Effects of stream topology on ecological community results from neutral models

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ABSTRACT

While neutral theory and models have stimulated considerable literature, less well investigated is the effect of topology on neutral metacommunity model simulations. We implemented a neutral metacommunity model using two different stream network topologies, a widely branched network (wide tree) and a narrowly branched network (high tree), both represented as binary trees. The wide tree had fewer exceedances of carrying capacity, higher final number of individuals per community, and greater community (α) diversity than the high tree. The difference in diversity increased with increasing dispersal rate. We infer that the greater connectivity of the wide tree facilitated more even spatial dispersal, which limited carrying capacity exceedances and associated random deletions, which, in turn, resulted in higher diversity. Effects specifically due to topology should be considered in analyses of community patterns for mobile aquatic species.

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1. Introduction

Hubbell's "unified neutral theory of biodiversity and biogeography" (2001) has successfully reproduced many observed patterns in species abundance and range size, using only a simple community model. The model and theory are neutral in the sense that all individuals within a community of ecologically similar interacting species are assumed to have the same birth and death rates. This theory has generated many theoretical and empirical investigations into its properties and validity (e.g., Alonso et al., 2006; Bell, 2000, 2001; Bell et al., 2006; Dornelas et al., 2006; Holyoak and Loreau, 2006; Hubbell, 2006; Leibold and McPeek, 2006; McGill et al., 2006; Muneepeerakul et al., 2007). Recently, neutral models been applied to fish diversity patterns in a large river system in the central United States (Muneepeerakul et al., 2008), the Panamanian tropical rain forest (Chisholm and Pacala, 2010), and avifaunal extinctions worldwide (Halley and Iwasa, 2011).

The influence of topological structure on neutral community ecology models has been investigated for terrestrial systems. White and Kiester (2008) used a model adapted from Bell (2000, 2001) neutral simulation model to show that several measures of community structure, including final number of individuals per community and Shannon diversity (α-diversity) differed among three topologies for terrestrial systems. The ordering of results corresponded directly to the degree of adjacency (measured as the number of adjacent communities), and the magnitude of differences increased as the dispersal rate of newborn individuals increased. Topological effects on an analytical version of Hubbell (2001) neutral model were recently studied by Economo and Keitt (2008). They examined the effects of different topologies on metacommunity (γ-) diversity using migration matrix models from population genetics to represent migration probabilities, and by developing the Malécot equation from the same literature to calculate Simpson diversity. They also showed that α-diversity increases with increasing migration rate and with more connected topologies, consistent with White and Kiester (2008).

The role of topology in determining community patterns within stream networks has applications for management of mobile species within watershed systems (Brown et al., 2011). An understanding of the role topology plays in the outcome of population dynamics allows management to set more accurate expectations for outcomes of activities in particular stream segments, such as allowing discharge permits or other activities that could decrease water quality and habitat, as well as restoration activities that can enhance these measures.

Here we examined the effect of two different stream topologies on the ecology of mobile species (e.g., fish) that actively navigate throughout the network. For this study we define a stream network as a linear branching structure with two upstream links or

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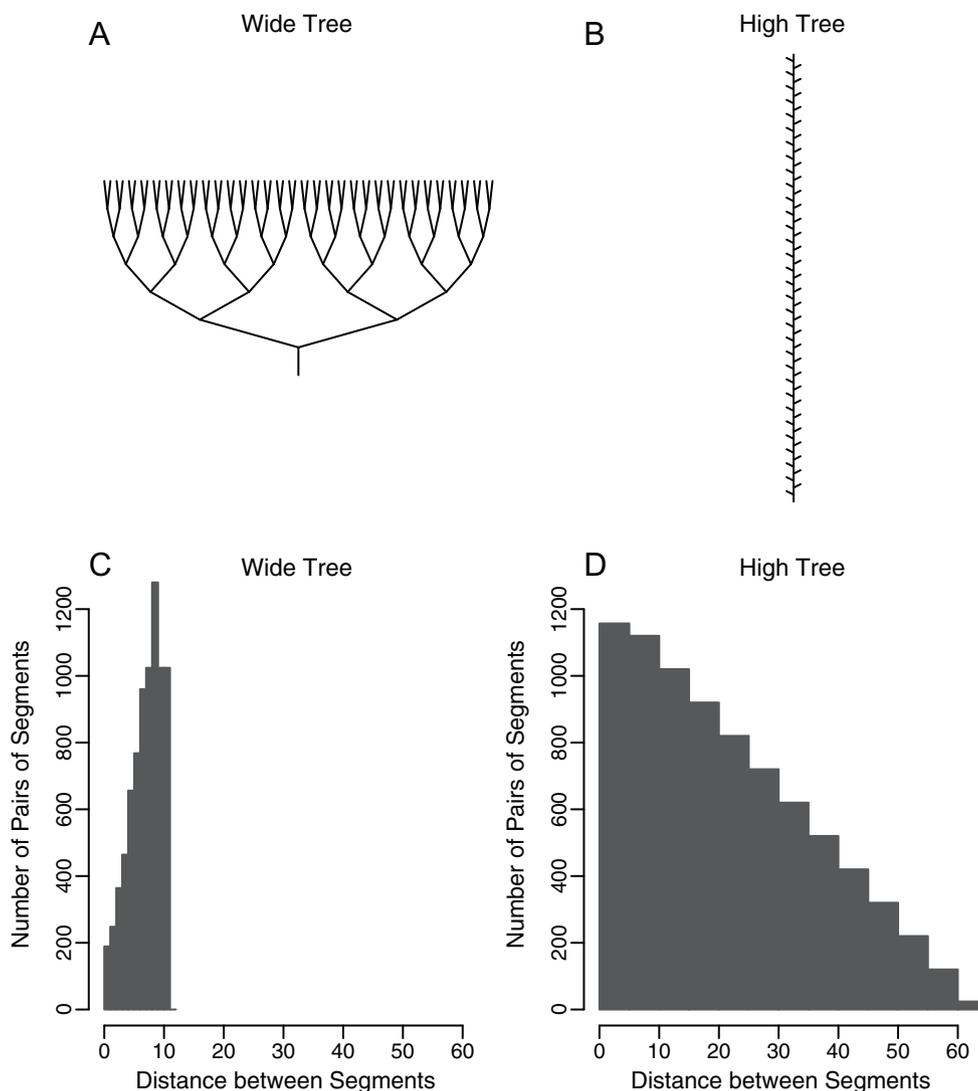E-mail addresses: whitede@onid.orst.edu (D. White), rashleigh.brenda@epa.gov (B. Rashleigh).

Fig. 1. The two contrasting topological shapes for a 127-segment stream network represented as binary trees that are the widest (A) and the highest (B) possible topologies for the size. The frequency distributions of distances between segments (measured as number of segments) are shown for these two topologies in (C) and (D).

segments for each downstream link or segment, i.e., a binary tree. We do not consider braided channels, lakes or reservoirs embedded in a network, deltaic distributaries, or any canals or other features that create closed cycles or loops in the network. We assume that a segment contains a multi-species fish community. The network is undirected and that individuals can move from one segment to any other adjacent segment. For our experiments we compared two topologies: a widely branched tree (wide tree) with a narrowly linear network (high tree) (Fig. 1). We chose these as two extremes, to see their effect on simulated metacommunity characteristics.

2. Methods

We created two stream network topologies of equal size, modeled as binary trees. Each tree included 127 stream segments, but was configured to be either the widest or the highest possible (Fig. 1). The trees differed in maximum topological depth (i.e., the maximum number of segments from bottom to top) and in the maximum topological width (i.e., the maximum number of segments at any depth). The wide tree had a maximum depth of 7 and a maximum width of 64 segments; the high tree had a maximum depth of 64 and a maximum width of 2

segments. The distribution of distances between pairs of segments also differed greatly (Fig. 1C and D). The wide tree distribution had a maximum distance of 11 segments, a median of 8, and a negative skew. The high tree distribution had a maximum distance of 63 segments, a median of 19, and a positive skew. Stream orders (Gregory and Walling, 1973) also differed between the two topologies. Strahler stream orders define stream size based on a hierarchy of tributaries: when two first-order streams come together, they form a second-order stream; when two second-order streams come together, they form a third-order stream, and so on. Both networks contained 64 Strahler first-order segments, but in the high tree, all 63 remaining segments were second-order. In the wide tree, the numbers of segments per stream order decreased by factors of two, reaching a single seventh-order segment at the bottom of the network. The bifurcation ratio is the ratio between the number of streams of one order and the number of the next higher order. Therefore the wide tree had a bifurcation ratio of 2 between any two orders and the high tree had only one bifurcation ratio, that of 64 between first and second orders. Because many streams in nature have ratios between 3 and 5 where geological structure does not overly influence the network (Gregory and Walling, 1973), the two extreme trees are outside the normal range, the high tree being less so than the wide tree.

We assumed that a multi-species community potentially occurred in each segment, and we 'simulated the dynamics of multiple species through time. Our simulations used the same neutral algorithm as in White and Kiester (2008), where the spatial units in White and Kiester (2008) function as communities, as do the segments in our stream network model. Our model had five parameters: (1) the size of the species pool (15); (2) carrying capacity, or the maximum number of individuals that can survive in a community (1000); (3) the probability that an individual of any species will give birth or die in each time step (0.3); (4) the probability that a newborn individual will disperse to an adjacent community (variable); and (5) the probability that an individual of any species will immigrate from outside the metacommunity into a community in each time step (0.001). Default parameters were selected based on Bell (2000, 2001), White and Kiester (2008), and preliminary simulations on river networks that allowed reasonable species survival.

In each time step we simulated immigration, birth and dispersal, and death (where death is due both to death rate effects and maintenance of carrying capacity). The population processes were implemented following Bell (2000, 2001) descriptions. Immigration was assumed to occur into each segment of the network according to the immigration probability. Immigrants were assigned to a random species. The population in each segment was increased according to the birth rate. At each time step, each newborn randomly dispersed to an adjacent location and continued moving until the probability of dispersal was not met. Boundaries of the system were reflective, in that individuals turned around at the headwaters or at the mouth to continue dispersing. Randomly chosen individuals died in each segment according to the death rate. After immigration, birth, dispersal of newborns, and death, if the number of individuals in a community exceeded the carrying capacity, excess individuals were deleted randomly. Consistent with Bell (2000, 2001), we assumed that speciation did not occur.

For the initial condition, each community was assigned the number of individuals equal to half of the carrying capacity; individuals were randomly distributed to each species. We ran 200 simulation replicates, each having 2000 time steps, for each combination of topology (wide vs. high), and dispersal probability (varied between 0.0 and 0.4 in increments of 0.05). We recorded the number of times carrying capacity was exceeded throughout the simulation; the mean number of individuals per community at the end of a simulation replicate; and community diversity (α-diversity). Exceedances of carrying capacity were used as a measure of the effects of topology because, according to our hypotheses, the wide tree should have fewer of these than the tall tree. Community diversity was measured as species richness, Shannon diversity, and inverse Simpson's index of diversity. Results were calculated on the pooled values of all communities and all replicates, to minimize the effects of outliers in the distributions of random variables used in the model.

3. Results

Differences in the three performance statistics occurred between the two stream network topologies. Moreover, these differences tended to increase with increasing probability of dispersal (Fig. 2). For both topologies, the number of times carrying capacity was exceeded was highest with no dispersal, declined at low dispersal probabilities, then gradually decreased as dispersal increased (Fig. 2A). Carrying capacity exceedance was greater for the high tree than for the wide tree, and this difference became more pronounced as birth and death rates increased.

Mean final number of individuals per community increased as dispersal increased (Fig. 2B). Final numbers of individuals per
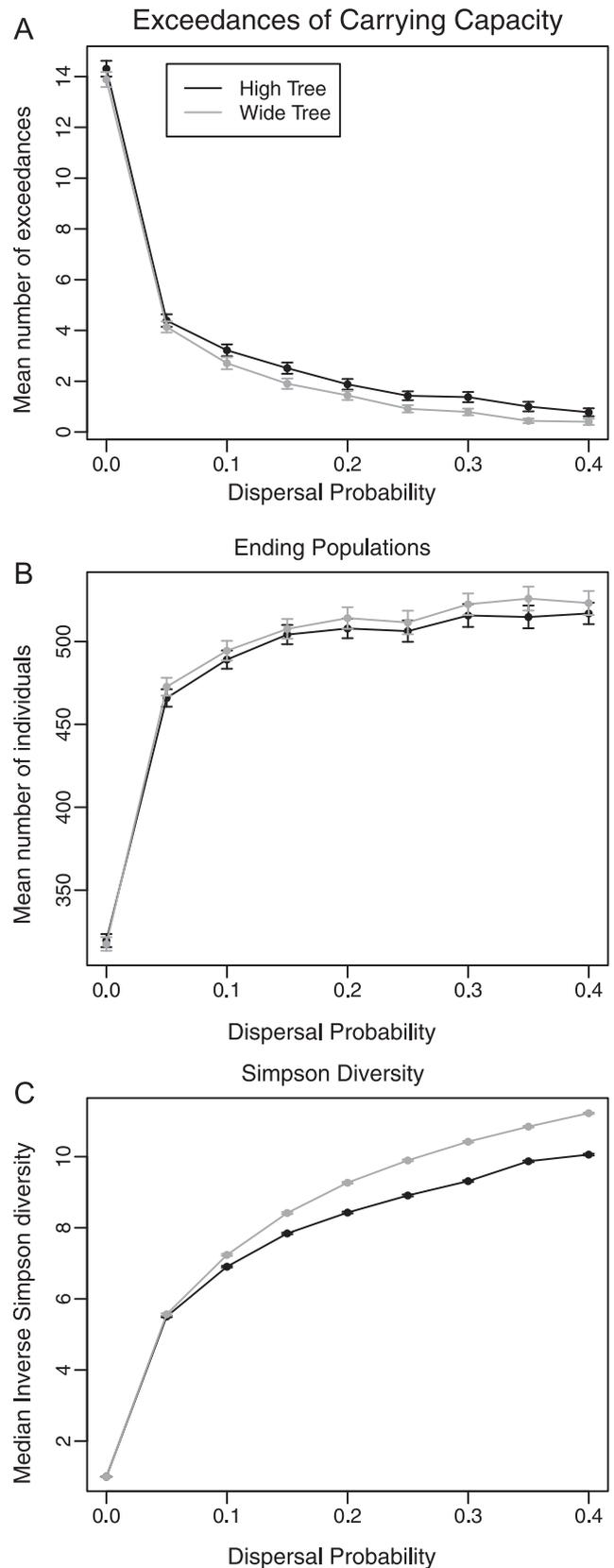
Fig. 2. Statistics calculated on the pooled values of all communities for all replicates across a range of dispersal probabilities: (A) the number of times carrying capacity was exceeded per community throughout the simulation; (B) the mean number of individuals per community, across all species, at the end of a simulation replicate; and (C) median values of inverse Simpson Diversity at the end of a simulation. These results are shown for the two topologies with 95% confidence limits at each dispersal value.

community for the high tree were lower than those for the wide tree, although this difference was not significant, as confidence intervals overlapped between the two results for most data points.

Diversity statistics also varied with dispersal and topology as shown by the median inverse Simpson diversity index (Fig. 2C; species richness and the Shannon diversity index had similar patterns). The index for both topologies was at a minimum with no dispersal and then sharply increased as dispersal increased. At a dispersal probability of 0.4, and birth and death rates of 0.3, there was a difference of about two units between the two topologies. Similar patterns for all metrics were observed for a set of smaller trees (with 15 stream segments each), although differences between the topologies were less pronounced.

4. Discussion

Our simulated communities were affected by dispersal probability and stream topology. At low levels of dispersal, communities in both topologies suffered from recruitment limitation and local exceedances of carrying capacity. Thus, lower numbers of individuals and lower diversity were more likely. Our finding that local diversity increased as dispersal increased is a common prediction of neutral models (Chase et al., 2005), and is also consistent with the general findings for experimental studies (Cadotte, 2006). We infer that the greater connectivity of the wide tree facilitated more even spatial dispersal, which limited carrying capacity exceedances and associated random deletions, which, in turn, reduced species extinctions and resulted in higher diversity. Thus, our supposition that the wide tree would produce higher diversity than the high tree and that the difference between the two topologies would increase with increasing dispersal probability was supported. This result is consistent with the finding of Hitt and Angermeier (2008) for river networks in the Mid-Atlantic U.S. that proximity of connected streams influence the distribution of fish in river networks.

Many modeling studies simulating spatial processes fail to consider the possible influences of topology on model outcomes (e.g., Carnevalea et al., 2008; Phillips et al., 2008; Sebert-Cuvillier et al., 2008). In our study we used two extremes of possible binary tree type networks. Most real stream networks are between these extremes of the distribution of possible topologies, and therefore the effects of topology would be smaller than what we measured. Our purpose was to bracket the effects of topology on metacommunity patterns and to highlight the importance of topology on tree-structured networks, using a simple neutral community model that includes dispersal. Topological structure affects dynamic spatial processes because adjacency and connectivity relationships both enable and limit dispersion of organisms, particles, or fluid media. In two dimensional planar systems the most dramatic effect is the difference between hexagon and square lattices in simulating fluid motion governed by the Navier-Stokes equation (Toffoli and Margolus, 1987, p. 178; Frisch et al., 1986). There are also differences in percolation thresholds (Stauffer and Aharony, 1992), optimal quantization (Conway and Sloane, 1999), and spatial sampling efficiency (Olea, 1984).

Our study was by necessity simplified. This study focused on one of the five model parameters; additional analysis could be done varying vital rates, the size of the species pool, carrying capacity, and the outside immigration. We designed the study to be consistent to the specifications of the neutral models of Hubbell (2001) and Bell (2000, 2001). The assumptions of these neutral models have received criticism (see McGill et al., 2006 for a meta-analysis of empirical evidence). Bell (2006) model represents variation in habitat that is implemented by variation in fitness with respect to birth and death rates; in the stream network application of the neutral model future simulations will vary carrying capacity by stream order to represent environmental variation, which

may influence the relationship between dispersal and diversity (Hiltunen et al., 2006). Also, we assumed symmetric dispersal among segments, even though asymmetric dispersal may commonly occur, due to mass flow of water, and can affect population dynamics (Goldberg et al., 2010). While we have attempted to isolate and identify effects of topology, a holistic view of stream ecosystems will incorporate many other factors, such as additional community processes, and evolutionary processes (Campbell Grant et al., 2007). This study presents a theoretical approach however future studies could increase realism, using parameters estimated from field data (Beeravolu et al., 2009), and scenarios of human alteration (Padgham et al., 2010).

Our approach to investigating alternative topologies used a simulation version of the neutral model, rather than the analytical version of Economo and Keitt (2008). Our results therefore complement Economo and Keitt by demonstrating similar effects with a Bell (2001) type model that can vary ecological parameters as well as topology. There is nothing particular to streams inherent in this work and it may apply generally to binary networks containing discrete objects moving through the network over time. Although empirical testing of neutral community models has provided mixed support for the neutral theory in general (McGill et al., 2006), synthesis has often been constrained by unclear definitions of spatial and temporal scale (Holyoak and Loreau, 2006). Nevertheless, neutral model research is proving to be a valuable stimulus to better understanding in community ecology and this study adopts that spirit in a cautionary tale for modeling in a spatial framework.

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