configurations described above using the LSODA differential equation solver in ODEPACK (https://computation.llnl.gov/casc/odepack/). Dynamics on each of the fifty replicates of each specific metacommunity structures and for each level of dispersal were

simulated twenty times with random initial conditions for each of the consumer and resource drawn uniformly from the interval [0.2, 1.8]. This range was chosen arbitrarily, although dynamics were frequently in this range and it provided enough variation to promote asynchrony. Furthermore, the twenty simulations per specific structure was found to generate representative results when compared to subsets of cases where more than 20 were used, providing a balance between replication and computation time. Each simulation was then run for 20,000 time steps to ensure long-run dynamics were reached (where a time step is defined as one unit defined by the dimensional analysis), and then, results from the final 2,000 time steps were selected for further analysis.

We focused our analyses on two features of metacommunity dynamics (Figure 2). First, we examined the amount and patterns of asynchrony observed across metacommunity structures and levels of dispersal. Because our models are deterministic, we used a strict definition of synchrony, with patches considered synchronised only if the abundances of each patch are within 0.01 of each other for at least the last twenty time steps. While this threshold is slightly less strict than previous related studies (e.g. Holland & Hastings, 2008), our results were not particularly sensitive to the exact value chosen.

While dynamics may be asynchronised in a metacommunity, subsets of local communities will synchronise with one another, forming distinct "clusters." These local communities in a cluster will be synchronous with each other, but not with communities in other clusters. The number of clusters was identified based on the number of unique sets of unsynchronised dynamics present within the metacommunity. The number of clusters and the average cluster sizes were directly related to the number of local communities in the metacommunity. Therefore, results are presented as the number of clusters/the metacommunity size.

As dynamics in our models were deterministic, we assessed the potential relationship between metacommunity asynchrony and amelioration of extinction risk using boundedness of population cycles away from zero. This metric was calculated by taking the minimum value of the total regional population of both the consumer and resource across a given metacommunity during the final 2,000 time steps.

We explored spatial patterns of asynchrony in the different simulated network types using the coefficient of variation (C.V.) in the population density of consumer and resources, where the C.V. is the ratio of standard deviation in population density to the mean of the same over the given time period. The C.V. was calculated using the final 2,000 time steps for both consumers and resources in each local community. Because there was strong and consistent overlap in the patterns exhibited by resources and consumers in their C.V.s, we present results for resources only.

3 | RESULTS

3.1 | Dynamics in deterministic metacommunities

Metacommunity size, dispersal rate and spatial configuration all have strong effects on asynchrony for all parameter ranges examined in the deterministically generated metacommunities (Figure 3). While the resulting patterns in observed dynamics are complex and somewhat idiosyncratic to particular combinations of parameters and initial conditions, generalities do emerge with straightforward ecological interpretations which we explore below.

Most simulations exhibited asynchrony with varying degrees of clustering (Figure 3). Synchronous dynamics only emerged in the smallest metacommunities; these were composed 7 or 15 communities in all cases with a small percentage of synchronous outcomes
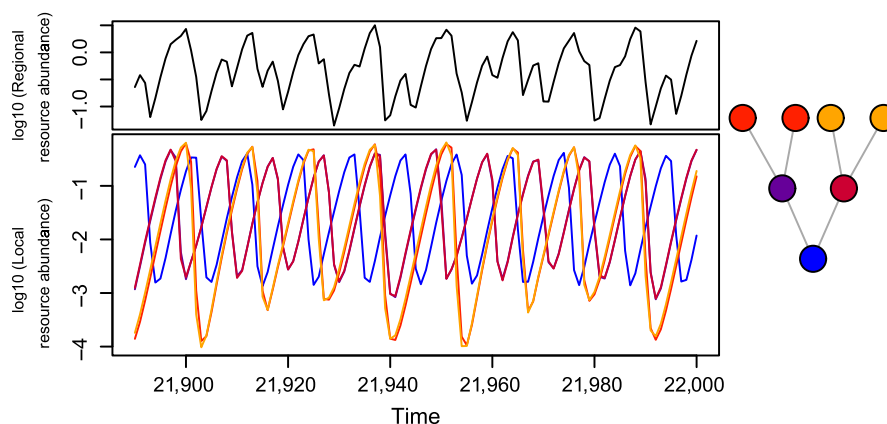
FIGURE 2 Examples of metacommunity dynamics examined in this study. Pictured above are time series for the included river metacommunity on the right. Only resource dynamics are shown, although corresponding consumer dynamics were also generated. Each time series in the bottom panel matches the local community with the same colour in the pictured river network. Local communities that share the same colour in the right-hand network represent "clusters" with synchronised dynamics. The example above has five clusters, noting that some time series are obscured because their dynamics are very similar to those that are more obviously pictured. The panel above pictures regional dynamics of the whole metacommunity, calculated as the sum total of individuals in each local community. Asynchrony causes the amplitude of oscillations to be reduced and minimum population sizes increased when comparing regional dynamics to those of individual local communities
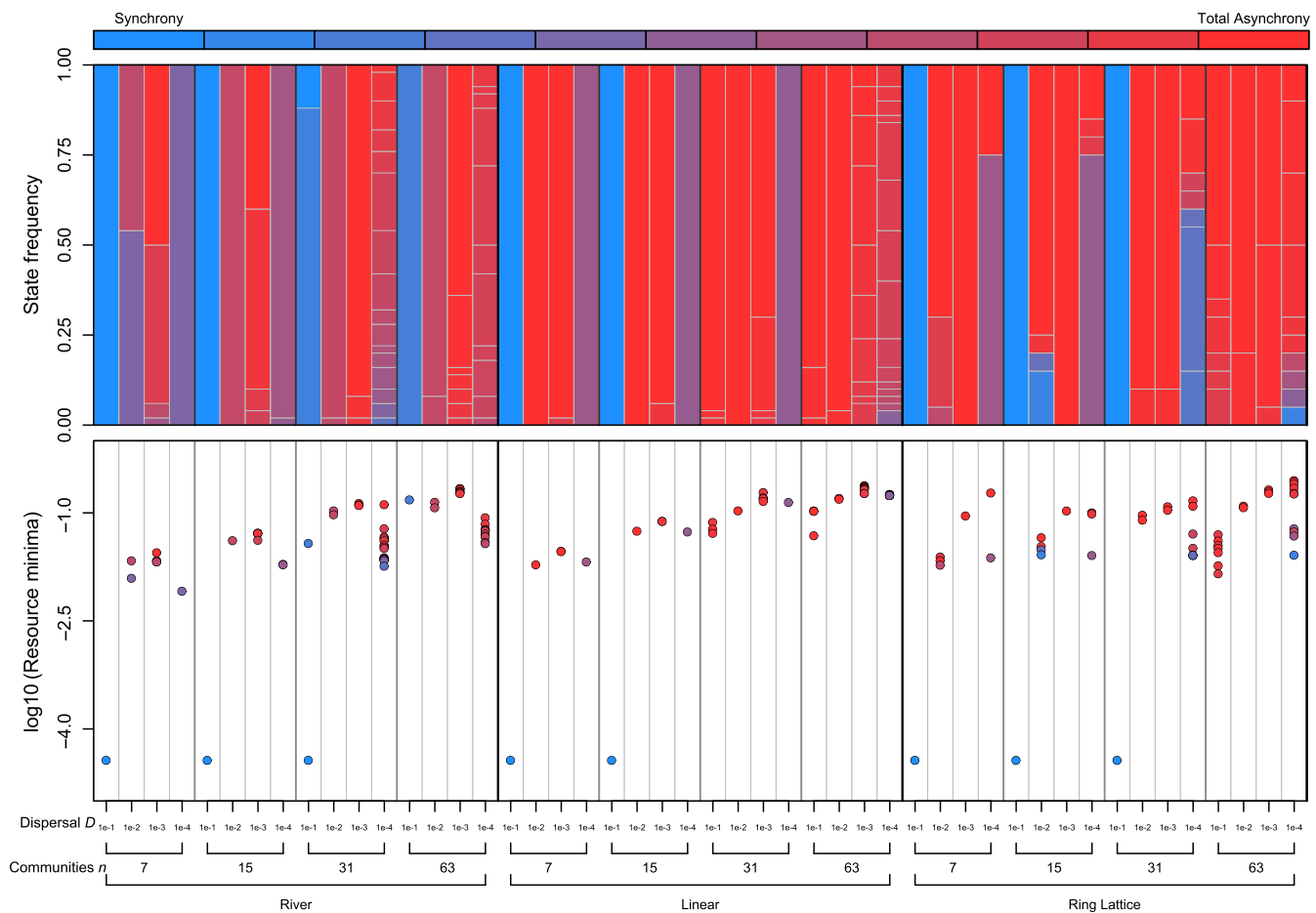
FIGURE 3 Asynchrony in metacommunities with deterministic spatial structures. The state frequency shows differences in the frequency of observed spatial patterns of asynchrony depending on spatial configuration, metacommunity size and dispersal rate. Asynchrony is classified by the amount of clustering in the system, ranging for total synchrony, where the number of clusters is 1, to total asynchrony, where the number of clusters is equal to the number of local communities. Because metacommunities can differ in size, we standardise the amount of clustering as the number of clusters/metacommunity size n. In the lower panels are corresponding regional population minima, calculated over the last 2,000 time steps of each simulation, where the regional population is the total resource abundance summed across the metacommunity. Consumers show nearly identical patterns, so only resources are shown. Point colours give the spatial asynchrony pattern that produces the observed regional resource minimum

occurring for 31 community river networks only. All other simulations showed asynchrony in oscillations among local communities, although the number synchronised clusters differed dramatically. Larger metacommunities exhibited greater asynchrony with higher numbers of clusters for all spatial configurations and dispersal rates.

Simulations at intermediate levels of dispersal had generally greater asynchrony and lower clustering than at lower or higher levels of dispersal (Figure 3). Completely synchronous dynamics were also confined to the highest dispersal rate used, $D = 1 \times 10^{-1}$ (Figure 3). At the opposite extreme, the largest metacommunities in all spatial configurations showed near-complete or complete asynchrony with no clustering (i.e. every local community is its own cluster) at intermediate dispersal of $D = 1 \times 10^{-2}$ or $D = 1 \times 10^{-3}$. The mechanisms here are largely intuitive: at high dispersal rates, local communities are more effectively "mixed" and therefore synchronised in their dynamics; at low dispersal rates, there is not enough exchange to influence local dynamics.

Our simulations demonstrated a tight link between the frequency of asynchrony, numbers of clusters and resource minima in all scenarios (Figure 3). In cases of complete synchrony, consumer–resource oscillations were completely in phase and had the same amplitude in every local community. Without asynchrony in local dynamics, regional minima are substantially lower, which would translate into to higher extinction risk in natural populations. In more asynchronous systems with large numbers of clusters, more local communities oscillated out-of-sync with one another, leading to greater regional averaging of dynamics and corresponding increases in resource population minima. The highest minima tended to fall around $D = 1 \times 10^{-3}$ where most simulations showed the highest number of clusters. Declines in minima at $D = 1 \times 10^{-4}$ corresponded to decreases in clustering in many cases.

Compared with the effects of metacommunity size and dispersal rate, the spatial configuration of the metacommunity dispersal

network had more subtle but still important influences on asynchrony and population minima. River metacommunities were the least prone to high asynchrony, generally showing higher clustering when asynchronous. Ring lattices in contrast were most prone to asynchrony. Despite these apparent differences, regional population minima were similarly high in large systems and at intermediate dispersal rates, with little obvious differences in comparison with linear and ring-lattice systems. At low dispersal, $D = 1 \times 10^{-4}$, river metacommunities exhibit the largest variation in outcomes, meaning that the degree of long-term asynchrony is more sensitive to the spatial pattern of the initial numbers of resources and consumers.

3.2 | Spatial patterns of asynchrony in deterministic metacommunities

The differences in the frequency of asynchrony and cluster numbers presented in Figure 3 reflect differences in underlying spatial patterns of asynchrony. The formation of asynchronous patterns proved quite complex and difficult to predict from specific initial conditions; oscillations in individual communities can have both differences in phase and differences in amplitude, and the two are not necessarily

related. Rather than summarising the complexity of these spatial patterns, we concentrate on the coefficient of variation in consumer–resource oscillations (Figures 4 and S1). Using this metric, we still can observe a diversity of different patterns. Yet, some consistent patterns do emerge.

The most consistent spatial pattern that emerges in river network configurations is that outlying boundary communities that are only connected to one other community have the highest C.V.s (Figure 4). This pattern also holds true for linear metacommunities, although the pattern inverts in a small number of these (Figure 1). The C.V.s of local communities in river configurations largely differentiated by branching level: differences between local communities within the same branching level were small, with much greater differences between local communities in different branching levels (Figure 4). The greatest differences were between those communities that were farthest from the outflow and others downstream. Different specific patterns of asynchrony emerged under the same dispersal rates, especially at high dispersal in river metacommunities. While this also occurred in linear and lattice metacommunities, the differences in spatial patterns were not nearly as great as in river metacommunities.
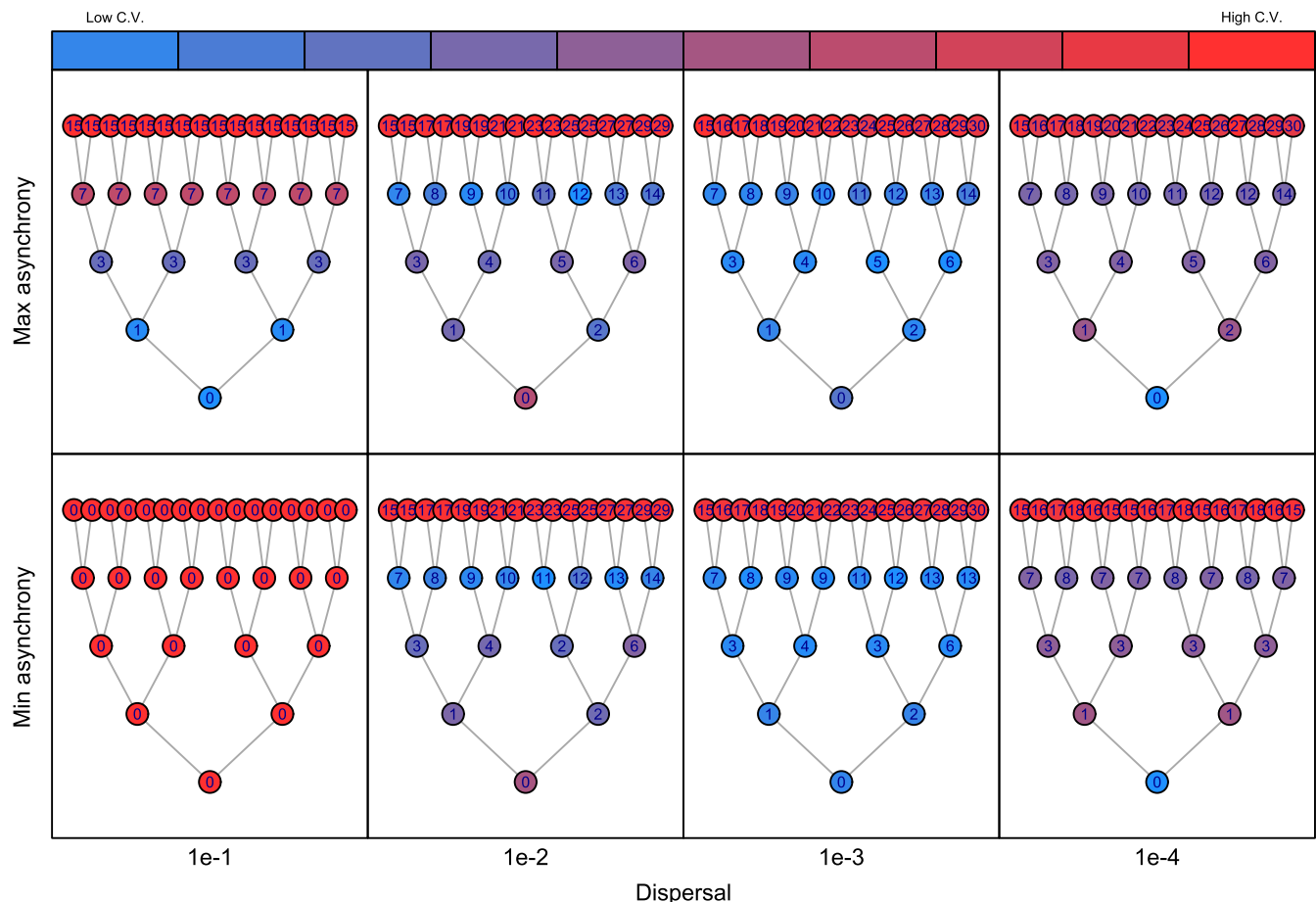
FIGURE 4 Example spatial patterns of asynchrony in deterministic river metacommunities. Shown are the most (max.) and least (min.) asynchronous pattern, measured as the number of clusters, of all patterns observed for each level of dispersal. Colours show the relative coefficient of variation among patches, with red being the highest variability patch and blue the lowest. Local communities sharing the same number belong to the same synchronised cluster

Patterns of asynchrony observed in river metacommunities were related to spatial patterns in population minima (Figure 5). The minima generally increased with increasing distance from the outflow community, indicating increasing boundedness from zero and buffering of population fluctuations due to asynchronous dispersal inputs. However, the community farthest from the outflow always had the lowest minimum, a pattern consistent with them having the highest C.V.s in population fluctuations. Because these communities only had one dispersal connection to other communities patches, their dynamics were relatively consistent across simulations with different metacommunity sizes, being almost indistinguishable among metacommunities with $n = 15$ or greater.

3.3 | Dynamics in stochastic metacommunities

Stochastically generated metacommunities showed similar influences of metacommunity size, dispersal rate and spatial configuration on asynchrony as with deterministic ones (Figure 6). The influence of stochastic variation in metacommunity spatial structure on dynamics is most readily observed in larger system sizes because of the greater number of possible metacommunity configurations. From here on, we focus on results from simulations where metacommunities are composed of $n = 31$ local communities, although patterns are consistent across other simulations.

Simulations lead to highly asynchronous outcomes in all cases except for those with the highest dispersal rates, $D = 1 \times 10^{-1}$ (Figure 6). At this high dispersal rate, river metacommunities with higher branching probabilities and ER metacommunities both showed higher variation in asynchrony outcomes owing to their more complex and less linear spatial structures. This greater number of observed cluster solutions corresponded to greater variation in the range of observed

population minima. At lower dispersal rates, particularly $D = 1 \times 10^{-4}$, these metacommunities showed almost total asynchrony; greater clustering and lower resource population minima were seen for the most linear river metacommunities with branching probability .15.

Dynamics were somewhat more asynchronous in stochastically generated river metacommunities relative to deterministically generated ones at the same dispersal rates and system sizes (Figures 3 and 6). The diversity of spatial asynchrony patterns appeared be enhanced in stochastic river metacommunities due to the complexity of dispersal linkages possible (Figures 4 and 7). While local communities linked to only one other community still showed the highest C.V.s, overall patterns and differences between individual communities are more variable given the spatial complexity of each metacommunity's structure. In some (but certainly not all) cases, individual branches show high C.V.s in all of the communities that comprise the branch, with confluences of these highly variable branches showing extensive buffering in the form of much lower C.V.s. Differences between branches were maintained to the greatest extent in rivers with high branching order, as these configurations possessed many more small branches than the more linear-shaped metacommunities with low branching order.

The relationship between population minima and distance to the outflow is obscured in stochastically generated river metacommunities (Figures 7 and S2). There is extensive variation in these patterns due to grouping many different stochastically generated structures. The clarity of patterns is therefore reduced because the maximum distance a patch can be from the outflow is not the same for all metacommunities with the same branching probability. In comparison with the deterministic river networks, where all terminal upstream communities are equal in distance from the outflow, an "upstream" community can be very close or very distant in a stochastic network.

In stochastic metacommunities, a better predictor of minimum population size is the "degree" of the local community, that is the number of other communities it is directly connected to by dispersal (Figure 8). Communities with degree 1 are the terminal upstream communities farthest from the outflow and the outflow itself, which have the lowest minima. This reflects the highest variability (C.V.) observed in these communities (Figure 7). In contrast, communities with degree 2 represent confluence communities, which have the lowest variation (Figure 7) and highest population minima (Figure 8). Because ER random networks are not constrained to having a dendritic spatial structure, they can possess communities with more than three connections. These communities continue the trend observable in river networks where a greater number of dispersal connections increases the population minimum.
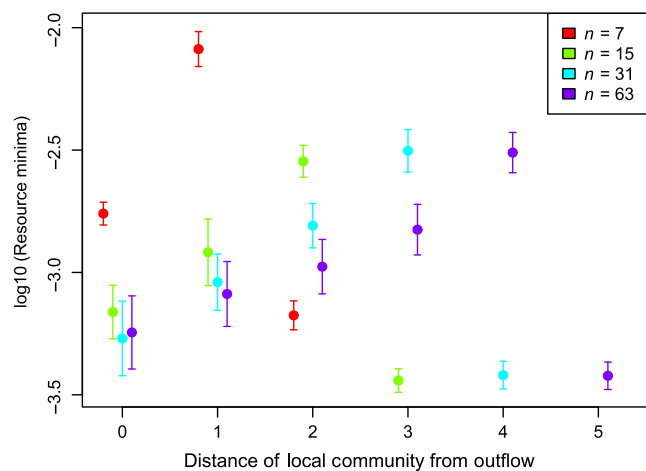
FIGURE 5 Resource minima vary as a function of distance for the outflow community in deterministic river metacommunities, calculated as the number of links. The maximum distance naturally varies depending on the metacommunity size n. Points shown are average minima ($\pm SD$) calculated in the last 2,000 time steps and then across all simulations of a given metacommunity size n. Results are shown for dispersal $D = 1 \times 10^{-1}$ as these had most variability in asynchrony outcomes

4 | DISCUSSION

The branching geometry of river networks has profound influences on fundamental instream physical and ecological processes (Grant
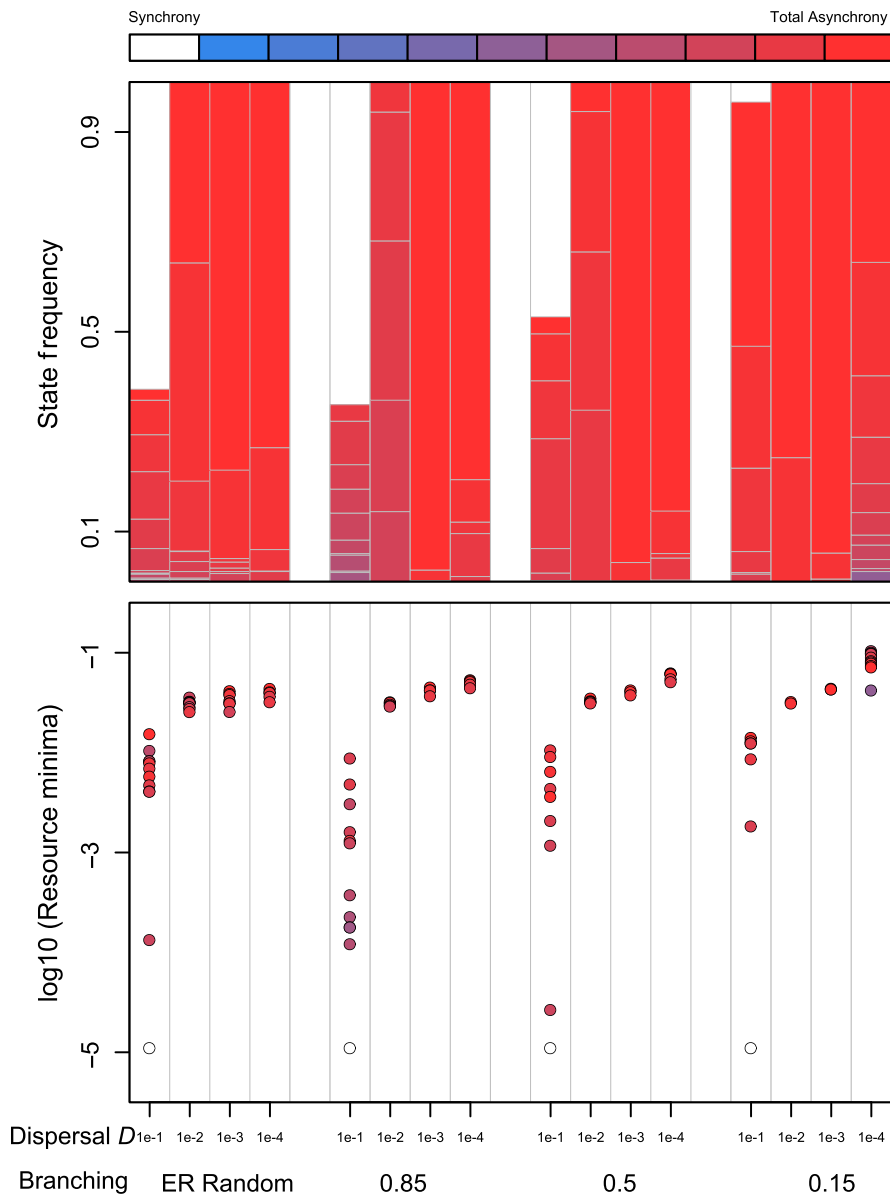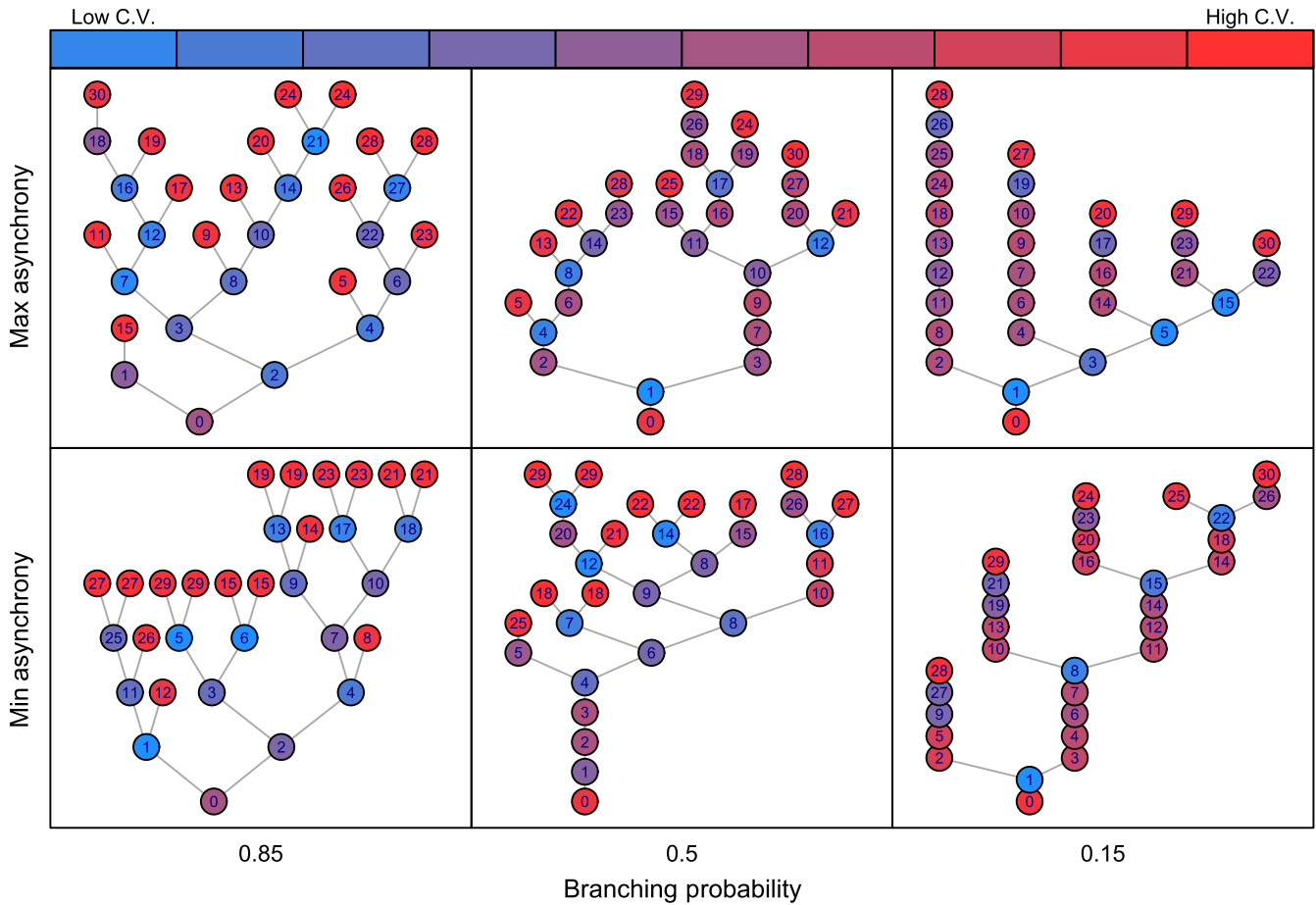
FIGURE 6 Examples of asynchrony in metacommunities with stochastic spatial structures. Asynchrony and resource minima are defined as in Figure 3. Results are shown for ER random metacommunities and river metacommunities with $n = 31$ local communities

et al., 2007). Freshwater systems exhibit strong trophic cascades when compared to other ecosystems (Borer et al., 2005; Shurin et al., 2002), yet despite this suggestion of consumption as a key organising process in rivers, the interplay between river network structure and consumer–resource interactions is not well characterised. We show that dispersal of consumers and resources in branching river networks can affect the degree of metacommunity asynchrony and persistence potential using mathematical models where trophic interactions lead to strong local oscillations. Asynchrony in these oscillations among communities frequently arose in river metacommunities, particularly in larger systems and at intermediate dispersal rates. A major consequence of asynchrony was that dispersal among communities appeared to buffer consumer and resource population oscillations, leading regional dynamics to be bounded further away from zero. While river networks did not consistently exhibit the greatest asynchrony among network types we examined, the spatial patterns of asynchrony most consistently

observed were unique to river networks and carry important ecological implications, which we explore below.

The most consistent pattern of spatial asynchrony that we observed in river networks was one where the highest population variability occurred in terminal upstream communities, which, because of their position, are most analogous to headwater communities in actual rivers. While nearby headwaters were sometimes clustered with each other, they would also oscillate asynchronously from one another and from communities at branch junctions. Dispersal from asynchronously oscillating terminal upstream communities tended to strongly buffer dynamics in communities at branch junctions, leading to lower variability and higher boundedness from zero in consumer and resource populations. Patterns were most distinctive in deterministically generated river networks; yet high headwater variability and buffering in junctions were also consistently observed in stochastically generated ones, suggesting these dynamics are robust. Similar results have been observed in models (Carrara

FIGURE 7 Example spatial patterns of asynchrony in stochastic river metacommunities for different levels of branching probability. Measures are as defined in Figure 4. Shown are example river metacommunities generated for $n = 31$ and $D = 1 \times 10^{-1}$
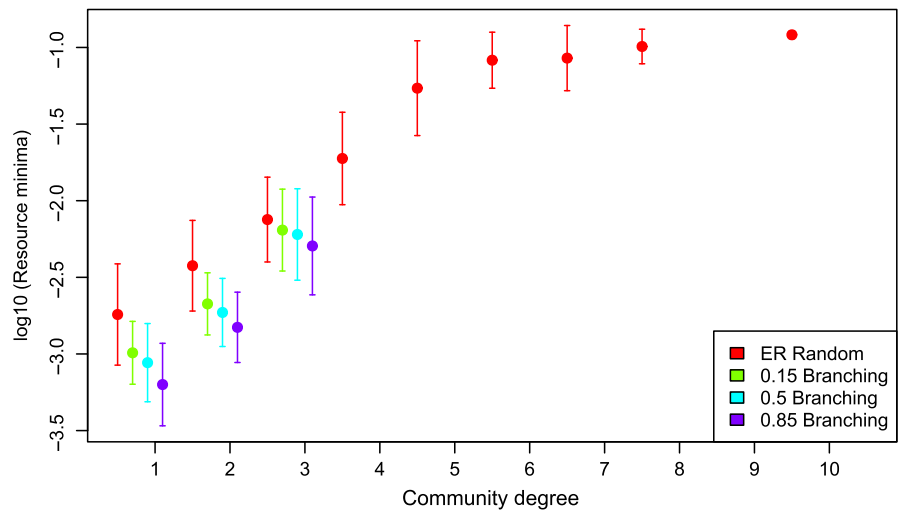
FIGURE 8 Resource minima as a function of the degree, or number of connections, that a community has with other communities in stochastic river metacommunities. Points shown average minima ($\pm SD$) calculated in the last 2,000 time steps and then across all simulations of metacommunities with $n = 31$ and the given branching probability. Results are again shown for dispersal $D = 1 \times 10^{-1}$

et al., 2012; Fronhofer & Altermatt, 2017; Yeakel et al., 2014) and microcosm experiments (Altermatt & Fronhofer, 2018; Carrara et al., 2012). These previous studies have focused on analogous outcomes as averaging of noisy population dynamics, whereas the dynamics we observed are deterministic oscillations that are generated from density-dependent feedbacks among consumers and resources rather than variability arising from processes such as demographic or environmental stochasticity. Spatial averaging of noisy dynamics does not cause changes in consumer–resource feedbacks in our local communities. Rather, it is the interaction of dispersal and nonlinear consumer–resource interactions that generates the wide variety of spatial dynamics in this study (Briggs & Hoopes, 2004; de Roos,

McCauley, & Wilson, 1998). This suggests the spatial patterns of asynchrony we observed are generalisable across a wide range of ecological conditions and interactions in branching networks.

High variability in headwater streams versus mainstem habitats has been observed in a wide range of ecological contexts. Population fluctuations and/or variable colonisation–extinction dynamics have been implicated in high genetic diversity in headwater populations (Besemer et al., 2013; Finn, Bonada, Murria, & Hughes, 2011), spatial portfolio effects in fish populations (Moore et al., 2015), higher β-diversity among headwaters (Besemer et al., 2013; Carrara et al., 2012; Finn et al., 2011; Seymour & Altermatt, 2014; Seymour et al., 2015) and altered patterns of species co-occurrence (Widder et al., 2014). The role of consumer–resource interactions in the patterns above has not however been explored. Our results show that because consumer–resource oscillations can generate population variation, they could be a strong potential contributor to all of these contexts. Terminal upstream communities most analogous to headwaters show the greatest overall variability as well as populations sizes that approach closer to zero in our models. Because higher variability and lower population minima should result in higher extinction rates in real populations, our modelling results are consistent with the extinction/colonisation dynamics hypothesised for producing high genetic and species turnover in headwater versus mainstem communities (Brown et al., 2011).

Many of the patterns observed in headwaters are potentially altered by out-of-network movement which can be high in some insects and vertebrates (Grant et al., 2007; Yeakel et al., 2014). For example, Lowe (2002) found that out-of-network dispersal stabilised headwater populations in a metapopulation model (see also Campbell Grant, Nichols, Lowe, & Fagan, 2010). For organisms with high out-of-network dispersal, dynamics would most resemble those of ER random networks where differences in the contributions of local communities to regional dynamics are less consistently dramatic. However, ER metacommunities in our study still exhibited substantial asynchrony and regional averaging of dynamics.

Different locations in river networks may of course exhibit quite distinct abiotic environmental conditions, a factor that we did not explore here. Headwaters in particular may have increased flow variability and otherwise more unique environmental abiotic conditions (Benda et al., 2004; Brown & Swan, 2010; Clarke, Mac, Bond, & Lake, 2008; Meyer et al., 2007). Because of this, such sites have been argued to be subject to higher environmental filtering or species sorting (Brown & Swan, 2010; Brown et al., 2011). Mainstems in contrast are more connected in a network sense and may have more buffered environments, leading to larger dispersal-influenced mass effects dynamics. Additionally, headwater habitats may be smaller, have lower autochthonous production and exist upstream of passage barriers, all together with high variability leading to lowered consumption pressure (McHugh, McIntosh, & Jellyman, 2010; Meyer et al., 2007; Sabo, Finlay, Kennedy, & Post, 2010; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). Despite not including underlying environmental heterogeneity in our model, we do still observe stronger dispersal influences and lower variability in headwaters versus mainstems. How these patterns might be altered by added environmental variability is unclear.

Spatial and temporal variability is easily introduced to Equation (1) by making parameters such as the resource carrying capacity K, consumer attack rate a or dispersal rate D dependent on location i and time t (note that doing this leads to alternative forms of Equation (2)). The effects of doing this will likely depend on where in the system different rates occur and the effects they have on local oscillatory tendency. For example, lowering enrichment by reducing the value of the carrying capacity K or consumption pressure in the attack rate a could locally reduce the tendency for consumer–resource oscillations (Murdoch et al., 2003). Upstream habitats that show reduced oscillations and greater species persistence may then increase rescue effects on downstream habitats. In contrast, oscillations and subsequent extinctions could actually be increased in mainstem habitats by build-up of nutrients and other resources that increase the value of K at network junctions (Power & Dietrich, 2002); spatial spread of consumer–resource oscillations initiated at these sites through dispersal could increase variability in otherwise stable upstream habitats. Studies examining the effects of spatial heterogeneity on persistence in rivers have examined gradients (Lutscher, McCauley, & Lewis, 2007) or patchy variability (Lutscher, Lewis, & McCauley, 2006; McKenzie, Jin, Jacobsen, & Lewis, 2012), although typically not in a network context (but see Auerbach & Poff, 2011) or in consumer–resource systems. Upstream habitats can in some cases lead to refuges for prey or weak competitors in these previous studies, although patchy variability can lead to weakened persistence depending on the relative quality of different patches. The lack of clear expectations arising from previous work therefore argues for the importance of integrating spatial heterogeneity into river network models.

The asynchronous spatial dynamics exhibited by our models are an example of ecological pattern formation (Kareiva, Mullen, & Southwood, 1990; Rietkerk & Van De Koppel, 2008). In ecological pattern formation, a small perturbation to an otherwise homogenous system grows into a persistent, spatially heterogeneous distribution of organisms and/or their resources. Pattern formation occurs in the system described by Equation (2) because of its oscillatory tendency in the absence dispersal, leading to a particular form of travelling wave spatial pattern formation where asynchrony in local oscillations travels as "waves" of population density through the system (Yang, Zhabotinsky, & Epstein, 2004). The interaction of dispersal with nonlinear feedbacks between resource consumption and the consumer numerical response alters the shape of oscillations, causing them to diverge in period or amplitude in such a way that generates persistently asynchronous fluctuations among sites. Such patterns of spatially asynchronous population fluctuations in consumer–resource systems have been observed experimentally, typically increasing population persistence (Ellner et al., 2001; Holyoak, 2000; Holyoak & Lawler, 1996; Liebhold et al., 2004).

Other mechanisms of spatial pattern formation that are relevant to river networks have been described that do not rely on systems

that oscillate in the absence of dispersal to form (Liu et al., 2013; Rietkerk & Van De Koppel, 2008; Wolfrum, 2012). For example, spatial asynchrony can still arise in cases of three or more interacting species as a result of Turing-type mechanisms where local inhibition (e.g. consumption and density dependence) and long-distance activation (e.g. dispersal) can lead to spatial pattern formation (Hata, Nakao, & Mikhailov, 2014). Three trophic-level food webs (e.g. algal resources → insect grazers → fish) are not uncommon in freshwater systems, providing ample opportunities for complex spatial patterns to arise by Turing mechanisms. Additionally, spatial pattern formation can arise due to "convective instabilities" wherein directional biases in dispersal or flow lead to spatial phase separation in oscillations among interacting populations (Anderson, Hilker, & Nisbet, 2012; Liu et al., 2013). We currently do not include directional dispersal in our model here; doing so would require reformulating the matrix A to be no longer symmetric. The strong unidirectional flow of water and materials in streams and rivers generates a perfect context for flow-based instabilities, although the sensitivity of these types of mechanisms to network connectivity and configuration is unknown.

The spatial complexity of our results demonstrates the importance of considering metacommunity dynamics in freshwater ecology and conservation. Despite each consumer and resource sharing identical parameter values to those in all other communities, they generated quite different dynamics depending dispersal rates, the amount of connectivity to other local communities, and their position within the river network. Thus, when species interactions are capable of generating emergent properties such as spatial asynchrony, using the behaviour of local communities to inform management outcomes can be misleading. Many previous studies have explored colonisation–extinction dynamics in regional population persistence, focusing on the importance of dispersal routes promoting persistence and the consequences of altering connectivity in river networks (Campbell Grant et al., 2010; Fagan, 2002; Lowe, 2002; Lowe & Bolger, 2002; Lynch et al., 2011; McKay, Schramski, Conyngham, & Fischenich, 2013; Samia, Lutscher, & Hastings, 2015). However, to our knowledge there has been no study of river networks that has considered dynamics that can arise in consumer–resource metacommunities, especially with emphasis on emergent regional patterns and the sensitivity of these to river network configuration. Our results show that even when both resources and consumers are distributed across a river network, asynchrony in their metacommunity dynamics can lead to spatial differences in variability and susceptibility to local extinction. Maintaining connectivity of headwaters to other habitats appears particularly necessary: without robust connection to the river network, recolonisation or rescue effects may not occur in protected or restored headwater reaches. Given the wide range of asynchrony outcomes observed in our simulations, altering dispersal pathways and network configuration (e.g. through dams or habitat destruction) could alter these patterns in unexpected ways. Thus, exploring the large range of dynamic outcomes possible in spatially complex river metacommunities can lead to more robust decision-making in the face of environmental change.

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SUPPORTING INFORMATION

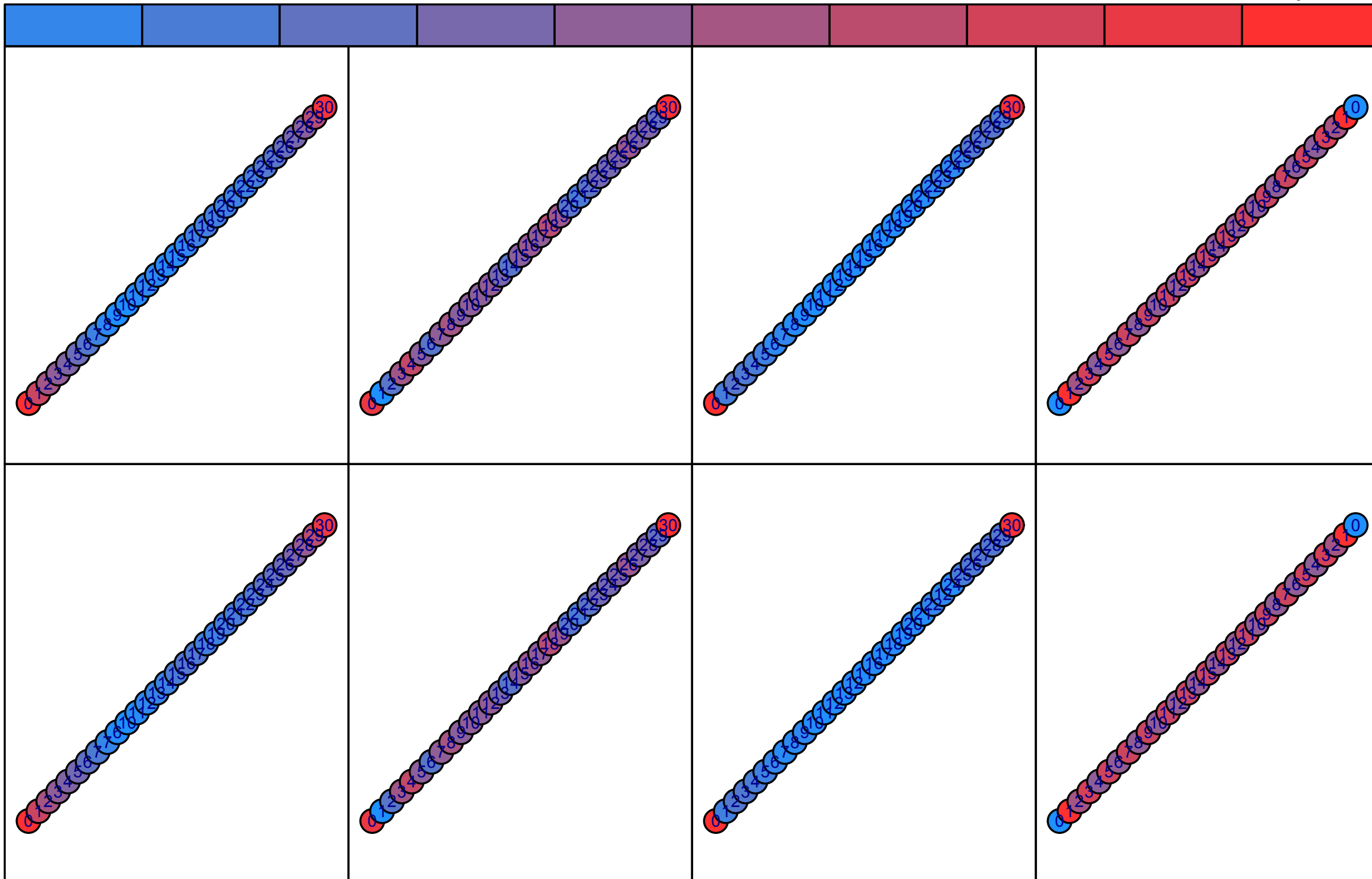Additional Supporting Information may be found online in the supporting information tab for this article.
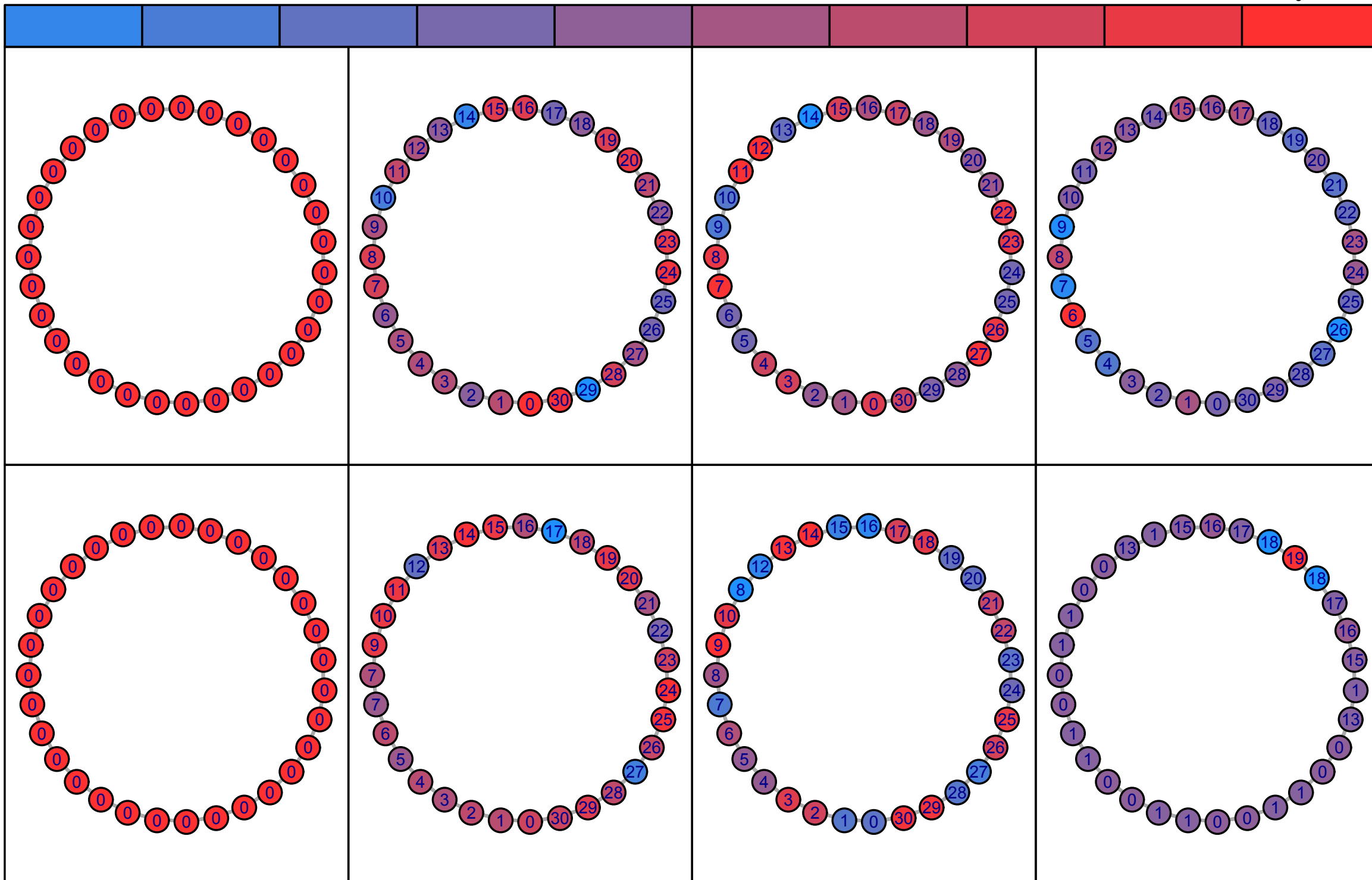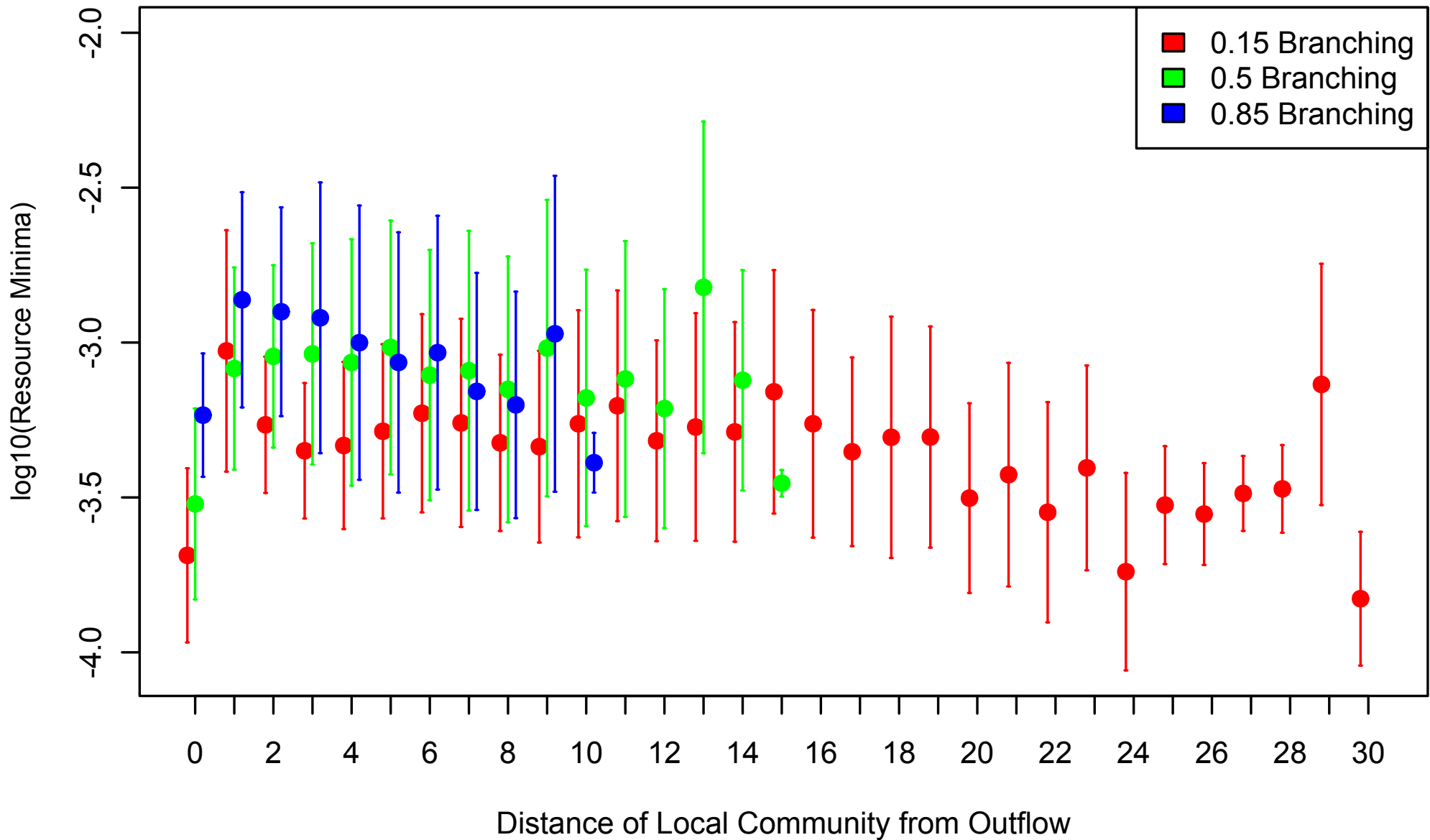

Figure S1. Example spatial patterns of asynchrony in deterministic a) linear and b) ring lattice metacommunities. Shown the most (max.) and least (min.) asynchronous pattern, measured as the number of clusters, of all patterns observed for each level of dispersal. Colors show the relative coefficient of variation among patches, with red being the highest variability patch and blue the lowest.

Figure S2. Resource minima as a function of distance from the outflow community in stochastic river metacommunities. Points shown average minima (+/- SD) calculated in the last 2000 time steps and then across all simulations of metacommunities with $n = 31$ and the given branching probability. Results are again shown for dispersal $D = 1 \times 10^{-1}$.