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Spatial variation in branch size promotes metapopulation persistence in dendritic river networks

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Abstract

1. Despite years of attention, the dynamics of species constrained to disperse within riverine networks are not well captured by existing metapopulation models, which often ignore local dynamics within branches.

2. We develop a modelling framework, based on traditional metapopulation theory, for occupancy dynamics subject to local colonization-extinction dynamics within branches and directional dispersal between branches in size-structured, bifurcating riverine networks. Using this framework, we investigate whether and how spatial variation in branch size affects species persistence for dendritic systems with directional dispersal.

3. Variation in branch size generally promotes species persistence more obviously at higher relative extinction rate, suggesting that previous studies ignoring differences in branch size in real riverine systems might overestimate species extinction risk.

4. Two-way dispersal is not always superior to one-way dispersal as a strategy for metapopulation persistence especially at high relative extinction rate. The type of dispersal which maximizes species persistence is determined by the hierarchical level of the largest, and hence most influential, branch within the network. When considering the interactive effects of up- and down-stream dispersal, we find that moderate upstream-biased dispersal maximizes metapopulation viability, mediated by spatial branch arrangement.

5. Overall, these results suggest that both branch-size variation and species traits interact to determine species persistence, theoretically demonstrating the ecological

significance of their interplay.

1 INTRODUCTION

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

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

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

In nature, river branches routinely display different sizes because of biological or geomorphological processes (Rodríguez-Iturbe, & Rinaldo, 2001). Differences in branch size (in which, following McIntosh et al. 2018, we include all physical aspects of a river branch that could affect capacity to support a population, e.g. branch length, width and depth, water area and catchment size) may be crucial for understanding the mechanisms of metapopulation persistence in river networks, as they can mediate the movement of populations among branches and therefore affect synchronization between "within-branch" and "among-branch" dynamics (Carrara et al., 2014; Yeakel et al., 2014; Terui et al., 2018). Likewise, spatial arrangement of different size branches in hydrological models plays a vital role in shaping basin-scale flow patterns (Rodríguez-Iturbe, & Rinaldo, 2001), and as such, dispersal interactions between river populations are often asymmetrically influenced by those upstream due to directional water flow (Grant, Lowe, & Fagan, 2007; Yeakel et al., 2014). Thus, the interaction between species dispersal and spatial variation in branch size can be expected to strongly affect the spatiotemporal dynamics of riverine metapopulations. Given all of this, it seems wise to explicitly consider variation in branch size when modeling ecological dynamics in river networks. However, this feature is absent from most previous dendritic ecological models, which have instead stressed the importance of dispersal among branches for population viability at the expense of branch size/length and/or local branch dynamics (Carrara et al., 2012, 2014).

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

2 METHODS

2.1 Theoretical framework

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

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

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

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

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

2.2 Simulation cases

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

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

While it is relatively easy to assess how each factor influences species persistence in an idealized system, these geometries are less realistic. In order to generalize our results for the effects of dispersal rates (λ and λ') to more realistic riverine structures we also calculate equilibrium occupancies on an ensemble of structures with randomly generated branch sizes. Branch sizes were drawn from a uniform distribution, with mean equilibrium occupancy and its standard deviation being calculated for 100 replicates (Figures 4 & S3 in *Appendix*).

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

For each experiment we calculated the non-trivial equilibrium occupancy of the systems using a numerical solver (ODE45 Matlab R2016a; see Matlab codes in *Appendix*). All patches were assumed to be initially occupied and simulations were run until the system approached its steady state. If global patch occupancy fell below 10^{-5}, the metapopulation was assumed to be extinct. Although we did not provide a formal sensitivity analysis (but see Figures S25-S26 in *Appendix* for a larger network with four hierarchical levels containing 15 branches), a broad range of biologically reasonable parameter combinations were explored and found to yield qualitatively similar outcomes, thus allowing us to present our general outcomes by choosing one of the parameter combinations as a reference case (Figures 1-5 & S1-S24 in *Appendix*). In our study, we assume that dispersal is limited to the colonization of neighboring branches. Longer range dispersal events, e.g. to neighbours of neighbours, could be included but would significantly increase the complexity of the model. An alternative, allowing global dispersal (i.e. from any patch to any patch) is straightforward to implement; we obtain $dp/dt=cp(1-p)-ep$, with $p^*=1-e/c$ at equilibrium. As such, global dispersal can maintain higher species abundance than neighbour dispersal, more obviously at higher relative extinction rates (e.g. Figure S4 in *Appendix*). However, it must be noted that global dispersal means that river structure, the focus of this study, has no effect on the occupancy dynamics.

3 RESULTS

3.1 Effects of branch size variation on species persistence in idealized riverine structures

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

For low relative extinction rates, dispersal bias has little effect on global occupancy (Fig. 2, see also S1 & S13-S14 in *Appendix*). Increasing the relative extinction rate makes smaller habitats less favorable, allowing effects of dispersal bias to emerge, in particular in relation to the underlying structure of river network. Regardless of the underlying riverine structure, an upstream-biased dispersal maximizes global occupancy (Figure 3), although the riverine structure does determine the optimal level of bias. The highest global occupancy is attained when the large branch is at the lowest hierarchical level (Figure 3II). In this case, upstream dispersal allows a large population in this branch to support the population of all other branches within the system (Figure S9). In the other configurations, some regions of the riverine network gain no benefit from the large branch (Figures S10 & S11). At high relative extinction rates, the optimal strategy for species survival is to disperse only in the direction of the largest branch. For example, if the largest branch is located at the lowest hierarchical level, then downstream-only dispersal leads to a highest global occupancy, in contrast to the case with the largest branch at headwaters (Figure S1II vs. IV). Consequently, our model predicts that the extinction threshold of a species is maximized if no dispersal from the large branch is possible (Figure S2). In particular, if the large branch is at one end of the network, the optimal dispersal bias is in the direction of that large branch (Figure S2). If the large branch is one of the intermediate branches, zero dispersal in both directions is optimal (Figure S2).

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

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

Increasing variation in branch size within the network (characterized by the coefficient of variation, *C.V*) increased global occupancy (Figure 5). This follows from, and generalizes, the observation that incorporating a large branch within the network increases the equilibrium population. In particular, variation in branch size means that some branches must be larger than others. Furthermore, since the size of the network as a whole is fixed, increasing this variation requires that the largest branch contains a greater proportion of the total habitat, i.e. become larger. We finally found that there is a significant difference in global occupancy between the three dispersal types (Friedman rank sum test with $P<0.01$), with upstream-inclusive dispersal generally yielding the higher levels of global patch occupancy than one-way downstream dispersal. Irrespective of dispersal type, we further observed high variability in patch occupancy, most likely resulting from the stochasticity in branch sizes and variation in branch arrangements.

4 DISCUSSION

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

Irrespective of other factors, variation in branch size increases the equilibrium population of the habitat and, consequently, reduces the risk that a species becomes extinct. In traditional metapopulation models (Levins, 1969; Hanski, 1998), one effect of the extinction process is that a fixed number of patches within each habitat are unoccupied in the equilibrium state. As a result, dividing a habitat into smaller sub-habitats (summing to the same size) decreases the overall population of the habitat (cf. habitat fragmentation; Fahrig, 2001, 2002; Liao, et al. 2013a,b). The effect of variation in branch size observed in this study can be understood as arising from a similar process. In particular, increasing branch size heterogeneity concentrates available habitat within a small number of large branches, thereby reducing effective habitat fragmentation relative to the system of all branches having the same size. Additionally, smaller populations are more vulnerable to small localized environmental perturbations (which are relatively common) than large populations, and thus that branch size heterogeneity provides a buffer against such extinction risks. A counter-point is that concentrating population within a smaller number of branches creates the potential that a small number of large perturbations (which are relatively rare) could drive the species to extinction. We note that our deterministic model does not include stochastic perturbations and thus does not directly capture either of these effects. These observations suggest that previous studies assuming a constant branch size may have overestimated species extinction risks (Anholt, 1995; Fagan, 2002; Goldberg, Lynch, & Neubert, 2010; Grant, 2011). As such, if we incorporate branch-size heterogeneity into the model of Anholt (1995), this might further strengthen the mechanism of density dependence that is proposed to resolve the stream drift paradox in that study.

A recent study by Terui et al. (2018) made the prediction, supported by empirical evidence, that greater variation in branch size would decrease metapopulation stability. While this appears to contrast with our findings, in fact the two studies consider different properties of a population within a riverine habitat. We consider the equilibrium size of the population, which gives an indicator of how far the population is from extinction. Of course, in practice populations fluctuate around this equilibrium due to environmental perturbations. Terui et al. (2018) considered the degree of synchrony in these fluctuations, to assess whether all sub-populations are simultaneously more vulnerable to a perturbation event. Which metric is more indicative of extinction risk depends on the size of the fluctuations relative to that of the sub-populations. Small fluctuations, relative to the size of a sub-population, do not typically present a significant threat to that population even if synchronized. As such, we suggest that branch size heterogeneity will tend to ameliorate the threat posed by synchronized fluctuations, as the larger sub-populations (in larger branches) will be subject to smaller (relatively) fluctuations.

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

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

For high relative extinction rates, where dispersal has a negative effect on global occupancy, no dispersal is, strictly speaking, the optimal strategy. In practice, if one end of the largest branch is closed, i.e. dispersal is not possible in one direction, dispersal in that direction does not negatively affect global occupancy. In this case there is no dispersal out of the optimal habitat, only dispersal into it from the other branches (for as long as they support a population). This is supported by the observation from Terui et al. (2014b) that some aquatic species display strongly downstream-biased dispersal in riverine systems with large downstream branches.

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

The modelling framework presented here is formulated by omitting some features known to occur in natural riverine systems, such as spatial environmental heterogeneity and temporal environmental variability (Liao et al., 2013b). Nevertheless, as a starting point, our model reflects that species traits (e.g. species dispersal and relative extinction rate) and spatial branch-size difference can jointly affect metapopulation dynamics in riverine systems that feature some forms of heterogeneity (Bertuzzo et al., 2011; Yeakel et al., 2014; Terui et al., 2018). Further extensions of this work could include disturbances (e.g. seasonal drought and flooding, and disruption in riverine connectivity by hydrodams; Vaughn, & Taylor, 1999; Ishiyama et al., 2018), species interactions, invasion dynamics, and the relationship between branch complexity and metacommunity stability. Overall, we found strong effects of variability of branch size on species persistence, suggesting that this realistic feature should be explored in future models of riverine metapopulations.

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Author contributions

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

Competing interests: The authors declare no competing interests.

Supporting information

Appendix accompanies this manuscript is also supplied.

Data accessibility

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

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Figure captions

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

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

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

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

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