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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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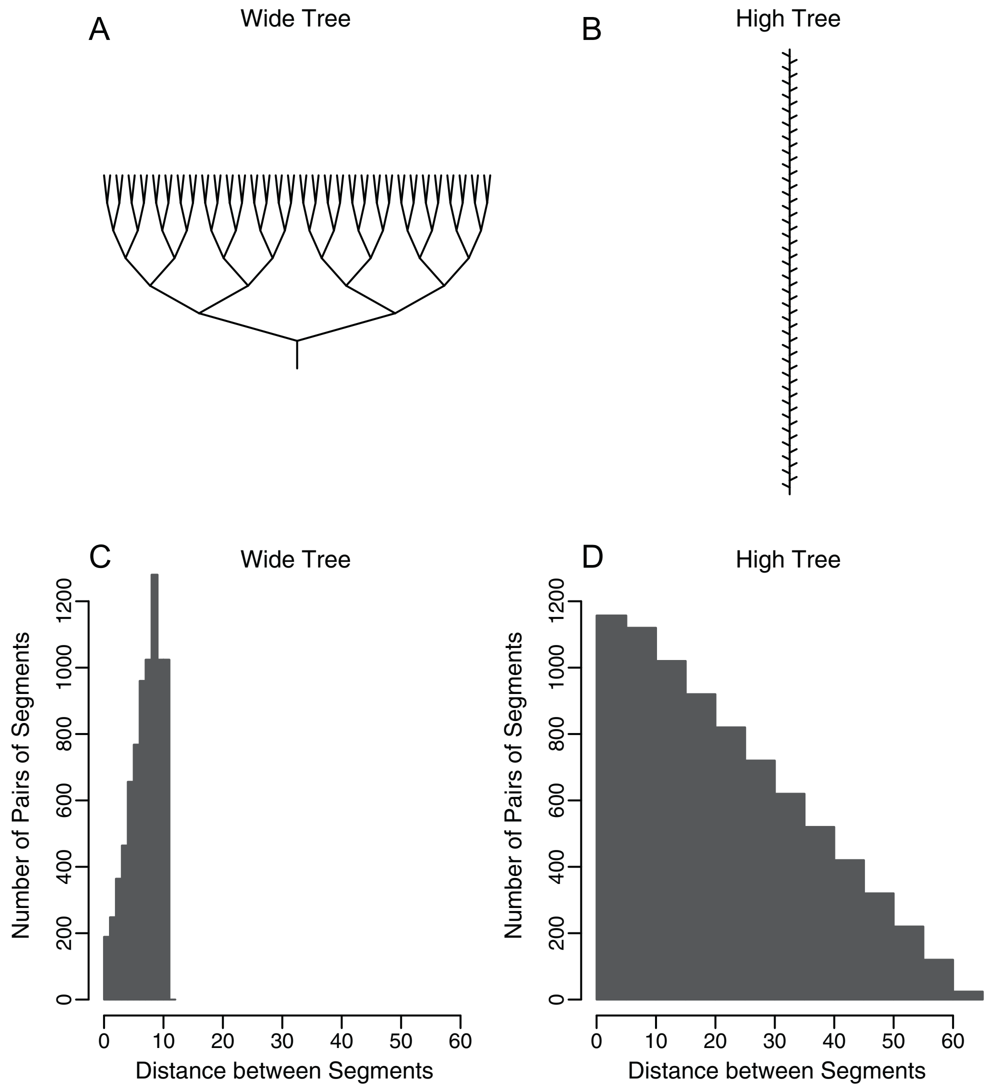

Fig. 1. The two contrasting topological shapes for a 127-segment stream network represented as binary trees that are the widest (A) and the highest (B) possible topologies for the size. The frequency distributions of distances between segments (measured as number of segments) are shown for these two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