

# Kent Academic Repository

## Full text document (pdf)

### Citation for published version

Ma, Chaoqun and Shen, Yang and Bearup, Daniel and Fagan, William F. and Liao, Jinbao (2019) Spatial variation in branch size promotes metapopulation persistence in dendritic river networks. *Freshwater Biology* . ISSN 0046-5070. (In press)

### DOI

### Link to record in KAR

<https://kar.kent.ac.uk/78514/>

### Document Version

Author's Accepted Manuscript

#### Copyright & reuse

Content in the Kent Academic Repository is made available for research purposes. Unless otherwise stated all content is protected by copyright and in the absence of an open licence (eg Creative Commons), permissions for further reuse of content should be sought from the publisher, author or other copyright holder.

#### Versions of research

The version in the Kent Academic Repository may differ from the final published version.

Users are advised to check <http://kar.kent.ac.uk> for the status of the paper. **Users should always cite the published version of record.**

#### Enquiries

For any further enquiries regarding the licence status of this document, please contact:

[researchsupport@kent.ac.uk](mailto:researchsupport@kent.ac.uk)

If you believe this document infringes copyright then please contact the KAR admin team with the take-down information provided at <http://kar.kent.ac.uk/contact.html>

1 **Spatial variation in branch size promotes metapopulation persistence**  
2 **in dendritic river networks**

3 Chaoqun Ma<sup>1</sup>, Yang Shen<sup>1</sup>, Daniel Bearup<sup>2</sup>, William F. Fagan<sup>3</sup>, Jinbao Liao<sup>1,\*</sup>

4 <sup>1</sup>Ministry of Education's Key Laboratory of Poyang Lake Wetland and Watershed  
5 Research, School of Geography and Environment, Jiangxi Normal University, Ziyang  
6 Road 99, 330022 Nanchang, China

7 <sup>2</sup>University of Kent, School of Mathematics, Statistics and Actuarial Sciences,  
8 Parkwood Road, Canterbury, CT2 7FS, UK

9 <sup>3</sup>Department of Biology, University of Maryland, College Park, MD 20742, USA

10 **\*Corresponding author:** Prof. Dr. Jinbao Liao (jinbaoliao@163.com)

11 Address: Ziyang Road 99, 330022 Nanchang, Jiangxi Province, China.

12 Tel.: +86-(0)791-88133622

Fax: +86-(0)791-88120538

13

14 **Keywords:** Metapopulation model, riverine networks, spatial branch-size  
15 heterogeneity, species dispersal, spatial branch arrangement.

16

17

18 **Abstract**

- 19 **1.** Despite years of attention, the dynamics of species constrained to disperse within  
20 riverine networks are not well captured by existing metapopulation models, which  
21 often ignore local dynamics within branches.
- 22 **2.** We develop a modelling framework, based on traditional metapopulation theory, for  
23 occupancy dynamics subject to local colonization-extinction dynamics within  
24 branches and directional dispersal between branches in size-structured, bifurcating  
25 riverine networks. Using this framework, we investigate whether and how spatial  
26 variation in branch size affects species persistence for dendritic systems with  
27 directional dispersal.
- 28 **3.** Variation in branch size generally promotes species persistence more obviously at  
29 higher relative extinction rate, suggesting that previous studies ignoring differences  
30 in branch size in real riverine systems might overestimate species extinction risk.
- 31 **4.** Two-way dispersal is not always superior to one-way dispersal as a strategy for  
32 metapopulation persistence especially at high relative extinction rate. The type of  
33 dispersal which maximizes species persistence is determined by the hierarchical  
34 level of the largest, and hence most influential, branch within the network. When  
35 considering the interactive effects of up- and down-stream dispersal, we find that  
36 moderate upstream-biased dispersal maximizes metapopulation viability, mediated  
37 by spatial branch arrangement.
- 38 **5.** Overall, these results suggest that both branch-size variation and species traits  
39 interact to determine species persistence, theoretically demonstrating the ecological

40      significance of their interplay.

41

## 42 **1 INTRODUCTION**

43 Riverine systems are inherently dendritic in structure, with mainstems connecting  
44 multiple blind-ended branches (Fagan, 2002; Muneeppeerakul et al., 2008; Altermatt,  
45 2013). These dendritic topologies feature unique structural and dynamic  
46 characteristics that deserve special attention (Grant, Lowe, & Fagan, 2007). Moreover,  
47 the biodiversity and functional integrity of rivers and streams are severely threatened  
48 by climate change (e.g. flooding and drought) and anthropogenic disturbance (e.g.  
49 hydrodams and pollution). This creates an urgent need for studies that explore how  
50 riverine structures affect ecological patterns and processes.

51 Over the past two decades, numerous theoretical and empirical studies have  
52 examined the effects of different riverine structures on species persistence and  
53 biodiversity, and great advances have already been made in our understanding of their  
54 ecological significance (Fagan, 2002; Muneeppeerakul et al., 2008; Fronhofer, &  
55 Altermatt, 2017). For example, metapopulation persistence in riverine ecosystems was  
56 higher in larger networks especially with greater topological complexity, but this  
57 relationship was greatly influenced by the specific nature of a species' dispersal, such  
58 as upstream or downstream biases (Altermatt, & Fronhofer, 2018; Anderson, & Hayes,  
59 2018; Tonkin et al., 2018; Tonkin, Heino, & Altermatt, 2018). Thus, the interaction of  
60 network topology with species dispersal can affect metapopulation stability in riverine  
61 networks (Mari et al., 2014; Seymour, Fronhofer, & Altermatt, 2016; Terui et al.,  
62 2018).

63 The importance of dispersal connectivity structured by riverine configurations has  
64 been widely appreciated for species persistence (Fagan, 2002; Lowe, 2003; Macneale,  
65 Peckarsky, & Likens, 2005; Grant, 2011), yet current metapopulation models often  
66 fail to capture the reality of riverine systems by ignoring local dynamics within  
67 branches. In fact, riverine branches can provide breeding habitats for many  
68 populations, and species movements observed at regional scales may both emerge  
69 from and influence processes occurring at much smaller scales (Anderson, & Hayes,  
70 2018). This suggests that the local colonization-extinction process within branches  
71 should be explicitly considered in metapopulation dynamics (Woodward, & Hildrew,  
72 2002; Goldberg, Lynch, & Neubert, 2010; Shen et al., 2018; Terui et al., 2018).

73 In nature, river branches routinely display different sizes because of biological or  
74 geomorphological processes (Rodríguez-Iturbe, & Rinaldo, 2001). Differences in  
75 branch size (in which, following McIntosh et al. 2018, we include all physical aspects  
76 of a river branch that could affect capacity to support a population, e.g. branch length,  
77 width and depth, water area and catchment size) may be crucial for understanding the  
78 mechanisms of metapopulation persistence in river networks, as they can mediate the  
79 movement of populations among branches and therefore affect synchronization  
80 between “within-branch” and “among-branch” dynamics (Carrara et al., 2014; Yeakel  
81 et al., 2014; Terui et al., 2018). Likewise, spatial arrangement of different size  
82 branches in hydrological models plays a vital role in shaping basin-scale flow patterns  
83 (Rodríguez-Iturbe, & Rinaldo, 2001), and as such, dispersal interactions between river  
84 populations are often asymmetrically influenced by those upstream due to directional

85 water flow (Grant, Lowe, & Fagan, 2007; Yeakel et al., 2014). Thus, the interaction  
86 between species dispersal and spatial variation in branch size can be expected to  
87 strongly affect the spatiotemporal dynamics of riverine metapopulations. Given all of  
88 this, it seems wise to explicitly consider variation in branch size when modeling  
89 ecological dynamics in river networks. However, this feature is absent from most  
90 previous dendritic ecological models, which have instead stressed the importance of  
91 dispersal among branches for population viability at the expense of branch size/length  
92 and/or local branch dynamics (Carrara et al., 2012, 2014).

93 Here we develop a modelling framework for metapopulation dynamics in  
94 size-structured, bifurcating riverine networks based on the traditional metapopulation  
95 model (Levins, 1969; Hanski, 1998), which has become increasingly prevalent in the  
96 modern ecological literature as it has already proven extremely useful for  
97 understanding the interactive effects of variation in patch size, network topology and  
98 dispersal asymmetry on metapopulation patterns (Vuilleumier et al., 2006; Shtilerman,  
99 & Stone, 2015). In our model, we further consider species dispersal directionality to  
100 reflect the reality that different species often display distinct dispersal behaviors, such  
101 as upstream only dispersal, downstream only dispersal, or two-way “upstream” and  
102 “downstream” dispersal (Schick, & Lindley, 2007). Local population dynamics within  
103 branches are thus subject not only to species regional dispersal but also to the local  
104 colonization-extinction process. With this model, we systematically investigate  
105 whether and how variability in branch size and the arrangement of branches of

106 different size, influence metapopulation persistence for bifurcating systems with  
107 directional dispersal.

## 108 **2 METHODS**

### 109 **2.1 Theoretical framework**

110 We model a bifurcating riverine network of total size one unit ( $F=1$ ), with  $n$   
111 hierarchical levels (total number of branches  $2^n - 1$ ). For model simplicity, each  
112 branch is divided into a variable number of identical patches representing colony sites  
113 for potential populations, disregarding spatiotemporal environmental variability. Thus,  
114 a larger branch contains more patches (illustrated in Figure 1; Muneeppeerakul et al.,  
115 2007). The population of a given branch, and the system as a whole, can be regarded  
116 as proportional to the number of colonized patches within it (Liao et al. 2017a,b,c).  
117 This framework allows us to model both within branch colonization-extinction  
118 processes and the effects of dispersal between branches. We consider three types of  
119 dispersal: one-way dispersal in either the upstream or downstream direction, and  
120 two-way dispersal (both down- and upstream movement). Thus, four processes  
121 determine riverine metapopulation persistence: colonizer production (with a rate  $c$ ),  
122 local extinction (with a rate  $e$ ), downstream dispersal (with a rate  $\lambda$ ) and upstream  
123 dispersal (with a rate  $\lambda'$ ).

124 For simplicity, we assume that species can disperse into the connected branches  
125 freely in each time unit (i.e. neighboring dispersal), unaffected by branch size (Fagan,  
126 2002; Grant, 2011). Based on the traditional metapopulation model (Levins, 1969;  
127 Hanski, 1998), we describe the patch occupancy dynamics for the given branch  $i$  by



$$128 \quad \frac{dp_i}{dt} = \left[ \begin{array}{c} cp_i \\ \text{Colonization} \end{array} + \lambda \begin{array}{c} (p_{j_1} + p_{j_2} - p_i) \\ \text{Net downstream dispersal} \end{array} + \lambda' \begin{array}{c} (p_k / 2 - p_i) \\ \text{Net upstream dispersal} \end{array} \right] \cdot \begin{array}{c} (F_i - p_i) \\ \text{Patch availability} \end{array} - \begin{array}{c} ep_i \\ \text{Extinction} \end{array} . \quad (1)$$

129 Here  $p_i$  represents the number of occupied patches within the branch divided by the  
130 total number of patches in the whole riverine system. We assume that each occupied  
131 patch within a branch produces colonizers at a constant rate  $c$  producing a  
132 *colonization potential*  $cp_i$ . The colonization potential from a given branch is then  
133 divided between local colonization and dispersal and thus, in particular, the dispersal  
134 out of a branch cannot exceed  $cp_i$ , i.e.  $\lambda + \lambda' \leq c$ . Local colonization is supplemented  
135 by dispersal from the neighboring branches  $j_1$  and  $j_2$  (upstream) and  $k$  (downstream).  
136 Thus, the net colonization potential for branch  $i$  is given by its own colonization  
137 potential plus the net dispersal in the up- and down-stream directions. Since only  
138 unoccupied patches can be colonized, the fraction of unoccupied patches within the  
139 branch  $(F_i - p_i)$  limits the overall colonization rate. Note that  $F_i$  denotes the number of  
140 patches within the  $i$ -th branch divided by the total number of patches within the  
141 system. Thus,  $F = \sum F_i = 1$  ( $0 \leq F \leq 1$ ) and the total occupancy of the system  
142 is  $p = \sum_{i=1}^{2^n-1} p_i$ .

143 The riverine networks are assumed to be a closed system without population inflow  
144 and outflow (i.e. completely isolated from external environments), thus in Equation 1,  
145  $-\lambda' p_i = 0$  and  $\lambda(p_{j_1} + p_{j_2}) = 0$  for those upstream blind-ended branches (headwaters),  
146 while  $\lambda' p_k / 2 = 0$  and  $-\lambda p_i = 0$  for the most downstream branch.

## 147 2.2 Simulation cases

148 In addition to the direct effect of varying branch size, the spatial arrangement of the

149 branches can also be expected to influence metapopulation dynamics. To investigate  
150 these effects on species persistence, we consider a small bifurcating riverine network  
151 with three hierarchical levels containing seven branches (total size  $F = \sum_{i=1}^7 F_i = 1$  with  
152 the mean  $\bar{F} = 1/7$ ; see Figure 1). We assume that branch sizes within a riverine  
153 network follow a randomly uniform (unbiased) distribution, which can yield a wider  
154 range of branch-size difference than a skewed (biased) distribution (though it is more  
155 realistic), allowing us to systematically explore the effect of spatial variation in  
156 branch size on metapopulation viability. We perform three distinct numerical  
157 experiments, detailed below.

158 We first consider an idealized riverine network containing a single large branch  
159 with all other branches being the same size (Figures 2-3 & S1-S11 in *Appendix*),  
160 allowing maximum control over the system characteristics. In particular, our system  
161 consisted of six branches with size  $F_i=1/10$  and one branch with size  $F_i=2/5$ . Using  
162 this system, we investigated the effects of the relative extinction rate ( $e/c$  in Figure 2)  
163 and the dispersal rates ( $\lambda$  and  $\lambda'$  in Figure 3), by comparing its three possible spatial  
164 configurations (Figure 1II-IV; though river branch size typically increases towards  
165 downstream) with the reference structure of all branches having the same branch size  
166 ( $F_i=1/7$  in Figure 1I). To ensure that the results obtained are not specific to this  
167 structure, we also considered a more complex, although still idealized, riverine  
168 structure, see *Appendix* (Figure S12-S24) for details.

169 While it is relatively easy to assess how each factor influences species persistence  
170 in an idealized system, these geometries are less realistic. In order to generalize our

171 results for the effects of dispersal rates ( $\lambda$  and  $\lambda'$ ) to more realistic riverine structures  
172 we also calculate equilibrium occupancies on an ensemble of structures with  
173 randomly generated branch sizes. Branch sizes were drawn from a uniform  
174 distribution, with mean equilibrium occupancy and its standard deviation being  
175 calculated for 100 replicates (Figures 4 & S3 in *Appendix*).

176 Finally, we carried out a similar investigation of the effects of variability in branch  
177 size and the relative extinction rate (Figure 5). Likewise, the branch sizes for each  
178 riverine network were randomly drawn from a uniform distribution, and the degree of  
179 variability in branch size in each structure was characterized using the coefficient of  
180 variation  $C.V = \sigma_{F_i} / \bar{F}$  (i.e. the relative dispersion of branch sizes  $F_i$  around the mean  
181  $\bar{F}$ ), with  $\sigma_{F_i}$  being the standard deviation. For each type of dispersal, we randomly  
182 generated 1000 riverine networks with different branch-size variations, and  
183 equilibrium system occupancy was calculated for each network.

184 For each experiment we calculated the non-trivial equilibrium occupancy of the  
185 systems using a numerical solver (ODE45 Matlab R2016a; see Matlab codes in  
186 *Appendix*). All patches were assumed to be initially occupied and simulations were  
187 run until the system approached its steady state. If global patch occupancy fell below  
188  $10^{-5}$ , the metapopulation was assumed to be extinct. Although we did not provide a  
189 formal sensitivity analysis (but see Figures S25-S26 in *Appendix* for a larger network  
190 with four hierarchical levels containing 15 branches), a broad range of biologically  
191 reasonable parameter combinations were explored and found to yield qualitatively  
192 similar outcomes, thus allowing us to present our general outcomes by choosing one

193 of the parameter combinations as a reference case (Figures 1-5 & S1-S24 in  
194 *Appendix*). In our study, we assume that dispersal is limited to the colonization of  
195 neighboring branches. Longer range dispersal events, e.g. to neighbours of neighbours,  
196 could be included but would significantly increase the complexity of the model. An  
197 alternative, allowing global dispersal (i.e. from any patch to any patch) is  
198 straightforward to implement; we obtain  $dp/dt=cp(1-p)-ep$ , with  $p^*=1-e/c$  at  
199 equilibrium. As such, global dispersal can maintain higher species abundance than  
200 neighbour dispersal, more obviously at higher relative extinction rates (e.g. Figure S4  
201 in *Appendix*). However, it must be noted that global dispersal means that river  
202 structure, the focus of this study, has no effect on the occupancy dynamics.

### 203 **3 RESULTS**

#### 204 **3.1 Effects of branch size variation on species persistence in idealized riverine** 205 **structures**

206 Including a single large branch within the riverine structure increases global species  
207 occupancy relative to the reference system (Figure 2 II-IV vs. I), regardless of other  
208 factors. This trend becomes stronger at higher relative extinction rates  $e/c$ . As a  
209 natural consequence of these trends, the species extinction threshold (i.e. the maximal  
210 value of  $e/c$  that a species can tolerate without going extinct) is lowest in the reference  
211 geometry but is much higher in the heterogeneous networks. Since the species is able  
212 to persist in the large branch at much higher values of  $e/c$  than it can in the smaller  
213 branches (Figures S5-S7 & S16-S18 in *Appendix*). Furthermore, dispersal from the

214 larger branch allows species to survive in the smaller branches at high relative  
215 extinction rates which would result in species extinction in the reference system.

216 For low relative extinction rates, dispersal bias has little effect on global occupancy  
217 (Fig. 2, see also S1 & S13-S14 in *Appendix*). Increasing the relative extinction rate  
218 makes smaller habitats less favorable, allowing effects of dispersal bias to emerge, in  
219 particular in relation to the underlying structure of river network. Regardless of the  
220 underlying riverine structure, an upstream-biased dispersal maximizes global  
221 occupancy (Figure 3), although the riverine structure does determine the optimal level  
222 of bias. The highest global occupancy is attained when the large branch is at the  
223 lowest hierarchical level (Figure 3II). In this case, upstream dispersal allows a large  
224 population in this branch to support the population of all other branches within the  
225 system (Figure S9). In the other configurations, some regions of the riverine network  
226 gain no benefit from the large branch (Figures S10 & S11). At high relative extinction  
227 rates, the optimal strategy for species survival is to disperse only in the direction of  
228 the largest branch. For example, if the largest branch is located at the lowest  
229 hierarchical level, then downstream-only dispersal leads to a highest global occupancy,  
230 in contrast to the case with the largest branch at headwaters (Figure S1II vs. IV).

231 Consequently, our model predicts that the extinction threshold of a species is  
232 maximized if no dispersal from the large branch is possible (Figure S2). In particular,  
233 if the large branch is at one end of the network, the optimal dispersal bias is in the  
234 direction of that large branch (Figure S2). If the large branch is one of the  
235 intermediate branches, zero dispersal in both directions is optimal (Figure S2).

236 **3.2 Effects of species characteristics on population persistence in networks with**  
237 **random branch sizes**

238 The trends we observe for the idealized riverine structures above are preserved for  
239 networks with random branch sizes. In particular, a moderate upstream-biased  
240 dispersal is optimal for low relative extinction rates (Figure 4) and no dispersal is  
241 optimal at high relative extinction rates (Figure S3). Moreover, increasing the relative  
242 extinction rate  $e/c$  decreases the global occupancy (Figure 5). The latter result follows  
243 from the fact that the effect of the relative extinction rate is independent of the  
244 network structure (cf. Figure 2), and, as such, randomizing that structure does not  
245 change the effect. Similarly, for low  $e/c$  upstream-biased dispersal is optimal  
246 regardless of the position of larger branches. Thus, while the degree of bias varies  
247 between systems within the ensemble, on average, the optimal bias must be upstream.  
248 For high  $e/c$ , dispersal out of the largest branch decreases global occupancy. In a  
249 random network, the position of this branch is random, thus zero dispersal is optimal.

250 Increasing variation in branch size within the network (characterized by the  
251 coefficient of variation,  $C.V$ ) increased global occupancy (Figure 5). This follows  
252 from, and generalizes, the observation that incorporating a large branch within the  
253 network increases the equilibrium population. In particular, variation in branch size  
254 means that some branches must be larger than others. Furthermore, since the size of  
255 the network as a whole is fixed, increasing this variation requires that the largest  
256 branch contains a greater proportion of the total habitat, i.e. become larger. We finally  
257 found that there is a significant difference in global occupancy between the three

258 dispersal types (Friedman rank sum test with  $P < 0.01$ ), with upstream-inclusive  
259 dispersal generally yielding the higher levels of global patch occupancy than one-way  
260 downstream dispersal. Irrespective of dispersal type, we further observed high  
261 variability in patch occupancy, most likely resulting from the stochasticity in branch  
262 sizes and variation in branch arrangements.

#### 263 **4 DISCUSSION**

264 Most existing models of riverine metapopulations treat all river branches as identical  
265 nodes (Fagan, 2002; Grant, Lowe, & Fagan, 2007; Grant, 2011). In reality, branch  
266 size/length often varies across a riverine network, and this variation is exactly what  
267 our theoretical framework seeks to capture. Using this model, we have identified key  
268 interactions between branch-size heterogeneity and species traits that determine  
269 species persistence, confirming the ecological significance of their interplay  
270 (Altermatt, 2013; Carrara et al., 2014).

271 Irrespective of other factors, variation in branch size increases the equilibrium  
272 population of the habitat and, consequently, reduces the risk that a species becomes  
273 extinct. In traditional metapopulation models (Levins, 1969; Hanski, 1998), one effect  
274 of the extinction process is that a fixed number of patches within each habitat are  
275 unoccupied in the equilibrium state. As a result, dividing a habitat into smaller  
276 sub-habitats (summing to the same size) decreases the overall population of the  
277 habitat (cf. habitat fragmentation; Fahrig, 2001, 2002; Liao, et al. 2013a,b). The effect  
278 of variation in branch size observed in this study can be understood as arising from a

279 similar process. In particular, increasing branch size heterogeneity concentrates  
280 available habitat within a small number of large branches, thereby reducing effective  
281 habitat fragmentation relative to the system of all branches having the same size.  
282 Additionally, smaller populations are more vulnerable to small localized  
283 environmental perturbations (which are relatively common) than large populations,  
284 and thus that branch size heterogeneity provides a buffer against such extinction risks.  
285 A counter-point is that concentrating population within a smaller number of branches  
286 creates the potential that a small number of large perturbations (which are relatively  
287 rare) could drive the species to extinction. We note that our deterministic model does  
288 not include stochastic perturbations and thus does not directly capture either of these  
289 effects. These observations suggest that previous studies assuming a constant branch  
290 size may have overestimated species extinction risks (Anholt, 1995; Fagan, 2002;  
291 Goldberg, Lynch, & Neubert, 2010; Grant, 2011). As such, if we incorporate  
292 branch-size heterogeneity into the model of Anholt (1995), this might further  
293 strengthen the mechanism of density dependence that is proposed to resolve the  
294 stream drift paradox in that study.

295       A recent study by Terui et al. (2018) made the prediction, supported by empirical  
296 evidence, that greater variation in branch size would decrease metapopulation stability.  
297 While this appears to contrast with our findings, in fact the two studies consider  
298 different properties of a population within a riverine habitat. We consider the  
299 equilibrium size of the population, which gives an indicator of how far the population  
300 is from extinction. Of course, in practice populations fluctuate around this equilibrium



301 due to environmental perturbations. Terui et al. (2018) considered the degree of  
302 synchrony in these fluctuations, to assess whether all sub-populations are  
303 simultaneously more vulnerable to a perturbation event. Which metric is more  
304 indicative of extinction risk depends on the size of the fluctuations relative to that of  
305 the sub-populations. Small fluctuations, relative to the size of a sub-population, do not  
306 typically present a significant threat to that population even if synchronized. As such,  
307 we suggest that branch size heterogeneity will tend to ameliorate the threat posed by  
308 synchronized fluctuations, as the larger sub-populations (in larger branches) will be  
309 subject to smaller (relatively) fluctuations.

310       The effect of dispersal within a heterogeneous riverine network on the overall  
311 population depends strongly on the extinction pressure imposed on the species. In  
312 particular, for low relative extinction rates, dispersal increases the equilibrium  
313 population. Populations in large branches produce an excess of colonizers which  
314 disperse into the smaller branches, increasing the population of these sub-optimal  
315 branches and thus the population of the habitat as a whole. However, at high relative  
316 extinction rates, the full colonization potential of a large population is required to  
317 sustain that population. Dispersal into smaller branches can allow the species to  
318 persist through a larger portion of the habitat, but at the cost of reducing the total  
319 population. This is supported by an empirical observation that upstream dispersal of  
320 Japanese freshwater mussel into cooler tributaries (poorer habitats) could cause net  
321 loss of the dispersing populations (Terui et al. 2014a, b).

322 In our systems, when dispersal has a beneficial effect, i.e. for low relative  
323 extinction rates, a moderate upstream bias is typically optimal. This results from the  
324 hierarchical branching structure of our networks, that is, upstream dispersal divides  
325 colonizers between branches, increasing the likelihood that they are able to find  
326 suitable colony sites. By contrast, downstream dispersing colonizers must compete for  
327 colony sites with those coming from another branch and thus are less likely to be  
328 successful. Nonetheless, some downstream dispersal remains beneficial since  
329 upstream branches can be population sources. Previous studies have predicted that  
330 two-way dispersal should always be superior to one-way dispersal in riverine  
331 networks (Fagan, 2002; Grant, Lowe, & Fagan, 2007; Goldberg, Lynch, & Neubert,  
332 2010; Grant, 2011; Shen et al., 2018). Our results refine this prediction, agreeing that  
333 two-way dispersal is generally preferable to one-way dispersal, but noting that the  
334 topology of the riverine network may produce a preferred direction. This refinement  
335 finds some support in empirical observations, in particular the prevalence of  
336 upstream-biased dispersal in stream-dwelling organisms (see Lowe, 2003; Macneale,  
337 Peckarsky, & Likens, 2005).

338 For high relative extinction rates, where dispersal has a negative effect on global  
339 occupancy, no dispersal is, strictly speaking, the optimal strategy. In practice, if one  
340 end of the largest branch is closed, i.e. dispersal is not possible in one direction,  
341 dispersal in that direction does not negatively affect global occupancy. In this case  
342 there is no dispersal out of the optimal habitat, only dispersal into it from the other  
343 branches (for as long as they support a population). This is supported by the

344 observation from Terui et al. (2014b) that some aquatic species display strongly  
345 downstream-biased dispersal in riverine systems with large downstream branches.

346 The diverse metapopulation patterns predicted in our model are supported by some  
347 field observations in riverine ecosystems. For example, studies on macroinvertebrate  
348 populations in New Zealand streams found that population structure was best  
349 explained by a combination of local and regional forces rather than by any  
350 scale-specific set of processes individually (Thompson, & Townsend, 2006). In  
351 contrast, in more isolated headwaters, populations of benthic macroinvertebrates were  
352 strongly influenced by local environmental factors (Heino, & Mykrä, 2008; Brown, &  
353 Swan, 2010; Patrick, & Swan, 2011). Because high dispersal rates are often sufficient  
354 to swamp the effects of local population dynamics, other investigations found that fish  
355 community dynamics in the Mississippi-Missouri drainage could be modeled with  
356 only regional dispersal-driven processes (Muneepeerakul et al., 2008; Azaele et al.,  
357 2009; Convertino et al., 2009).

358 The modelling framework presented here is formulated by omitting some features  
359 known to occur in natural riverine systems, such as spatial environmental  
360 heterogeneity and temporal environmental variability (Liao et al., 2013b).  
361 Nevertheless, as a starting point, our model reflects that species traits (e.g. species  
362 dispersal and relative extinction rate) and spatial branch-size difference can jointly  
363 affect metapopulation dynamics in riverine systems that feature some forms of  
364 heterogeneity (Bertuzzo et al., 2011; Yeakel et al., 2014; Terui et al., 2018). Further  
365 extensions of this work could include disturbances (e.g. seasonal drought and flooding,

366 and disruption in riverine connectivity by hydrodams; Vaughn, & Taylor, 1999;  
367 Ishiyama et al., 2018), species interactions, invasion dynamics, and the relationship  
368 between branch complexity and metacommunity stability. Overall, we found strong  
369 effects of variability of branch size on species persistence, suggesting that this  
370 realistic feature should be explored in future models of riverine metapopulations.

371

372 **Acknowledgements**

373 This study was supported by the National Science Foundation of China (No.  
374 31901175 and 31760172), the Thousand Young Talents Plan of China, the Jiangxi  
375 Provincial Education Department (No. GJJ160274), and the Key Joint Youth Project  
376 of Jiangxi Province (No. 20192ACBL21029).

377 **Author contributions**

378 C.M. and J.L. designed this study; C.M., Y.S., D.B., W.F.F. and J.L. performed  
379 numerical simulations and analyzed the results; J.L., C.M. and D.B. wrote the first  
380 draft of the manuscript and all authors contributed substantially to revisions.

381 **Competing interests:** The authors declare no competing interests.

382 **Supporting information**

383 *Appendix* accompanies this manuscript is also supplied.

384 **Data accessibility**

385 This is a theoretical modelling study and does not use data.

386

387 **References**

- 388 Altermatt, F. (2013). Predicting novel trophic interactions in a non-native world.  
389 *Ecology Letters*, 16(8), 1088-1094. DOI:10.1111/ele.12143
- 390 Altermatt, F., & Fronhofer, E.A. (2018). Dispersal in dendritic networks: ecological  
391 consequences on the spatial distribution of population densities. *Freshwater*  
392 *Biology*, 63, 22-32. DOI: 10.1111/fwb.12951
- 393 Anderson, K.E., & Hayes, S.M. (2018). The effects of dispersal and river spatial  
394 structure on asynchrony in consumer–resource metacommunities. *Freshwater*  
395 *Biology*, 63, 100-113. DOI: 10.1111/fwb.12998
- 396 Anholt, B.R. (1995). Density dependence resolves the stream drift paradox. *Ecology*,  
397 76, 2235-2239. DOI: 10.2307/1941697
- 398 Azaele, S., Muneeppeerakul, R., Maritan, A., Rinaldo, A., & Rodriguez-Iturbe, I.  
399 (2009). Predicting spatial similarity of freshwater fish biodiversity. *Proceedings*  
400 *of the National Academy of Sciences*, 106(17), 7058-7062.  
401 DOI:10.1073/pnas.0805845106
- 402 Bertuzzo, E., Suweis, S., Mari, L., Maritan, A., Rodríguez-Iturbe, I., & Rinaldo, A.  
403 (2011). Spatial effects on species persistence and implications for biodiversity.  
404 *Proceedings of the National Academy of Sciences*, 108(11), 4346-4351.  
405 DOI:10.1073/pnas.1017274108
- 406 Brown, B. L., & Swan, C. M. (2010). Dendritic network structure constrains  
407 metacommunity properties in riverine ecosystems. *Journal of Animal Ecology*,  
408 79(3), 571-580. DOI:10.1111/j.1365-2656.2010.01668.x
- 409 Carrara, F., Altermatt, F., Rodriguez-Iturbe, I., & Rinaldo, A. (2012). Dendritic  
410 connectivity controls biodiversity patterns in experimental metacommunities.  
411 *Proceedings of the National Academy of Sciences*, 109(15), 5761-5766.  
412 DOI:10.1073/ pnas.1119651109

- 413 Carrara, F., Rinaldo, A., Giometto, A., & Altermatt, F. (2014). Complex interaction of  
414 dendritic connectivity and hierarchical patch size on biodiversity in river-like  
415 landscapes. *The American Naturalist*, 183(1), 13-25. DOI:10.1086/ 674009
- 416 Convertino, M., Muneeppeerakul, R., Azaele, S., Bertuzzo, E., Rinaldo, A., &  
417 Rodriguez-Iturbe, I. (2009). On neutral metacommunity patterns of river basins  
418 at different scales of aggregation. *Water Resources Research*, 45(8), 4972-4974.  
419 DOI:10.1029/2009WR007799
- 420 Deiner, K., Fronhofer, E. A., Mächler, E., Walser, J. C., & Altermatt, F. (2016).  
421 Environmental DNA reveals that rivers are conveyer belts of biodiversity  
422 information. *Nature Communications*, 7, 12544. DOI:10.1038/ncomms12544
- 423 Fagan, W. F. (2002). Connectivity, fragmentation, and extinction risk in dendritic  
424 metapopulations. *Ecology*, 83(12), 3243-3249. DOI:10.2307/3072074
- 425 Fahrig, L. (2001). How much habitat is enough? *Biological Conservation*, 100, 65-74.  
426 DOI:10.1016/s0006-3207(00)00208-1
- 427 Fahrig, L. (2002). Effect of habitat fragmentation on the extinction threshold: A  
428 synthesis. *Ecological Applications*, 12, 346-353. DOI:10.2307/3060946
- 429 Fronhofer, E. A., & Altermatt, F. (2017). Classical metapopulation dynamics and  
430 eco-evolutionary feedbacks in dendritic networks. *Ecography*, 40, 1455-1466.  
431 DOI:10.1111/ecog.02761
- 432 Goldberg, E. E., Lynch, H. J., & Neubert, M. G. (2010). Effects of branching spatial  
433 structure and life history on the asymptotic growth rate of a population.  
434 *Theoretical Ecology*, 3(3), 137-152. DOI:10.1007/s12080-009-0058-0
- 435 Grant, E. H. C., Lowe, W. H., & Fagan, W. F. (2007). Living in the branches:  
436 population dynamics and ecological processes in dendritic networks. *Ecology*  
437 *Letters*, 10(2), 165-175. DOI:10.1111/j.1461-0248.2006.01007.x
- 438 Grant, E. H. C. (2011). Structural complexity, movement bias, and metapopulation

439 extinction risk in dendritic ecological networks. *Freshwater Science*, 30(1),  
440 252-258. DOI:10.1899/09-120.1

441 Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396(6706), 41-49.  
442 DOI:10.1038/23876

443 Heino, J., & Mykrä, H. (2008). Control of stream insect assemblages: roles of spatial  
444 configuration and local environmental factors. *Ecological Entomology*, 33(5),  
445 614-622. DOI:10.1111/j.1365-2311.2008.01012.x

446 Ishiyama, N., et al. (2018). Predicting the ecological impacts of large dam removals  
447 on a river network based on habitat network structure and flow regimes.  
448 *Conservation Biology*, 32(6), 1403-1413. DOI:10.1111/cobi.13137

449 Kleinhans, D., & Jonsson, P. R. (2011). On the impact of dispersal asymmetry on  
450 metapopulation persistence. *Journal of Theoretical Biology*, 290, 37-45.  
451 DOI:10.1016/j.jtbi.2011.09.002

452 Levins, R. (1969). Some demographic and genetic consequences of environmental  
453 heterogeneity for biological control. *Bulletin of the Entomological Society of*  
454 *America*, 15(3), 237-240. DOI:10.1093/besa/15.3.237

455 Liao, J., Li, Z., Hiebeler, D.E., El-Bana, M., Deckmyn, G., & Nijs, I. (2013a).  
456 Modelling plant population size and extinction thresholds from habitat loss and  
457 habitat fragmentation: effects of neighbouring competition and dispersal strategy.  
458 *Ecological Modelling*, 268, 9-17. DOI:10.1016/j.ecolmodel.2013.07.021

459 Liao, J., et al. (2013b). Species persistence in landscapes with spatial variation in  
460 habitat quality: a pair approximation model. *Journal of Theoretical Biology*,  
461 335(20), 22-30. DOI:10.1016/j.jtbi.2013.06.015

462 Liao, J., et al. (2017a). Robustness of metacommunities with omnivory to habitat  
463 destruction: disentangling patch fragmentation from patch loss. *Ecology*, 98(6),  
464 1631-1639. DOI:10.1002/ecy.1830



- 465 Liao, J., Bearup, D., & Blasius, B. (2017b). Food web persistence in fragmented  
466 landscapes. *Proceedings of the Royal Society B*, 284, 20170350.  
467 DOI:10.1098/rspb.2017.0350
- 468 Liao, J., Bearup, D., & Blasius, B. (2017c). Diverse responses of species to landscape  
469 fragmentation in a simple food chain. *Journal of Animal Ecology*, 86, 1169-1178.  
470 DOI:10.1111/1365-2656.12702
- 471 Lowe, W. H. (2003). Linking dispersal to local population dynamics: A case study  
472 using a headwater salamander system. *Ecology*, 84, 2145-2154.  
473 DOI:10.2307/3450038
- 474 Macneale, K. H., Peckarsky, B. L., & Likens, G. E. (2005). Stable isotopes identify  
475 dispersal patterns of stonefly populations living along stream corridors.  
476 *Freshwater Biology*, 50, 1117-1130. DOI:10.1111/j.1365-2427.2005.01387.x
- 477 Mari, L., Casagrandi, R., Bertuzzo, E., Rinaldo, A., & Gatto, M. (2014).  
478 Metapopulation persistence and species spread in river networks. *Ecology Letters*,  
479 17(4), 426-434. DOI:10.1111/ele.12242
- 480 McIntosh, A. R., Mchugh, P. A., Plank, M. J., Jellyman, P. G., Warburton, H. J., &  
481 Greig, H. S. (2018). Capacity to support predators scales with habitat size.  
482 *Science Advances*, 4, eaap7523. DOI:10.1126/sciadv.aap7523
- 483 Muneeppeerakul, R., Weitz, J. S., Levin, S. A., Rinaldo, A., & Rodriguez-Iturbe, I.  
484 (2007). A neutral metapopulation model of biodiversity in river networks.  
485 *Journal of Theoretical Biology*, 245(2), 351-363. DOI:10.1016/j.jtbi.2006.10.005
- 486 Muneeppeerakul, R., Bertuzzo, E., Lynch, H. J., Fagan, W. F., Rinaldo, A., &  
487 Rodriguez-Iturbe, I. (2008). Neutral metacommunity models predict fish  
488 diversity patterns in Mississippi–Missouri basin. *Nature*, 453(7192), 220-222.  
489 DOI:10.1038/nature06813
- 490 Patrick, C. J., & Swan, C. M. (2011). Reconstructing the assembly of a stream-insect

491 metacommunity. *Freshwater Science*, 30(1), 259-272. DOI:10.1899/09-169.1

492 Rodríguez-Iturbe, I., & Rinaldo, A. (2001). Fractal river basins: chance and  
493 self-organization. Cambridge University Press.

494 Schick, R. S., & Lindley, S. T. (2007). Directed connectivity among fish populations  
495 in a riverine network. *Journal of Applied Ecology*, 44(6), 1116-1126.  
496 DOI:10.1111/j.1365-2664.2007.01383.x

497 Seymour, M., Seppälä, K., Mächler, E., & Altermatt, F. (2016). Lessons from the  
498 macroinvertebrates: species-genetic diversity correlations highlight important  
499 dissimilar relationships. *Freshwater Biology*, 61, 1819-1829.  
500 DOI:10.1111/fwb.12816

501 Shen, Y., Xu, Z., Nijs, I., & Liao, J. (2018). Spatial arrangement of size-different  
502 patches determines population dynamics in linear riverine systems. *Ecological*  
503 *Modelling*, 385, 220-225. DOI:10.1016/j.ecolmodel.2018.07.021

504 Shtilerman, E., & Stone, L. (2015). The effects of connectivity on metapopulation  
505 persistence: network symmetry and degree correlations. *Proceedings of the*  
506 *Royal Society B*, 282(1806), 20150203. DOI:10.1098/rspb.2015.0203

507 Terui, A., et al. (2014a). Dispersal of larvae of *Margaritifera laevis* by its host fish.  
508 *Freshwater Science*, 33, 112-123. DOI:10.1086/674577

509 Terui, A., et al. (2014b). Asymmetric dispersal structures a riverine metapopulation of  
510 the freshwater pearl mussel *Margaritifera laevis*. *Ecology and Evolution*, 4,  
511 3004-3014. DOI:10.1002/ece3.1135

512 Terui, A., et al. (2018). Metapopulation stability in branching river networks.  
513 *Proceedings of the National Academy of Sciences* 115, E5963-E5969.  
514 DOI:10.1073/pnas.1800060115

515 Thompson, R., & Townsend, C. (2006). A truce with neutral theory: local  
516 deterministic factors, species traits and dispersal limitation together determine

517 patterns of diversity in stream invertebrates. *Journal of Animal Ecology*, 75(2),  
518 476-484. DOI:10.2307/3505591

519 Tonkin, J. D., Heino, J., & Altermatt, F. (2018). Metacommunities in river networks:  
520 the importance of network structure and connectivity on patterns and  
521 processes. *Freshwater Biology*, 63, 1-5. DOI:10.1111/fwb.13045

522 Tonkin, J. D., et al. (2018). The role of dispersal in river network metacommunities:  
523 patterns, processes, and pathways. *Freshwater Biology*, 63, 141-163.  
524 DOI:10.1111/fwb.13037

525 Vaughn, C. C., & Taylor, C. M. (1999). Impoundments and the decline of freshwater  
526 mussels: A case study of an extinction gradient. *Conservation Biology*, 13,  
527 912-920. DOI:10.1046/j.1523-1739.1999.97343.x

528 Vuilleumier, S., & Possingham, H. (2006). Does colonization asymmetry matter in  
529 metapopulations? *Proceedings of the Royal Society B*, 273(1594), 1637.  
530 DOI:10.1098/rspb.2006.3469

531 Woodward, G., & Hildrew, A. G. (2002). Food web structure in riverine landscape.  
532 *Freshwater Biology*, 47(4), 777-798. DOI:10.1046/j.1365-2427.2002.00908.x

533 Yeakel, J. D., Moore, J. W., Guimaraes, P. R., & de Aguiar, M. A. M. (2014).  
534 Synchronisation and stability in river metapopulation networks. *Ecology Letters*,  
535 17, 273-283. DOI:10.1111/ele.12228

536

537 **Figure captions**

538 **Figure 1.** Four size-structured bifurcating riverine networks consisting of seven  
539 branches (represented by circles). Graph (I): the reference structure with all branches  
540 having the same size  $F_i=1/7$ . Graphs (II-IV): three network structures with different  
541 spatial branch arrangements, containing one large branch  $F_i=2/5$  and six small  
542 branches with the same size  $F_i=1/10$ . Each branch is partitioned into a number of  
543 size-equal patches (denoted by grids), with larger branch having more patches. The  
544 solid lines denote species dispersal pathways.

545 **Figure 2.** Species persistence in different riverine structures (as shown in Figure 1I-IV;  
546 denoted by colored lines) by varying relative extinction rate ( $0 < e/c < 1$  at fixed  $c=1$ ),  
547 comparing three types of dispersal: (a) only downstream dispersal (with rate  $\lambda=0.25$  &  
548  $\lambda'=0$ ), (b) only upstream dispersal ( $\lambda=0$  &  $\lambda'=0.25$ ), and (c) two-way down- and  
549 up-stream dispersal ( $\lambda=\lambda'=0.125$ ).

550 **Figure 3.** Interactive effects of downstream and upstream dispersal on global patch  
551 occupancy at steady state in different bifurcating networks (graphs I~IV  
552 corresponding to the riverine structures as shown in Figure 1I-IV). Dash lines  
553 represent species symmetric dispersal with  $\lambda=\lambda'$ . Other parameters:  $c=1$  and  $e=0.1$ .  
554 Note that  $\lambda+\lambda' < c$ , as the total dispersal rate out of a branch should be less than the  
555 propagule production rate.

556

557 **Figure 4.** Interactive effects of downstream and upstream dispersal on average patch  
558 occupancy at steady state in size-structured bifurcating networks with three  
559 hierarchical levels containing seven branches. Graphs (a & b) with different color  
560 ramp scales: mean  $\pm$  standard deviation (*SD*) of global patch occupancies on 100  
561 riverine networks of varying branch sizes ( $F_i$ ), which were randomly generated from a  
562 uniform distribution around the mean  $\bar{F} = 1/7$ . Dash lines represent species symmetric  
563 dispersal with  $\lambda = \lambda'$ . Invalid region:  $\lambda + \lambda' > c$ . Other parameters: see Figure 3.

564 **Figure 5.** Effect of variation in branch size (coefficient of variation – *C.V*) on global  
565 patch occupancy at steady state in bifurcating riverine networks with three  
566 hierarchical levels containing seven branches by varying  $e/c$  (panels a-d:  $e/c = 0.1, 0.15,$   
567  $0.2, 0.25$  at  $c = 1$ ). Branch sizes ( $F_i$ ) are randomly generated from a uniform  
568 distribution around the mean  $\bar{F} = 1/7$ , with 1000 replicates for each type of dispersal  
569 (colored circles; including only downstream dispersal  $\lambda = 0.25$  &  $\lambda' = 0$ , only upstream  
570 dispersal  $\lambda = 0$  &  $\lambda' = 0.25$ , and two-way dispersal  $\lambda = \lambda' = 0.125$ ), fitted by fourth-degree  
571 polynomial curves. Different dispersal modes lead to a significant difference in  
572 species occupancy by using Friedman rank sum test: (a) Chi-square = 1404.3 &  
573  $P < 0.01$ ; (b) Chi-square = 1204 &  $P < 0.01$ ; (c) Chi-square = 436.14 &  $P < 0.01$ ; (d)  
574 Chi-square = 169.68 &  $P < 0.01$ .