

# The role of branching in the maintenance of diversity in watersheds

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**Abstract:** Stream systems are characterized by a hierarchical dendritic branching pattern, which is thought to have important consequences for stream community structure. However, branching is associated with many other changes in stream condition, which make disentangling the effects of branching from associated environmental changes challenging. Moreover, much difficulty arises in scaling up local effects of branching within a watershed to the watershed as a whole, which is where diversity is arguably maintained and management and restoration efforts are assessed. Here, we show that branching can be present with no associated changes to community dynamics, either locally or in the watershed as a whole when branching affects only dispersal patterns and not environmental structure. We explore violations of these conditions to identify how branching can modify environmental conditions affecting coexistence in the watershed. We show that the strength of coexistence in the watershed depends in all essentials on the amount of environmental heterogeneity with only a small role for other factors. Only when streams are small relative to the scales of environmental change or dispersal can branching affect the strength of watershed-scale coexistence independently of changes to environmental heterogeneity in the watershed, but these effects are small and depend on interactions with environmental variation. We suggest that focusing on environmental heterogeneity rather than branching patterns will yield the greatest understanding of the drivers of stream community structure and the greatest benefits for management and restoration of stream communities.

**Key words:** environmental variation, species coexistence, diversity maintenance, streams and rivers, dendritic ecological networks, stream branching, dispersal

A key feature of stream habitats is a hierarchical dendritic branching structure (Strahler 1957, Campbell Grant et al. 2007), which is well studied in geomorphology to understand material transport patterns, physical changes along the stream, and discharge (e.g., Strahler 1957, Leopold et al. 1964). In ecology, branching affects the movement of organisms and the diversity of stream habitats, so it is thought to be an important determinant of patterns of local composition, species interactions, and environmental relationships in streams (Cuddington and Yodzis 2002, Fagan 2002, Benda et al. 2004, Campbell Grant et al. 2007, Muneeppeerakul et al. 2008, Brown and Swan 2010, Auerbach and Poff 2011, Brown et al. 2011, Altermatt 2013). It is well established that species diversity is strongly related to habitat diversity (Rosenzweig 1995), and because branching increases habitat diversity, it is expected to increase species diversity (Benda et al. 2004, Campbell Grant et al. 2007, Finn et al. 2011).

Different branches have different environmental characteristics because of different physical structures of the local

drainage basins, and confluences alter channel characteristics, such as shape, gradient, and substrate (Leopold et al. 1964, Frissell et al. 1986, Benda et al. 2004). Moreover, the branching topology of the stream affects connectivity between local populations and habitats, leading to consistent findings of increased local diversity near confluences and lower in the watershed (Heino and Mykrä 2008, Brown and Swan 2010, Finn et al. 2011, Carrara et al. 2012, Altermatt et al. 2013, Swan and Brown 2014, Kuglerová et al. 2015). Beyond patterns of local diversity, various lines of evidence, both theoretical (Tilman 1994, Amarasekare et al. 2004, Snyder and Chesson 2004, Aiken and Navarrete 2014, Holt and Chesson 2016) and empirical (Campbell Grant et al. 2010, Carson et al. 2010, Pedruski and Arnott 2011, Bode et al. 2011, Perkin and Gido 2012), suggest that connectivity has major effects on spatial coexistence mechanisms and, thus, has the potential to affect species diversity in the watershed as a whole. The resulting watershed-scale species pool then feeds into local populations.

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One recurrent finding is that low, but not zero, connectivity can favor high diversity at the landscape scale (e.g., Bolker and Pacala 1999, Forbes and Chase 2002, Tscharrnke et al. 2002, Fahrig 2003, Snyder and Chesson 2003, Miller and Chesson 2009, Gavish et al. 2012, May et al. 2013, Holt and Chesson 2016), which in the present context is the watershed scale. This outcome is also a prediction of neutral models (Thompson and Townsend 2006, Muneeppeerakul et al. 2007, Economo and Keitt 2008, White and Rashleigh 2012), but it also has a major role in models of stable coexistence, which depends on the distinctive biology of the various species. Thus, branching potentially affects watershed-scale diversity by influencing both habitat diversity and connectivity. Factors that increase watershed-scale diversity increase the potential for high local diversity. We asked whether these various effects can be teased apart. Specifically, if the branching structure of a stream is varied independently of habitat diversity, what is the effect of branching on coexistence mechanisms and, hence, the diversity in the stream as a whole, and what are the implications for local diversity?

Diversity is necessarily a multiscale phenomenon, with watershed-scale diversity being the collective outcome of varying and interacting local processes, whereas local diversity depends on the maintenance of diversity regionally coupled with dispersal, local environments, and local-scale interactions. However, studies of diversity patterns in streams typically treat the regional pool as a given (e.g., Brown et al. 2011, Finn et al. 2011, Carrara et al. 2012, Heino et al. 2012, Altermatt 2013, Swan and Brown 2014). Authors of some theoretical studies have examined watershed-scale persistence or community composition, but the restrictions imposed by neutral dynamics (Muneeppeerakul et al. 2008, White and Rashleigh 2012) or single sites/reach (Auerbach and Poff 2011) have limited their ability to detect the mechanisms maintaining diversity at the watershed scale. The diversity of species at the watershed scale must be maintained by processes occurring within the watershed, provided the watershed is effectively closed, i.e., dynamics at the watershed scale are not appreciably affected by locations outside the watershed on ecological time scales. Coexistence mechanisms, as established by scale-transition theory, scale local interactions up to regional dynamics, thereby determining the maintenance of watershed-scale diversity as the outcome of heterogeneous interactions occurring at lower scales and dispersal (Chesson 2000a, 2012). We used these mechanisms to investigate the effect of branching on watershed-scale diversity, accounting for its simultaneous effects on local communities and maintenance of watershed-scale diversity.

We show that branching can be manipulated without changing other environmental factors to reveal the effects of stream topology alone. This result leads to a series of instructive null cases that assess how branching and its interactions with other stream properties affect diversity at the scale of the watershed. The spatial storage effect and fitness–density covariance coexistence mechanisms emerge from scale

transition theory and quantify the strength of coexistence at the regional scale (Chesson 2000a, 2008). Watershed-scale diversity, which is the natural goal of modern conservation efforts (Roni et al. 2008, Palmer et al. 2014), places an upper bound on local-scale diversity. These coexistence mechanisms measure the strength of coexistence at the watershed scale, but they depend on the patterns of environmental conditions and abundances of organisms within the watershed. We studied the effect of branching on these coexistence mechanisms to develop a theoretical foundation for diversity maintenance in watersheds. We found that branching is not inherently important for diversity in the watershed, but environment heterogeneity is. In nature, branching is often associated with changes in the environment, but these changes, not branching per se, are key to maintenance of diversity.

## MODELING STREAM COMMUNITIES

To analyze the effects of branching and associated changes on the maintenance of diversity in the watershed, we develop a flexible model of streams as environmentally structured branching sequences of habitat patches (sites), e.g., pools or riffles depending on the focal community, which define local communities in our model. Communities consist of guilds of competing species that disperse according to the specified stream network topology and respond differentially to environmental conditions.

### Community dynamics model

We model community dynamics as a 2-step process of local dynamics followed by dispersal. We treat local dynamics as an input–output process. The input of species  $j$  to site  $x$  is the local density  $N_{j,x}(t)$ , which then gives an output 1 time unit later equal to  $N_{j,x}(t)\lambda_{j,x}(t)$  where  $\lambda_{j,x}(t)$  is the local fitness. Dispersal kernels determine how the output of each site disperses to other locations and is retained locally. Local fitness consists of per capita reproduction and survival as a function of the species-specific responses of the organisms to local environmental conditions and competition. We do not model particular physical environmental variables such as temperature directly. Rather, we define an *environmental response*,  $E_{j,x}$ , of each species  $j$  at each site  $x$ . The environmental response defines the integrated effect of density-independent effects of the environment of a site on the fitness in the absence of competition. Competition reduces local fitness, and we assume that these effects are negative exponential in form, following Holt and Chesson (2016), to give  $\lambda_{j,x}(t)$  as:

$$\lambda_{j,x}(t) = S_x E_{j,x}(t) e^{-C_{j,x}(t)}. \quad (\text{Eq. 1})$$

$S_x$  is a site-specific survival rate determined by dispersal mortality. Strictly speaking, in the terminology of Chesson (2000a),  $S_x$  is a component of the environmental response, and would be incorporated in  $E_{j,x}(t)$ . For clarity, we kept it separate in the presentation, but it is treated fully as part of

the environmental response in the analysis of coexistence mechanisms (Holt and Chesson 2016).  $E_{j,x}$  reflects physiological activity such as growth or reproductive rates, which lead to resource consumption, so larger values increase competition. We model competition,  $C_{j,x}$ , as a reflection of total physiological activity according to the formula:

$$C_{j,x}(t) = \sum_l \alpha_{j,l} E_{l,x}(t) N_{l,x}(t), \quad (\text{Eq. 2})$$

where  $N_{l,x}(t)$  is the density of species  $l$  in site  $x$  at time  $t$  and  $\alpha_{j,l}$  is a competition coefficient that scales the importance of the density of species  $l$  in determining competition. As long as  $\alpha_{j,l}$  is the same for all species, it cannot affect coexistence.

We model dispersal using a negative binomial dispersal kernel both up- and downstream, which can be made asymmetric to examine the effects of drift. However, in our previous work (Holt and Chesson 2016), drift had little effect on regional coexistence, so it is not a focus of this work. Dispersal mortality is not included in the kernel because we account for it in  $S_x$  according to the procedure of Chesson (1998). We assume that organisms dispersing beyond the stream mouth die and, therefore, dispersal mortality ( $1 - S_x$ ), depends on the position of a site with respect to the mouth and the dispersal kernel. Individuals cannot disperse beyond the headwaters, and instead are reflected back downstream. At stream confluences, the upstream dispersal kernel divides in half.

Our exact and asymptotic analytical development does not depend on the specific functional form of  $\lambda_{j,x}(t)$  or the specific details of the dispersal kernel, but applies generally to models with the same qualitative features (Appendix S1). Our other results are expected to be qualitatively similar for models of similar structure, where the competitive effect of a species increases with the favorability of the environment because such effects are generic (Chesson 2000b). Likewise, different dispersal kernels would yield quantitative differences, but the critical aspect is the extent to which branching connects variable habitats compared with an unbranched stream having the same dispersal kernel. Hence, our results would remain qualitatively similar over quantitative variations in the dispersal kernel.

### Characterizing the stream

We model watersheds as a series of connected sites. The environmental response,  $E_{j,x}$ , is a positive random variable, correlated in space. For simplicity, we assume independence between environmental responses of different species. To obtain spatially autocorrelated positive random variables, we assume that  $E_{j,x}$  is log-normal and, therefore, can be obtained from the formula:

$$E_{j,x} = e^{Y_{j,x} + m_j}, \quad (\text{Eq. 3})$$

where  $\{Y_{j,x}\}$  is an autocorrelated sequence of mean 0 normal random variables, and  $m_j$  defines the mean of  $\ln$

$E_{j,x}$ . The sequence  $\{Y_{j,x}\}$  is obtained as an autoregressive process defined by the equation:

$$Y_{j,x} = \rho Y_{j,x-1} + \varepsilon_{j,x}, \quad (\text{Eq. 4})$$

where  $\rho$  is the autocorrelation and  $\varepsilon_{j,x}$  is an independent mean 0 normal random variable with variance  $\sigma_\varepsilon^2$  and  $x$  is the distance from the mouth of the stream. Upstream from confluences, the autoregressive process becomes 2 processes. For a confluence occurring at  $x = c$ , the environmental variable  $Y_{j,c}$  serves as the starting value of environmental sequences up the right ( $R$ ) and left ( $L$ ) tributaries, which change according to the difference equations:

$$\begin{aligned} Y_{j,x}^R &= \rho Y_{j,x-1}^R + \varepsilon_{j,x}^R \\ Y_{j,x}^L &= \rho Y_{j,x-1}^L + \varepsilon_{j,x}^L \end{aligned} \quad (\text{Eq. 5})$$

Further branching simply iterates this process (Fig. 1, Appendix S2).

We consider 2 different cases for the relationship between the environments of the left and right branches. In the 1<sup>st</sup> case (parallel environments), the  $\{\varepsilon_j^R\}$  and  $\{\varepsilon_j^L\}$  sequences are identical and, therefore, the environmental conditions in the 2 tributaries are the same. In the 2<sup>nd</sup> case, the  $\{\varepsilon_j^R\}$  and  $\{\varepsilon_j^L\}$  sequences are independent, and so the environmental conditions of each tributary change independently of the other relative to the common value at the confluence. The key difference between these 2 cases is the number of distinct environmental conditions occurring in the stream. Independence of the environments in the tributaries doubles the number of distinct conditions that a split contributes to the watershed as a whole.

The resulting sequence of environmental responses has a characteristic length scale at which the environment changes, known as the correlation length (Janke 1996). The autocorrelation function of the  $Y$  distribution, i.e., the correlation  $A(d)$  between  $Y_{j,x}$  and  $Y_{j,x-d}$  as a function of the separation of the sites in space,  $d$ , can be expressed as a negative exponential, where  $\tau$  is the correlation length:

$$A(d) = e^{-d/\tau}. \quad (\text{Eq. 6})$$

The negative exponential (Eq. 6) holds only approximately for the  $E$  distribution, but integration (Appendix S2) gives a more precise value. These correlation lengths are little different; so we simply use the correlation length defined on the log scale, which then satisfies Eq. 6.

### Environmental heterogeneity of the stream

The environmental heterogeneity of the stream is determined by 3 quantities: the number of sites, the fraction of distinct environments, and the correlation length. The correlation length determines how rapidly the environment changes in space and must be measured relative to the dispersal distance. The ratio of mean dispersal distance ( $\bar{D}$ ), to

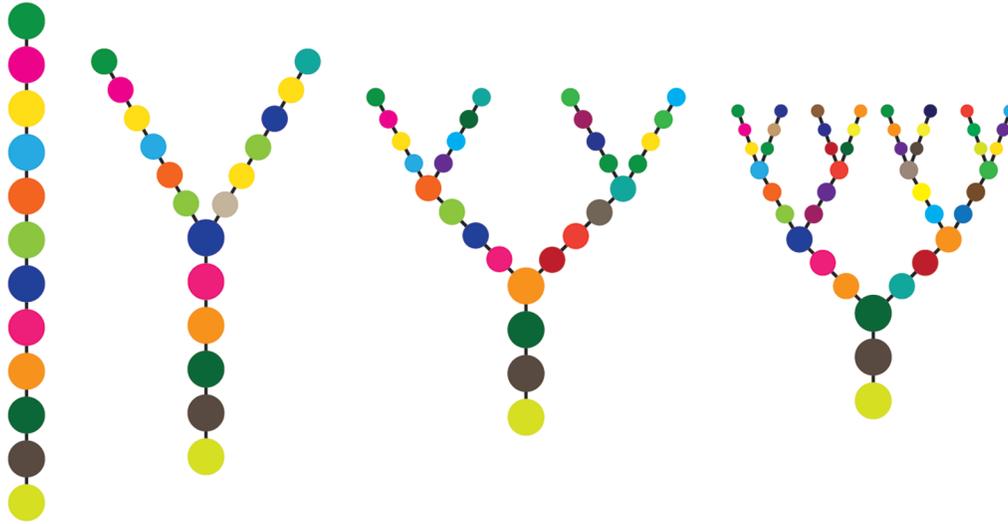


Figure 1. Watersheds constructed as a series of sites (dots) with autocorrelated environmental conditions (colors) connected by dispersal. Branching patterns are denoted by Strahler order (Strahler 1957); streams shown here have Strahler orders 1, 2, 3, and 4 (left to right). For simplicity, all numerical results consider symmetric bifurcations, which are the simplest topologies yielding their respective Strahler order. Except where otherwise noted, the total amount of habitat a given distance from the mouth (summed across tributaries) is held constant, illustrated here by area.

correlation length ( $\tau$ ) determines how the population is distributed relative to environmental change, thereby controlling the strength of spatial partitioning (Holt and Chesson 2016). The fraction of distinct environments is defined as the number of distinct environments divided by the total number of sites. It depends on the amount of branching and whether environmental deviations (the  $\{\varepsilon_j^R\}$  and  $\{\varepsilon_j^L\}$  sequences of Eq. 5) are the same or independent up tributaries sharing a confluence. Given the correlation length and fraction of distinct environments, the total number of sites determines how much of the potential variation given by the underlying stochastic processes is actually realized in the stream. For instance, a small number of distinct environments (low number of sites or low fraction of distinct sites) will not sample the tails of the log-normal distribution of  $E_j$  very well, especially when correlation lengths are long. The log-normal distribution is highly skewed in accordance with what is often found in nature; so large values of  $E_{j,x}$  occur, although with low probability. A few high values can profoundly influence the outcome, and are much more likely in a watershed with many distinct sites and short correlation lengths.

In our previous work (Holt and Chesson 2016), we varied the ratio  $\bar{D} : \tau$  (relative dispersal) to study how the distribution of organisms relative to environmental change affected coexistence strength, while holding the total amount of environmental heterogeneity constant. Here, we hold relative dispersal constant in our simulations to compare different branching scenarios without changing the way organisms are distributed relative to environmental change. Thus, total environmental heterogeneity can be altered in 2 ways, changing environmental correlation length and changing

the number of sites in the watershed, but any changes in the distribution of organisms relative to the environment come from branching.

## APPROACH

### Null cases

We first develop an exact null case that splits streams into identical tributaries to identify when branching does not affect the strength of coexistence in the watershed. Informed by these conditions, we go further to develop asymptotic null cases as streams increase in size relative to branching, which identify situations when the effects of branching would be minimal. These null cases allow us to identify necessary conditions for branching to affect community dynamics and species coexistence in watersheds. We quantify the effect of branching in terms of the strength of coexistence at the watershed scale, where diversity is maintained.

### Quantifying the strength of coexistence in the watershed

We assume that watersheds are closed, i.e., no immigration occurs from other watersheds. With our model, coexistence comes from habitat partitioning, which is quantified by the magnitudes of 2 contributing mechanisms, fitness–density covariance and the spatial storage effect. Fitness–density covariance relies on the correlation between the distribution of a species and the favorability of the environment for that species. However, to have a coexistence-promoting effect at the watershed level, distributional patterns must change as densities change. Such changes naturally come about when species are favored in different localities, and

competition occurs both within and between species (Holt and Chesson 2016). A species at high regional density has a distributional pattern less strongly determined by the pattern of environmental favorability because intraspecific competition limits its accumulation in favorable locations. In contrast, no such limitation exists when a species is at low density regionally. Thus, when at low density, a species is better able to take advantage of favorable conditions through its distribution in space. Another mechanism also is present, the spatial storage effect, which relies on physiological responses to environmental conditions independently of the distribution of the organisms in space. This mechanism can be important when high dispersal or frequent changes in environmental patterns weaken fitness–density covariance. Otherwise fitness–density covariance is dominant, as it is here (Appendix S3).

Formulae for the fitness–density covariance and spatial storage effect coexistence mechanisms are given in Table 1. As stabilizing mechanisms, they boost the watershed-scale fitness,  $\tilde{\lambda}_j$ , of each species as its density declines (Chesson 2000b). For any species  $j$ , the watershed-scale fitness, is defined by

$$\tilde{N}_j(t+1) = \tilde{\lambda}_j(t)\tilde{N}_j(t), \quad (\text{Eq. 7})$$

where  $\tilde{N}_j(t)$  is the mean density of species  $j$  over the watershed at time  $t$ . Coexistence requires all species to have watershed-scale fitness  $>1$  when perturbed to low density (the invader state, denoted  $i$ ) in the presence of all other species at their natural densities (the resident state). The watershed-scale fitness of invaders can be expressed as the sum of the 3 quantities in Table 1,

$$\tilde{\lambda}_i - 1 = \xi_i + \overline{\Delta I} + \overline{\Delta \kappa}, \quad (\text{Eq. 8})$$

(Chesson 2008, Holt and Chesson 2016). The first term,  $\xi_i$ , represents the average difference in fitness between species  $i$  and its competitors. In the absence of stabilizing mecha-

nisms, only the species with the largest  $\xi_i$  persists in the long run. If the environment varies, a species with negative  $\xi_i$  (below average fitness) can have a positive invader fitness if the stabilizing mechanisms, the spatial storage effect ( $\overline{\Delta I}$ ) and fitness–density covariance ( $\overline{\Delta \kappa}$ ), are positive and large enough to counteract a negative  $\xi_i$ . Thus, the sum of the storage effect and fitness–density covariance is the strength of coexistence, which, in conjunction with average fitness differences, determines watershed-scale diversity as the number of species with  $\tilde{\lambda}_i > 1$ .

How do the formulae in Table 1 capture the ecological understanding described above? The analytical expression for fitness–density covariance captures the benefit to invader growth that arises from the superior ability of invaders to accumulate in favorable locations. Relative density,  $v_{j,x} = N_{j,x}/\tilde{N}_j$ , gives the distribution of the species in the watershed independently of absolute density. Therefore, the covariance between local fitness ( $\lambda_{j,x}$ ) and relative density ( $v_{j,x}$ ) quantifies how the distribution of a species is related to local fitness. Coexistence is promoted when a species is more concentrated in favorable sites when perturbed to low regional density than at its higher natural regional density. The formula for the fitness–density covariance mechanism is an invader–resident (low-vs-high density) comparison of these covariances.

The spatial storage effect quantifies the growth rate benefit for invaders at the watershed scale that arises if sites that are favorable to invaders impose less competitive limitation than sites that are favorable to residents. The covariance between  $E$  and  $C$  measures the extent to which competition limits fitness in favorable environmental conditions. Coexistence is promoted when residents have a larger covariance between  $E$  and  $C$  than do invaders. This density dependence of the covariance between  $E$  and  $C$  tends to come about because residents have high physiological activity in favorable conditions, generating more competition. In contrast, because invaders are at low density, they can have high physiological activity in favorable locations without causing high competition. In this situation, the covariance between  $E$  and  $C$  declines with density, promoting coexistence, provided the species are favored in different environmental conditions.

Here, we study the effects of branching on these coexistence mechanisms to quantify its effect of diversity maintenance in streams. The functional forms of these mechanisms provide ecologically meaningful interpretation of the results. However, their particular values generally cannot be determined analytically when space is explicit. Thus, to quantify the effects of branching on coexistence, we simulate communities and calculate the strength of the mechanisms from the resulting covariances as defined in Table 1. Fitness–density covariance is by far the dominant contributor to total coexistence strength in this model (Appendix S3) and others with limited dispersal and spatial variation (Snyder and Chesson 2003, Holt and Chesson 2016). Thus, we focus on fitness–density covariance as the dominant

Table 1. Components of invader fitness. Subscript  $i$  = invader; superscript  $-j$  = in the absence of species  $j$  (species  $j$  is invader),  $\bar{E}$  = mean environmental response over space and species, superscript  $i \neq j$ , average over all other species in turn as invader with species  $j$  as resident,  $\mathcal{E}_{j,x}$  = effect of  $S_x E_{j,x}$  expressed in units of multiplication rate,  $\mathcal{C}_{j,x}$  = effect of  $C_{j,x}$  expressed in units of multiplication rate,  $v_{j,x}$  = relative density:  $v_{j,x} = N_{j,x}/\tilde{N}_j$ . Covariances are taken over space. Derivations of these equations are given by Holt and Chesson (2016).

Mechanism	Formula
$\xi_i$ (Average fitness difference)	$(\bar{E}_i^x - \overline{\bar{E}_i^{x^{i \neq j}}})/\bar{E}$
$\overline{\Delta I}$ (storage effect)	$\frac{\overline{\text{cov}(\mathcal{E}_j, C^{-i})^{i \neq j}} - \text{cov}(\mathcal{E}_j, C^{-j})}{\overline{\text{cov}(\mathcal{E}_j, C^{-i})^{i \neq j}}}$
$\overline{\Delta \kappa}$ (fitness–density covariance)	$\frac{\text{cov}^{-j}(\lambda_j, v_j) - \overline{\text{cov}^{-i}(\lambda_j, v_j)^{i \neq j}}}{\overline{\text{cov}^{-i}(\lambda_j, v_j)^{i \neq j}}}$

component of coexistence strength in our results and their interpretation.

### PARALLEL ENVIRONMENTS: THE EXACT NULL CASE

If a linear stream were split partway up so that it takes on a Y form, would the organisms notice? A split in a stream does not have any intrinsic effects on dynamics separate from associated changes in the environment of the tributaries. We show this for an exact null case, defined as follows:

A linear stream can be split into a branched stream with no changes in dynamics either locally or regionally if the following assumptions are met:

1. The environment of each locality in a stream is strictly a function of distance from the mouth, i.e., environmental change proceeds in parallel up branches from the same confluence (Fig. 2A).
2. The total amount of habitat contained in localities at a given distance upstream of the mouth (summing across all tributaries) is the same regardless of the extent of branching.
3. Branches can be unequal in cross-sectional area, but dispersal up a branch is proportional to the cross-sectional area of the branch, or more generally, the amount of habitat per unit length.
4. Demographic stochasticity can be ignored because local populations remain reasonably large despite being split upstream of confluences.

Given these conditions, branching has no effect on community dynamics or coexistence mechanisms (Fig. 3A, Appendix S1). The fundamental reason is that when a stream is

divided in 2 in this null model, neither the densities of the organisms nor the environment are changed. Moreover, dispersal measured in density units into or from any locality is not changed. Hence, local fitness is not changed. The only change is that populations at given distances from the mouth are subdivided between the tributaries, but their dynamics are identical. This result is Theorem 1 of Appendix S1 and is illustrated by simulation in Fig. 3A (black line). This finding generalizes to show no effect of splitting a stream at any point into unevenly sized tributaries, provided that the total amount of habitat remains fixed. Environmental variation can be purely spatial through all grades of spatiotemporal (where the spatial pattern varies through time) to purely temporal, as long as the environment remains perfectly correlated between the 2 parts of the split watershed (see Appendix S1 for proofs and illustrations). For clarity, we restrict our presentation here to pure spatial variation. These assumptions are not realistic, but they nevertheless demonstrate that the topology of the watershed is not inherently important for either community dynamics or watershed-scale coexistence. For branching to have an effect, it must be associated with violation of at least one of these assumptions. In real streams, violation of these assumptions is common. In particular, changes in the environment (violations of assumption 1) are highly likely with branching in nature. However, our point with this null model is to isolate the effect of branching topology alone.

### NUMERICAL RESULTS

#### Effect of environmental heterogeneity

We consider violations of assumption 1 by allowing changes in the environment to accrue independently up the tributaries, i.e., the  $\epsilon$  sequences of Eq. 5 are independent

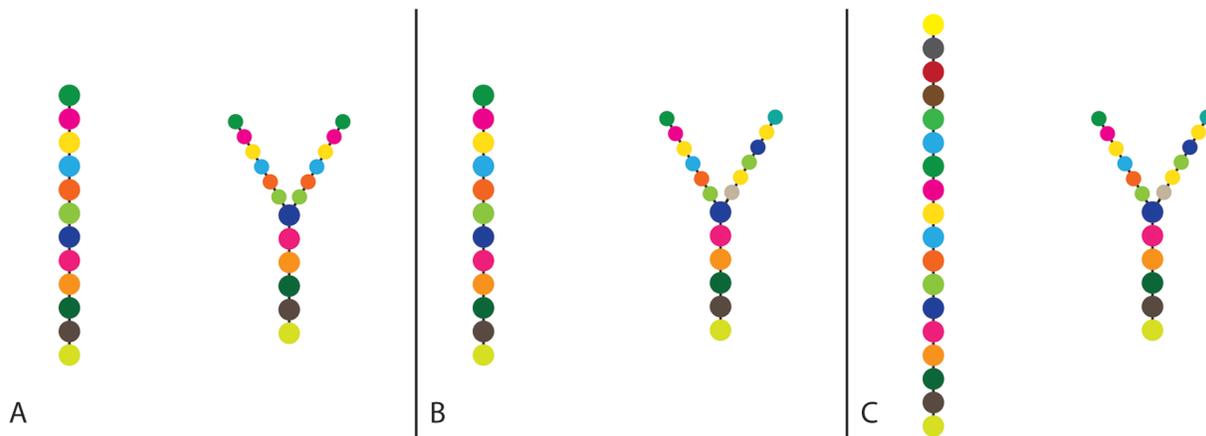


Figure 2. Illustration of cases with different structure of environmental conditions in branched networks. Colors represent environmental conditions and total habitat size at a given distance from the mouth is the same between topologies. A.—Parallel environments case: tributaries have identical habitats; number of sites increases and fraction of distinct sites decreases with branching. B.—Environmental conditions diverge between tributaries; fraction of distinct environmental conditions = 1, number of sites increases between branching patterns. C.—Number of distinct environmental conditions held constant between branching patterns; fraction of distinct environmental conditions = 1.

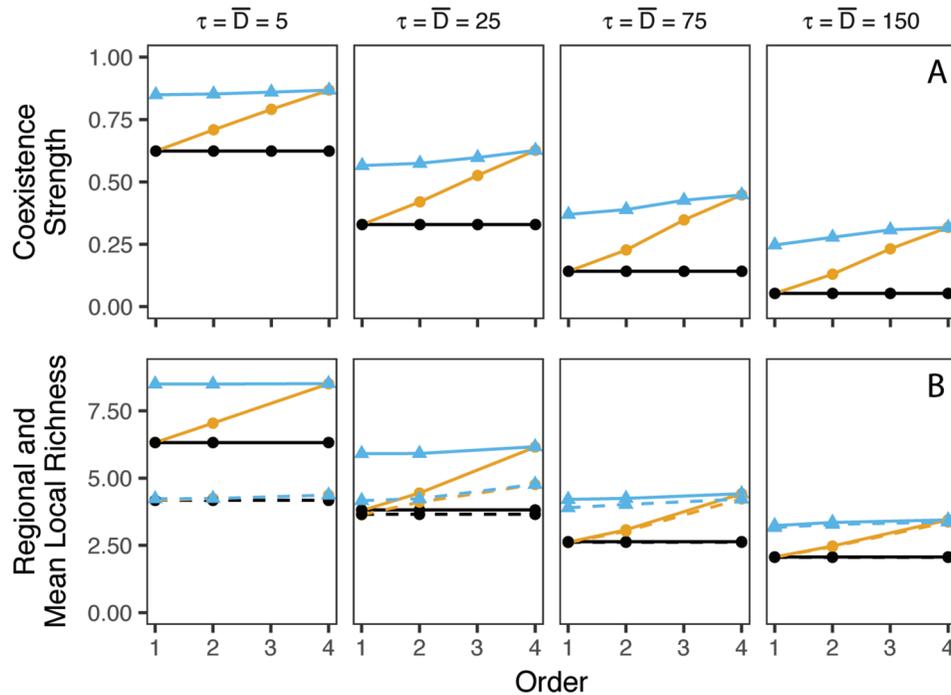


Figure 3. Effect of branching on the strength of coexistence (A) and species richness (B) for environmental cases illustrated in Fig. 2A–C. Black line = parallel environments, as in Fig. 2A; Orange line = tributaries differ but watershed size increases with branching, as in Fig. 2B; Blue line = tributaries differ and watershed size remains constant, as in Fig. 2C. In panel B, solid lines indicate regional richness, and dashed lines indicate mean local richness. Order is the Strahler order of the watershed (see Fig. 1). Panels from left to right have increasing mean dispersal distance ( $\bar{D}$ ) and environmental correlation length, ( $\tau$ ), which are held in fixed proportion (1:1) to make coexistence strength comparable. Circles = number of sites in the watershed increases with branching, whereas triangles = number of sites in watershed remains constant. Regional richness is defined as the number of species with invader fitness ( $\tilde{\lambda}_i \geq 1$ ), given 10 possible species and average fitness differences created by spacing mean environmental responses by 0.15 between species. Mean local richness is found in the same conditions with local occupancy determined by a detection threshold of  $10^{-5}$ . This detection threshold is needed to convert continuous local population densities to high and low, with high being treated as ‘present’ to assign a local species richness value. The units are local density, so patch size and system size have no effect on the outcome.

between tributaries. The environmental conditions remain autocorrelated, but the environments of the tributaries diverge with distance from their confluence (Fig. 2B). The outcome is an increase in the strength of coexistence with branching (orange lines, Fig. 3A). Branching in this case has the effect of increasing the number of distinct environments in the watershed, thereby including a greater range of local environments (see ‘Environmental heterogeneity of the stream’ above). In other words, branching increases overall environmental heterogeneity in the watershed. In contrast, in the parallel environments case, branching increases the number of sites, but not the amount of environmental heterogeneity (Fig. 2A), showing that branching without environmental differences between tributaries has no effect. Is the increase in coexistence strength seen when tributaries differ caused solely by increased environmental heterogeneity, or does branching itself become important by interacting with the variation between tributaries?

To decouple branching from increased environmental heterogeneity, we hold the number of sites in the watershed constant between branching patterns and keep the fraction

of distinct environments = 1, i.e., all sites have distinct environments (Fig. 2C). Thus, environmental heterogeneity is fixed across branching patterns. In this case, branching has only a small positive effect on the strength of coexistence (blue lines, Fig. 3A).

The results shown in Fig. 3A for coexistence strength are mirrored for regional diversity (solid lines, Fig. 3B), provided species have average fitness differences, i.e., all species but one require stabilizing coexistence mechanisms to persist. The particular values for the regional species pool will depend on the average fitness differences, but the critical point is that increasing coexistence strength increases the opportunity for diversity at the watershed scale. In contrast, the average species richness of single sites (dashed lines, Fig. 3B) exhibits different responses to branching and dispersal because of changing importance of turnover between sites and limitation by the regional pool (see ‘Implications for local diversity’ below).

The individual panels in Fig. 3A, B show the effect of correlation length. Increasing environmental correlation length reduces the strength of coexistence (Fig. 3A). This

result is understandable because neighboring sites become more similar in their environments, and total heterogeneity in the watershed is reduced. However, all panels show essentially the same patterns of branching effects, with a small interaction between correlation length and the degree of branching seen in the slopes of the blue lines.

Overall, the results in Fig. 3A show that the strength of coexistence is explained in all essentials by the amount of environmental heterogeneity rather than the amount of branching. Major changes in the strength of coexistence associated with branching occur only when branching increases the number of distinct environments. Environmental correlation length has an important effect on the strength of coexistence, but it has only a minor interaction with branching. The small interaction that is found might be driven at least partially by dispersal, because the ratio between mean dispersal distance and correlation length is fixed in these analyses. Thus, as correlation length increases, so does mean dispersal distance.

### Why is there any effect of branching?

The amount of heterogeneity, explained by the number of sites and the correlation length, has the dominant effect on coexistence, but some effect of branching is still seen from the slopes of the blue lines. When tributaries differ,

branching can interact with correlation length and dispersal distance in 3 ways. First, the branched autocorrelation structure means that sites in different tributaries are correlated by the common environments at confluences (Appendix S2). Second, sites downstream of confluences receive propagules from multiple sites at a given distance upstream. If those upstream sites have different environmental conditions, the downstream sites receive a more diverse group of propagules than do equivalent sites in a linear stream. Dispersal distance and correlation length determine the extent of this effect. Third, with a fixed number of sites, more branching decreases the maximum distance of a site from the mouth and from the headwaters (length of the stream, Fig. 2C). Thus, increased branching increases the relative importance of boundary conditions for dynamics in the watershed. These differences lead to the small differences in fitness–density covariance between streams of different topology that take equivalent samples from the  $E_i$  distribution (blue lines, Fig. 3A; comparison between lines, Fig. 4A–C). We emphasize that these effects are minor relative to the effect of environmental heterogeneity: the slopes of the blue lines in Fig. 3A are small relative to those of the orange lines, and in Fig. 4A–D, watershed size and correlation length determine fitness–density covariance with only slight deviations between linear and 2<sup>nd</sup>-order streams.

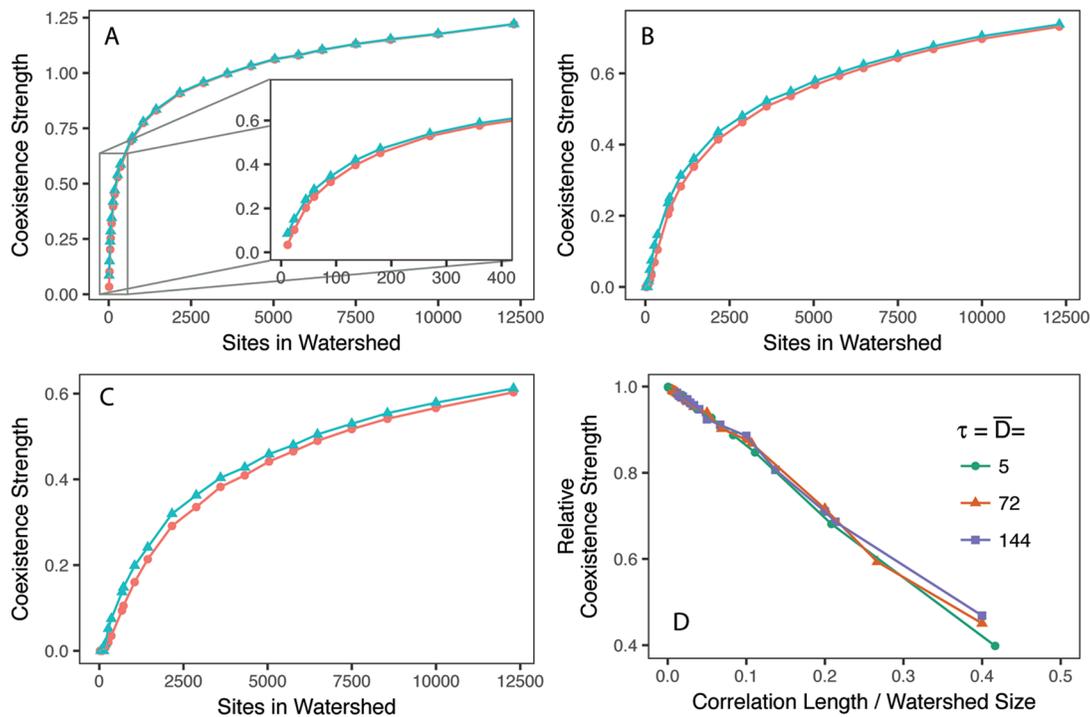


Figure 4. Coexistence strength converges between linear (red) and 2<sup>nd</sup>-order (blue) streams as watershed size increases. Number of distinct environments = sites in watershed. A.—Correlation length ( $\tau$ ) = mean dispersal distance  $\bar{D} = 5$ . Inset shows area of divergence between topologies. B.— $\tau = \bar{D} = 75$ . C.— $\tau = \bar{D} = 150$ . D.—Strength of fitness–density covariance in linear streams relative to in 2<sup>nd</sup>-order streams, plotted against the relative scales of correlation length and watershed size for data from panels A–C. Only cases where  $\tau$ :watershed-size ratios  $< 0.5$  are considered because  $\bar{D} > \frac{1}{2}$  of the stream tends to cause extinction.

### Increasing stream size: the asymptotic null case

The small differences in the strength of coexistence that remain between branching patterns after environmental heterogeneity is accounted for are eliminated as watersheds increase in size. This result is illustrated in Fig. 4A–D and is explained analytically in Appendix S1. As streams increase in size, the effects of branching on correlation structure, distance to boundaries, and composition near confluences become negligible for overall community dynamics. In Fig. 4A, where correlation length and dispersal distance are low, appreciable effects of branching are evident only for very small streams, but for larger correlation lengths and dispersal distances the effects of branching disappear only for streams of large size (Fig. 4B, C). These differences are explained by the ratio of the correlation length to the number of sites in the watershed. This result is illustrated in Fig. 4D, which shows the ratio of coexistence strength for 1<sup>st</sup>- relative to 2<sup>nd</sup>-order streams plotted against the ratio of correlation length to watershed size. This view shows that the results in Fig. 4A–C are explained by essentially the same relationship.

### Eliminating branching effects on correlation structure and boundary conditions

Real watersheds may, in fact, be short relative to environmental correlation length or dispersal distance. In terms of Fig. 4A–D, this scenario corresponds to small numbers of sites or high correlation length relative to watershed size

where branching has a small, but appreciable, effect on coexistence. These effects may come from interactions between branching and 3 factors: environmental correlation structure, community composition near confluences, and boundary effects (see ‘Why is there any effect of branching?’ above). We now eliminate the effects of branching on correlation structure and boundary effects, comparing the strength of coexistence when these effects are eliminated to the strength of coexistence when they are present. These comparisons show how correlation length and dispersal determine the small remaining effect of branching on coexistence once environmental heterogeneity is accounted for in small watersheds.

We eliminate the effects of branching on the correlation structure of the environmental conditions by holding the environmental responses at the mouth, confluences, and tips of the tributaries at the same value, while retaining the correlation length of the environmental sequence. Autoregressive processes adjusted to have fixed values at certain points are known as autoregressive bridges (Corlay 2014). Fixing the mouth, confluences, and headwaters at the same environmental response results in each segment of the stream being an independent realization of an autoregressive process with the same endpoints. These segments have the same endpoints, so they can be stacked to form a linear stream without altering the autocorrelation structure of the environment along the stream, unlike unbridged streams (Fig. 5A, B, Appendix S2).

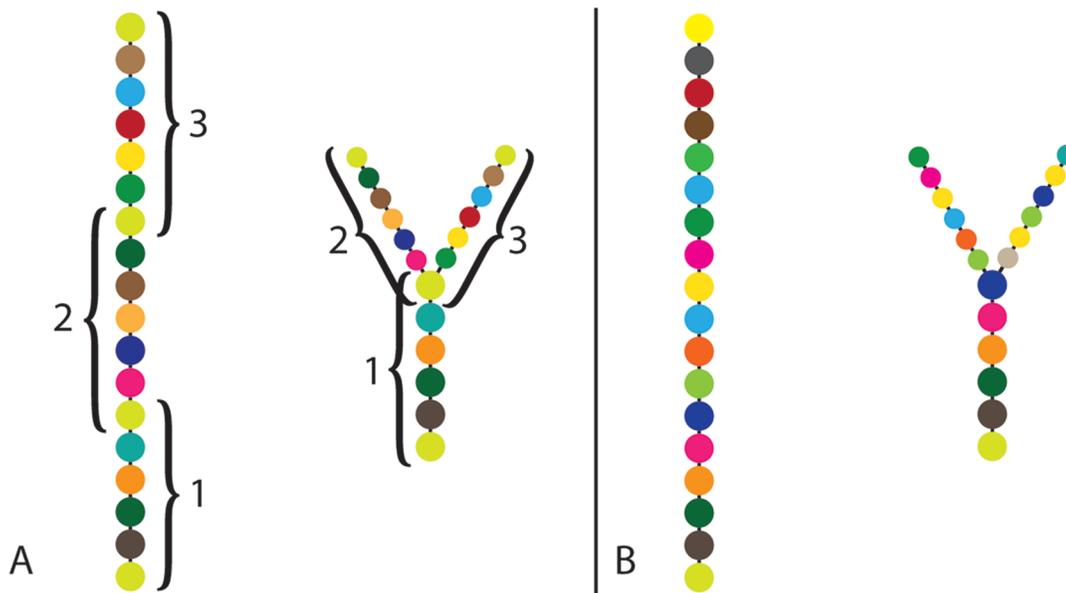


Figure 5. Streams constructed with and without environmental bridges. A.—Stream with environmental bridges. The indicated stream segments return to the first environmental state at the end of the segment. Adjacent segments include a common site, and so stacking tributaries to form a linear stream preserves the sequences of environmental states. B.—Stream without environmental bridge (same as Fig. 2C); linear stream is not equivalent to stacking the segments of a branched stream because independent divergence between tributaries would result in a break in the autocorrelation structure if stacked. This figure illustrates the concept of bridging with 1<sup>st</sup>- and 2<sup>nd</sup>-order streams constructed of 3 bridged reaches. Model results consider bridging in a 4<sup>th</sup>-order stream too large to illustrate here. The 1<sup>st</sup>-, 2<sup>nd</sup>-, and 4<sup>th</sup>-order streams are each constructed of 15 bridged reaches.

We eliminate the effects of branching on boundary effects by considering looped dispersal: organisms leaving the top of the stream reappear at the bottom of the stream and vice versa. When looped dispersal is considered with environmental bridges, the identical start and endpoints preserve relationships between dispersal and environmental structure. Thus, streams still change length with branching, but no concurrent change occurs in the importance of boundary conditions for dynamics.

We consider how the strength of coexistence changes with branching for a factorial combination of environmental bridges and looped dispersal. By comparing these cases, we show how each factor contributes to the small effect of branching on coexistence strength in small watersheds. The combinations of environmental bridges and looped dispersal eliminate the effects of branching as follows: 1) environmental bridges (e.g., Fig. 5A) eliminate the effect of branching on correlation structure; 2) looped dispersal and environmental bridges eliminate the effect of branching on boundary conditions and correlation structure; 3) looped dispersal eliminates the effect of boundary conditions, but severe discontinuities in correlation structure are experienced by dispersing organisms; 4) with neither looped dispersal nor environmental bridges (e.g., Fig. 2C, Fig. 5B) correlation structure and boundary effects both change with branching. In all 4 cases, dispersal still affects community composition in the vicinity of confluences.

Figure 6 shows cases with environmental bridges in blue and unconstrained environmental structure in red. Environmental bridges decrease coexistence strength, evidently because of a reduction in heterogeneity when points along the stream are constrained to the same environmental value. In the absence of looped dispersal, the slope of coexistence as a function of stream order is little affected by environmental bridges; branching still increases coexistence strength. However, looped dispersal has a large effect. Instead of increasing with branching, coexistence strength decreases (dashed lines, Fig. 6). Looped dispersal reduces heterogeneity in the stream by eliminating washout mortality and diminishes the tendency for unique communities to develop in the headwaters of different branches. Combining looped dispersal with environmental bridges yields a lower decline in coexistence strength with branching than occurs without bridges, reflecting constrained correlation structure. Combined looped dispersal and environmental bridges still yields branching effects, but they are subtle.

### Implications for local diversity

Our focus has been on maintenance of diversity in the watershed as a whole, whereas empirical studies tend to focus on patterns of diversity within a watershed. Thus, the most immediate comparison with empirical findings is to within-watershed patterns. Our model reproduces the finding that sites near confluences have elevated local diversity

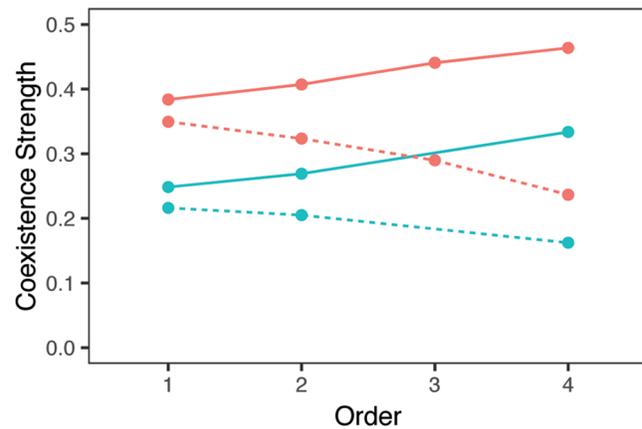


Figure 6. Coexistence strength for streams with and without environmental bridges and looped dispersal. All streams have 1800 sites. Correlation length ( $\tau$ ) = mean dispersal distance ( $\bar{D}$ ) = 75. Blue line = with environmental bridge, red line = without bridge, solid line = no loop (boundary effects), dashed line = looped dispersal. Solid red line is the same data as blue line in Fig. 3A with  $\tau = \bar{D} = 75$ .

relative to the rest of the stream and to streams with less branching (Fig. 7A, B). Our models emphasize that this outcome depends on differences in environmental conditions between tributaries because it does not occur when tributaries contain identical environmental sequences (proved in Appendix S1, illustrated in Appendix S4, Fig. S4.1). When tributaries differ, correlation length and dispersal distance determine both the magnitude and spatial extent of diversity increases near confluences (Figs 7A, B, S4.2). Long dispersal reduces the increase in local diversity near confluences, but extends those increases over a larger scale. The outcome is that both branching and long dispersal boost average local diversity as a fraction of the regional species pool, but in general, the regional species pool decreases with increases in dispersal distance and is only slightly enhanced by branching separately from environmental heterogeneity (Fig. 3B).

Our model also finds a distinctive hump in local diversity in the middle of the stream, particularly at low dispersal distances (Fig. 7A, B), which occurs even in the absence of branching. Like the peaks in diversity near confluences, this pattern arises because sites near the boundaries receive propagules from a less diverse set of environmental conditions than do sites in the middle of the stream. The pattern is similar to a mid-domain effect, but it is driven by the patchy distribution of suitable environmental conditions and dispersal rather than a monotonic environmental gradient with more species ranges overlapping in the middle.

### DISCUSSION

In nature, regional diversity constrains local diversity, and the two are often closely related (Caley and Schluter

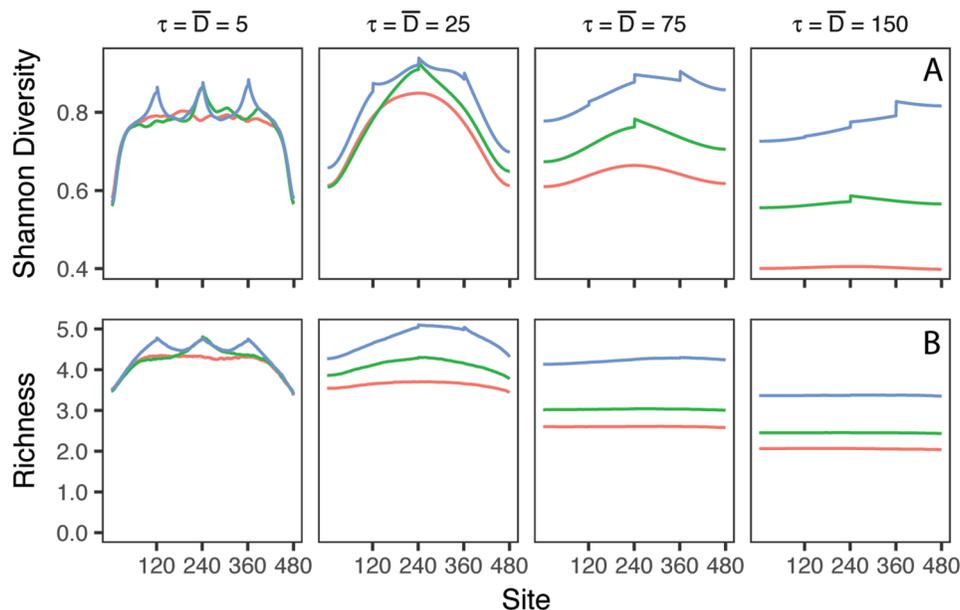


Figure 7. Shannon diversity (A) and local richness (B) at sites a given distance along a single flow path from the headwaters (site 0) to the mouth (site 480) averaged over 500 model runs for different branching patterns. Blue line = 4<sup>th</sup> order, green line = 2<sup>nd</sup> order, red line = linear. Tributaries differ and watershed size increases with branching, as in Fig. 2B, and so all branching patterns have the same distance from headwaters to mouth along a single flow path. Thus, total environmental heterogeneity increases with stream order. Other scenarios (parallel environments and constant heterogeneity) are considered in Appendix S4. Confluences occur at site 240 in the 2<sup>nd</sup>-order stream, and at sites 120, 240, and 360 in the 4<sup>th</sup>-order stream. Panels from left to right have increasing mean dispersal distance ( $\bar{D}$ ) and environmental correlation length ( $\tau$ ), which are held in fixed proportion (1:1) to make coexistence strength comparable. Simulations were conducted with average fitness differences for 10 possible species created by spacing mean environmental responses by 0.15 between species. Local richness was determined by the number of species present at a site with a detection threshold of  $10^{-5}$ , as for Fig. 3A, B.

1997, Shurin et al. 2000, Heino et al. 2003, Cornell et al. 2008, Grönroos and Heino 2012, Gonçalves Souza et al. 2013, Al-Shami et al. 2014), a phenomenon that also emerges in our theoretical study. Many investigators take regional diversity as a given and focus on local diversity, but our primary concern is the role of stream branching patterns in the maintenance of diversity at the watershed scale, which is the regional scale in our study. Investigators typically assume that local communities are assembled from a regional species pool without asking about maintenance of diversity in the pool itself, although the pool, in general, constrains local diversity (Brown et al. 2011, HilleRisLambers et al. 2012, Cornell and Harrison 2014). Our previous work (Holt and Chesson 2016) demonstrated an interplay between environmental structure in a watershed, local diversity, and regional diversity maintenance, but we did not consider the role of branching in that environmental structure. Overall, we find here that the amount of environmental heterogeneity is the dominant factor determining diversity maintenance at the watershed scale, whereas the role of branching is minimal apart from changes in physical environmental characteristics that might go hand in hand with branching. Moreover, our results imply that the common observation, reproduced in our models, that local diversity often peaks at confluences (Rice et al. 2001, Fernandes

et al. 2004, Hitt and Angermeier 2008) may weaken diversity maintenance at the watershed scale. Diversity maintenance is strengthened by a tendency for species to segregate in space according to their environmental responses (the fitness–density covariance mechanism), but confluences diminish this segregation, weakening diversity maintenance.

We came to these conclusions by first considering the effect of branching alone on the dynamics of the species in the watershed, and the implications of these dynamics for species coexistence. To do this, we set up null cases in which branching changed without any changes in environmental structure. Thus, sites the same distance from the mouth were given the same environment in different tributaries. A bifurcation in the stream then leads to 2 environmentally identical tributaries (parallel environments). In these null cases, the environmental patterns are identical, but the tributaries need not have identical cross-sectional area. We show that in this case, the branching pattern has no effect on community dynamics when 2 additional conditions are met: 1) total habitat at a given distance from the mouth is unaffected by branching, and 2) demographic stochasticity is unimportant. The strength of coexistence does not differ between streams with different topologies because the branching pattern of the stream has no effect on local community

dynamics at any given distance from the mouth. Thus, branching itself does not inherently affect the strength of coexistence in stream communities. These results do not rely on numerics or simulation but are exact general mathematical conclusions, proved in Appendix S1. In Appendix S5, we relax the assumptions on habitat size and demographic stochasticity and find by simulation only small absolute effects of these factors on coexistence and a very small interaction with branching.

If the parallel-environment conditions are violated, the strength of coexistence can change with branching. The strength of coexistence increases with branching if branching increases the total amount of environmental variation. Tributaries in nature generally do diverge in their environmental patterns (Leopold 1994, Montgomery et al. 1996, Montgomery and Buffington 1997, Benda et al. 2004, Heino and Mykrä 2008, Boughton et al. 2009), and our results here mean that these environmental differences rather than branching patterns per se define the key effects on diversity maintenance. The introduction of more sites with distinct environmental conditions increases the total range of environmental variation, regardless of branching pattern and increases the total potential variation in local fitness. Coexistence strength in our model system depends largely on the fitness–density covariance coexistence mechanism. Thus, increasing the potential variation in local fitness increases the coexistence strength provided the different species are affected differently by the environmental conditions.

To see whether the total amount of environmental variation is sufficient to explain coexistence independently of branching when the parallel environmental assumption is violated, we used various devices to keep the amount of environmental heterogeneity constant as the branching structure was varied. Effects of branching cannot be entirely eliminated in small streams, but as watershed size increases, coexistence-strength differences between branched and unbranched streams disappear. This situation is our asymptotic null case in which the dynamics within a sufficiently long reach are not appreciably influenced by dynamics in other reaches. Thus, a long reach can satisfy the effective closure requirement (Chesson 2000a) for independent dynamics. The scale at which branching effects are unimportant is not absolute, but is relative to the scales of dispersal and environmental variation because these factors determine the ways in which different reaches influence each other. As the watershed increases in size, the number of sites affected by other reaches does not change, but they are a decreasing fraction of the total stream system. Thus, the relative importance of these sites to overall dynamics decreases until it becomes negligible, explaining the asymptotic elimination of branching effects on species coexistence.

The asymptotic null case also allows for branching in which the resulting tributaries are of different length. In that case, the scale at which individual reaches approach effective closure (essentially independent dynamics) may vary within

the watershed, but coexistence strength in streams with different branching patterns will still converge asymptotically as streams get larger. If tributaries are asymmetric in width, but not length, the parallel environments case continues to hold provided the total amount of habitat at a given distance from the mouth remains constant (Appendix S1).

When streams are not large relative to the scales of environmental variation and dispersal, coexistence strength shows some small increase with branching. In these situations, branching reduces the average distance of a site from the mouth and allows distinct communities to develop in the headwaters of different branches. Thus, environmental gradients induced by the peculiar environments at the ends of the stream have more influence, effectively increasing environmental heterogeneity, and so increasing coexistence strength. In contrast, when these gradients are eliminated by considering streams as a loop, coexistence strength declines with branching (Fig. 6). Because confluences receive propagules from multiple reaches, sites near confluences tend to have higher local diversity, smaller population sizes of any given species, and reduced influence of the local environmental conditions on local community composition. The outcome is to diminish the tendency of a species to build up in favorable locations. In other words, fitness–density covariance is reduced, reducing coexistence strength. Similar reductions in the strength of fitness–density covariance associated with increased local diversity are studied in detail in Holt and Chesson (2016), where they arise from the relative scales of dispersal and environmental correlation length.

The coexistence mechanism of focus here, namely fitness–density covariance (see ‘Quantifying the strength of coexistence in the watershed’ above), in part reflects diversity patterns. It tends to be stronger with high species turnover, and thus, with high  $\beta$ -diversity and low  $\alpha$ -diversity. This relationship depends on species turnover being driven by changes in the environment, thereby reflecting associations between local density of a species and its local fitness. In contrast, when the coexistence mechanism is the spatial storage effect, local diversity patterns minimally affect coexistence because the spatial storage effect depends on spatial patterns of physiological responses of organisms, not on spatial density patterns (Appendix S3; Holt and Chesson 2016). Although generally much weaker than fitness–density covariance, the spatial storage effect does contribute to coexistence strength (Appendix S3). Most important for our study, the spatial storage effect is relatively insensitive to dispersal and branching patterns. Its effect is to further reduce the effects of branching on diversity maintenance overall, but this outcome is of much importance only with spatiotemporal variation or long dispersal when fitness–density covariance tends to be weak, and the spatial storage effect becomes the main coexistence mechanism.

We consider spatiotemporal variation, in which the spatial pattern of environmental conditions changes through

time, in Appendix S5. These analyses show that the strength of coexistence remains relatively unchanged even when branching increases total environmental heterogeneity, which was the only scenario that yielded large effects of branching on coexistence strength with pure spatial variation. This outcome can be understood from the dominance of the spatial storage effect over fitness–density covariance in that case. As stream size is increased while the variance in the environment is held fixed, more sites with extreme environmental conditions will be present as the tails of the distribution of environmental variation become represented in the stream. This outcome occurs with both pure spatial variation and spatiotemporal variation, but the effects on coexistence strength are quite different. Pure spatial variation with short dispersal means that densities can accumulate dramatically in extremely favorable sites, a situation that becomes increasingly important as sites are added. This density accumulation drives increasing coexistence strength with the number of sites (Figs 3A, B, 4A–D). With spatiotemporal variation, accumulation of density in favorable locations is limited, fitness–density covariance is weak, and coexistence strength, which is largely determined by the spatial storage effect, does not change with the number of sites. Coexistence strength simply reflects the variance of the environmental distribution, not the tails.

Under spatiotemporal variation, the small effect of branching on coexistence strength seen in small streams also goes away (Appendix S5). Long dispersal and spatiotemporal variation both reduce the accumulation of density in favorable locations, but anything less than infinite dispersal still continues to reflect the branching structure of the stream when environmental variation is purely spatial, thereby retaining the small effects of development of unique headwater communities and the higher diversity at confluences seen in Fig. 6. In contrast, because of the continuing change in the environmental pattern in the stream under spatiotemporal variation, unique headwaters communities cannot develop, and higher local diversity arises from changes in the local environment rather than connectivity. Thus, spatiotemporal variation provides even less opportunity for branching to affect regional coexistence strength than does pure spatial variation.

### Links to previous theory

The metacommunity concept (Leibold et al. 2004) emphasizes consideration of both local conditions and dispersal to understand community composition, and application of this framework to streams has generated much interest (e.g., Brown et al. 2011, Göthe et al. 2013, Heino et al. 2015, Downes et al. 2017). However, the metacommunity framework has been used primarily as a way of understanding the pattern of local diversity within a stream, not the maintenance of watershed-scale diversity that is our focus. Nevertheless, local- and watershed-scale diversity are related because the pattern of local diversity directly affects maintenance of watershed-scale diversity. In particular, the fitness–

density covariance coexistence mechanism is strengthened when species are separated in space (low  $\alpha$ -diversity, but high  $\beta$ -diversity) according to their fitnesses (Holt and Chesson 2016, Shoemaker and Melbourne 2016).

Our work shows that in any stream with many sites, environmental heterogeneity and dispersal distance determine the major patterns of local diversity within the stream and the strength of coexistence in the watershed. Sharp peaks in local diversity can occur at confluences, but these branching effects have, at most, minor influence on coexistence strength. The development of unique communities in headwater tributaries increases fitness–density covariance and is associated with low local diversity and high turnover, a pattern often seen empirically and described as species sorting (Finn et al. 2011, Swan and Brown 2014, Kuglerová et al. 2015). In contrast, increased mass effects leading to high local diversity near confluences reduce the ability of species to reach high densities in favorable environments, weakening fitness–density covariance. These 2 effects pull overall watershed-scale coexistence strength in opposite directions (Fig. 6). Investigators often assume that a large effect of dispersal on local community composition or low correlations between local composition and environmental conditions are associated with neutrality (e.g., Thompson and Townsend 2006, Heino and Mykrä 2008), but we show here and elsewhere (Holt and Chesson 2016) that even when local community diversity is elevated by high dispersal, the regional species pool can still be maintained by the spatial storage effect (Appendix S3), which functions by partitioning the underlying environmental variation physiologically rather than numerically.

Our simulation results consider only fixed environmental variation, i.e., purely spatial variation, but natural variation often has a spatiotemporal component, wherein the spatial pattern varies through time. Spatiotemporal environmental variation includes the possibility that the finite rate of increase is affected by fluctuating mortality events, as would be the case with disturbance (Poff and Ward 1990, Townsend and Hildrew 1994, Fagan 2002, Auerbach and Poff 2011). In general, such fluctuations will lead to diversity maintenance by the spatial storage effect, similar to the disturbance model of Miller and Chesson (2009). For branched streams, we show that the exactly null parallel environments case is independent of the nature of the variation (Appendix S1), so the presence of spatiotemporal variation will not alter our conclusion that branching per se has no effect on regional coexistence. Moreover, as discussed above, we find that spatiotemporal variation provides much less opportunity than spatial variation for branching to affect the strength of coexistence.

Our model development depends on environmental conditions directly affecting the finite rate of increase. However, other models have focused on spatiotemporal fluctuations in population densities arising from small population sizes. These sorts of spatiotemporal fluctuations have led to much

interest in local extinction and recolonization and are an essential feature of patch-dynamics models of lotic systems (Townsend 1989, Winemiller et al. 2010), where branching affects recolonization and the persistence of populations (Fagan 2002), and neutral models, where these local extinctions determine the distribution of species throughout the network (Muneepeerakul et al. 2007, Auerbach and Poff 2011, White and Rashleigh 2012). In our simulation model, we consider local extinction by including demographic stochasticity (Appendix S5). We find that local extinctions do not cause branching to affect regional coexistence appreciably, even when mean local population sizes are as low as 4. Thus, the probability of local extinction is high. Our model considers quantitative population sizes, so rescue of low or extinct local populations occurs readily but is much less important than dynamics once the patches are occupied. Moreover, the stabilization provided by environmental variation quickly overwhelms any neutral effects. These findings are similar to those of Shoemaker and Melbourne (2016), where neutral and patch-dynamics models yielded no or very little stabilization and contributed little when operating in conjunction with species sorting.

Stream size is also key to relating our findings to previous models of branched networks. Models with patches only at confluences (e.g., Fagan 2002, Campbell Grant et al. 2007, Auerbach and Poff 2011, Carrara et al. 2012), or a single or few patches per tributary (e.g., Campbell Grant et al. 2007, Goldberg et al. 2009, Campbell Grant 2011) include the implicit assumption that dispersal and environmental variation are long relative to reach size. These scenarios are more extreme versions of our finding that branching can affect coexistence strength when streams are very small relative to dispersal and environmental variation (Fig. 3A, left-most points in Fig. 4A–C). Our analysis isolating these small-stream effects (Fig. 6) ascribes them to the contrasting effects of increased local diversity near confluences and increased heterogeneity caused by washout and unique headwater communities. Of most importance, our work shows that these effects are negligible in streams of realistic size. Moreover, these other studies were focused predominantly on patterns of local diversity within the watershed, which understandably increases near confluences.

### Links to stream communities in nature

The natural history of real stream communities is more complex and structured than we have considered here, and we do not claim to have shown exactly how branching affects real communities. What we have shown is the much greater importance of environmental variation than branching per se on watershed-scale coexistence. Branching may contribute a small but theoretically appreciable amount to the strength of coexistence, if dispersal is long relative to watershed size. However, the effects we have demonstrated

probably are too small to be detectable empirically with present technology. Our analyses identify the following key questions for the capacity of a watershed to support high diversity: 1) What is the extent of environmental variation in the watershed? 2) Do tributaries differ in their environmental conditions? 3) If so, are the scales of environmental correlation or dispersal long enough for conditions in one reach to appreciably affect dynamics in another? We expect these key questions to be generally applicable, not constrained by the specific details of our model.

We show that branching per se is not important for coexistence, but branching cannot be separated from environmental conditions in nature as we have done here. The branched structure of streams has important implications for the physical characteristics of the stream, including channel geometry, substrate, and flow (Leopold et al. 1964, Schumm 1977, Benda et al. 2004). Moreover, branching can modify the headwaters-to-mouth gradients in the stream environment that are fundamental to conceptual models of stream community organization (Vannote et al. 1980, Frissell et al. 1986, Rice et al. 2001, Benda et al. 2004). However, the resultant environmental structure itself, not the branching, is the hypothesized driver of ecological responses in these empirical studies and conceptual models. Likewise, such changes would be accommodated most appropriately in our model by varying the environmental responses. Thus, environmental changes may depend on the branched structure of the stream network (e.g. Leopold et al. 1964, Schumm 1977, Benda et al. 2004), but our results imply that their effects on the maintenance of diversity in ecological communities are best understood as driven by the increased environmental heterogeneity rather than the associated branching patterns. This result underlines the importance of empirical studies investigating the drivers and structure of environmental heterogeneity within watersheds.

Beyond the general correspondence between branching and environmental variables, such as substrate size, depth, and insolation (Leopold 1994, Benda et al. 2004), these variables and many others also change within reaches at smaller scales (Schumm 1977, Ward et al. 2002). For example, pool-riffle sequences and meanders cause within-reach variation in substrate, temperature, depth, velocity, and dissolved O<sub>2</sub>, and riparian vegetation causes variation in insolation and coarse woody debris (Frissell et al. 1986, Poff 1997, Webb et al. 2008, Wolter et al. 2016). The environmental response, *E*, we considered is the integrated effect on fitness of all environmental factors, and so its scale of variation is unlikely to match any particular physical factor and is expected to vary within and between reaches.

In addition to influencing qualitative changes in the environment, branching changes the amount of habitat in different reaches of the stream. Unlike our null model and the simulation results presented above, streams in nature are expected to have a greater proportion of habitat area up-

stream of confluences than downstream because of the combined effects of channel geometry (Leopold et al. 1964, Schumm 1977, Leopold 1994) and the greater dependence of many species on the benthic than the cross-sectional area. Larger upstream habitat area increases the influence of headwater reaches on overall community dynamics and changes the relative importance of boundary conditions. We used our simulation model to explore these issues (Appendix S5) and found that they do not alter the findings that branching minimally affects watershed-scale species coexistence. Changing the size of habitats does not introduce additional environmental heterogeneity, and so little opportunity exists to affect the maintenance of watershed diversity.

Once environmental heterogeneity is taken into account, the small effect of branching on coexistence that occurs in small streams arises as a consequence of mean dispersal distance, although long dispersal has contrasting effects on coexistence strength. High mean dispersal weakens coexistence by increasing diversity near confluences, but strengthens coexistence by increasing the importance of the environmental gradient created by washout at the mouth. These contrasting effects may not be linked in nature as they are in our model. Many highly dispersive species are adapted to avoid dispersing into uninhabitable environments beyond the stream, and we expect this avoidance to reduce the net effect on coexistence of the interaction between dispersal and branching. Dispersal in nature can come in many forms including habitat selection (Haskins 1997, Peckarsky et al. 2000, Reich and Downes 2003, Downes and Lancaster 2010, Guillemette et al. 2010), out-of-network dispersal, and leptokurtic dispersal (Skalski and Gilliam 2000, Lowe 2009, Campbell Grant et al. 2010). Many of these dispersal characteristics make dispersal less constrained by the network than we consider here, which would further reduce the importance of branching on diversity maintenance and would accentuate the already dominant contribution of environmental variation. In general, dispersal characteristics should be considered in terms of how strongly they connect the dynamics of different reaches and how they affect the importance of washout.

The way branching and dispersal interact to link dynamics of different reaches can be understood in terms of the concept of effective closure. Linkages between the dynamics of different reaches require more than just the existence of connectivity. Small numbers of organisms can move between reaches without causing appreciable changes to dynamics. The requirement of linked dynamics makes drawing conclusions directly from field data difficult. For example, flighted insects and many fish have the ability to disperse long distances relative to the branched structure of watersheds, but such long-dispersal events may not be common enough to link dynamics. Hitt and

Angermeier (2008) found that the species richness of fishes near confluences typically is elevated over relatively short distances, in line with findings that fish are capable of long-distance dispersal, but most individuals move short distances and remain within their natal reach (Radinger and Wolter 2014, 2015). Moreover, the dynamics of species with low dispersal capabilities, such as flightless insects (Preziosi and Fairbairn 1992, Phillipsen and Lytle 2013) or amphibians (Lowe 2003), are unlikely to be linked throughout the watershed.

One dispersal characteristic that has received much attention in the literature is downstream drift of organisms. We consider only symmetric dispersal in the text, which probably is representative of many species, where net dispersal and settlement distributions may show little net downstream bias for various reasons (Müller 1982, Hershey et al. 1993, Lowe 2003, Downes and Lancaster 2010, Lancaster and Downes 2014). Moreover, the results for the exact parallel environments case do not depend on the nature of dispersal. Thus, drift does not make the strength of coexistence depend on topology per se, provided the amount of drift is not affected by branching (Appendix S1). However, when the environment differs between tributaries, drift increases the influence of upstream reaches on downstream reaches. Drift also increases the effect of boundary conditions at the mouth relative to boundary conditions in the headwaters. We investigate these effects in Appendix S5 and find that drift only slightly increases the already small positive effect of branching on coexistence.

Stream communities worldwide are under threat and are experiencing dramatic changes, often because of anthropogenic effects. Mitigating these negative effects requires knowledge of the processes maintaining diversity in watersheds to guide restoration and management interventions that typically occur at a smaller scale (Lake et al. 2007, Roni et al. 2008, Heino 2012, Palmer et al. 2014). Our results suggest that primary emphasis should be placed on maintaining and restoring areas of high-quality habitat. These findings provide theoretical support for Fahrig's (2003, 2017) reviews of empirical studies showing that the amount of habitat is far more important than connectivity and that once habitat is taken into account, the vast majority of empirical evidence shows that lower connectivity tends to favor higher values of response variables, such as species richness. This conclusion is not to say that restoring connectivity is unimportant. Connectivity is one of the restoration activities that has yielded the most success (Roni et al. 2008, Palmer et al. 2010, Neeson et al. 2015), probably because of improvement of the condition and amount of available habitat and provision of a route for recolonization, rather than the restoration of topology. A focus on topology and local diversity might sometimes have an effect opposite to that intended. Local diversity

at confluences is an outcome of regional maintenance of diversity. Focusing on patterns of local diversity within the watershed obscures the overall reduction in diversity at the watershed scale caused by confluences.

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Author contributions: the authors jointly conceived of the idea for this study. PC developed the null and environmental models, GH wrote the code, conducted the simulations, and performed the analyses. Both authors contributed to the interpretation of the results and the preparation of the manuscript. PC developed the analytical results in Appendix S1.

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