

Topology matters: Network topology affects outcomes from community ecology neutral models

Denis White^{a,*}, A. Ross Kiester^b

^a *US Environmental Protection Agency, 200 SW 35th Street, Corvallis, OR 97333, USA*

^b *Biodiversity Futures Consulting, 5550 SW Redtop, Corvallis, OR 97333, USA*

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Abstract

Topology affects outcomes of processes in planar networks. Hexagon tessellations have different performance than, and are often superior to, square tessellations in applications such as fluid dynamics, percolation theory, self-avoiding walks, survey sample design, and quantization. Hexagon tessellations and square tessellations using both von Neumann and Moore neighborhoods were examined as a network topology for neutral ecology community models, following the simulation approach of Graham Bell. These models, which assume identical life history and movement properties for each individual of each species, produce collective properties of communities, such as abundance distributions, range distributions, spatial variation in abundance, species–area curves, and spatial variation in species composition, that match many empirical patterns. The simulations in this study varied the dispersal rate but kept birth, death, and immigration rates constant. For these experiments, ending community populations, species richness, Shannon diversity, and Simpson diversity were clearly different for the different topologies, but the relationship between the topologies varied as the dispersal rate changed. Empirical distributions of the performance measures also showed clear differences among topologies. The interaction of topology with dispersal, spatial boundary effects, and other parameters of these models appears to be quite complex and warrants further research.
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1. Introduction

Models of spatial processes in two dimensions often use one of the only three regular tessellations in the plane: squares, hexagons, or triangles. Triangles are seldom used, hexagons infrequently, and the vast majority of regular grid applications uses squares. While square tessellations are easy to use there is one significant problem. Hexagons have six neighbors each with the same border length (Fig. 1a). Squares have four orthogonal neighbors each with the same border length and four diagonal neighbors adjacent only at a vertex. The orthogonal neighbors are called the von Neumann neighborhood (Fig. 1b), and those

plus the diagonal neighbors are called the Moore neighborhood (Fig. 1c).

Using the von Neumann neighborhood neglects the close proximity of the diagonal neighbors, but using the Moore neighborhood implicitly assumes, in effect, that the cell is an octagon and octagons do not tile the plane. Of course, the diagonal neighbors can be weighted (see Birch, 2006 for an example), but it is not obvious what the weighting should be, depending on whether the process assumes locations are points or areas. An alternative used in some cellular automata applications is the Margolus neighborhood, which can be visualized as the six closest neighbors in a tilted square tessellation (Fig. 1d). The Margolus neighborhood is implemented with two 4x4-cell blocked square tessellations which are offset from one another by one row and one column. The Margolus neighborhood then consists of a cell and its three block

* Corresponding author. Tel.: +1 541 754 4476; fax: +1 541 754 4799.
E-mail addresses: white.denis@epa.gov (D. White), rkiester@gmail.com (A.R. Kiester).

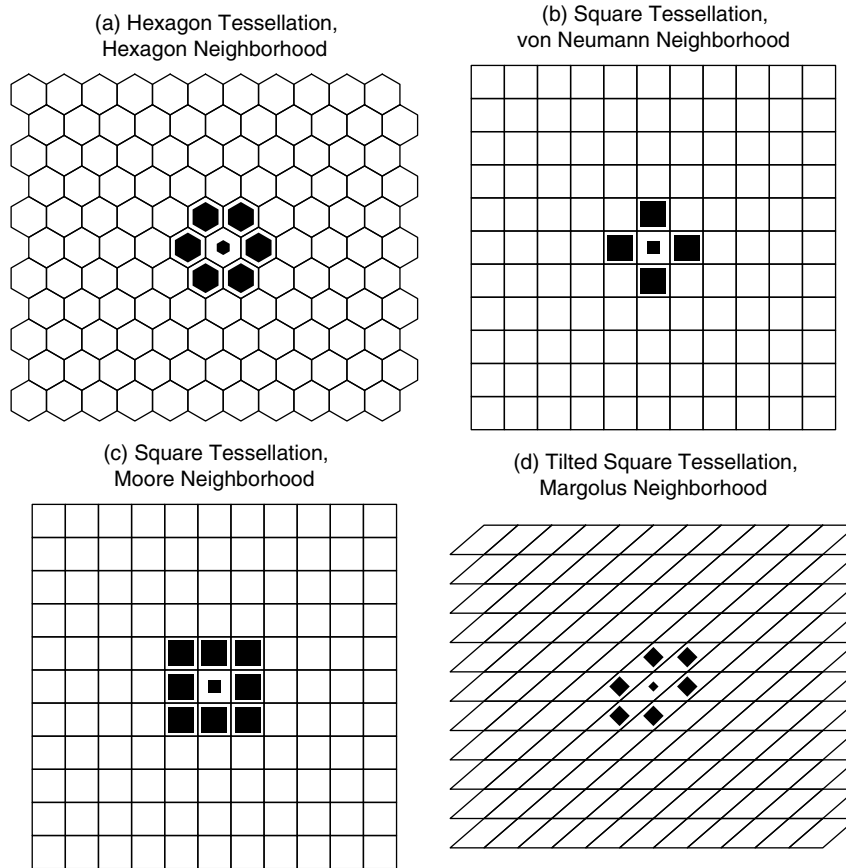


Fig. 1. Topologies analyzed in the paper are (a) hexagons, (b) squares with the von Neumann neighborhood, and (c) squares with the Moore neighborhood. Some cellular automata applications use (d) squares with the Margolus neighborhood in order to achieve hexagon neighborhood properties.

neighbors in one tessellation plus its three block neighbors in the other tessellation. This procedure essentially simulates hexagonal adjacency relations.

The motivation for examining this issue in the context of community ecology population models comes from a wide literature that describes the differential performance of alternative topologies on a number of physical properties and processes when represented in a plane.

The most important of the findings on topological effects is probably in the simulation of the Navier–Stokes equations for fluid dynamics in two dimensions. Both analytical results and simulations show not only differences between square and hexagonal tessellations, but also that the square tessellation (using the von Neumann neighborhood) has an anisotropic viscosity that is an artifact resulting, apparently, from the ambiguity in connectivity between adjacent side neighbors and adjacent vertex neighbors (Frisch, Hasslacher, & Pomeau, 1986; Toffoli & Margolus, 1987, p. 178). The Navier–Stokes results raise a question for ecology: is particle movement such as that found in ecological processes subject to similar artifactual effects when implemented in a square tessellation?

Another finding is from analysis of the percolation movement model, or graph connectivity property, in two (and greater) dimensions. This model has a critical para-

meter that is topology dependent. This parameter is the threshold of density of occupancy beyond which it is guaranteed that a path will exist from one boundary of the study area to another, connecting occupied locations. If the locations are conceived of as vertices, the model is called site percolation, and if edges, bond percolation. For both types of percolation the critical value for a hexagon tessellation (considered as a triangular lattice representing the movement graph) is less than that for a square tessellation (using the von Neumann neighborhood) (Stauffer & Aharony, 1992; Wolfram Mathworld, 2006).

In geostatistics, a hexagonal tessellation of sampling sites has a lower minimum average standard error, a lower maximum standard error, a larger screen effect (ability of sample points to minimize influence of points farther from the estimation point), and a smaller number of nearest neighbors for stable kriging, than a square tessellation (or any other pattern of sample points) (Olea, 1984).

In the quantization of continuous or highly detailed discrete data into chunks or bins more suitable for data analysis or graphical display, hexagons are the optimal solution in two dimensions (Conway & Sloane, 1999).

Recent work questions simulations using square tessellations (and other types) and quantifies some of the problems. Flache and Hegselmann (2001) found that in

agent-based social cooperation simulations, actors will migrate in search of other cooperating actors in hexagon tessellations at a higher rate than in square tessellations, and it takes approximately six times as long for the rates to stabilize. Cioffi-Revilla (2002) points out that the average number of territorial neighbors in political systems is close to six, that is, close to the number of hexagon neighbors, and that the use square tessellations in agent-based model simulations may affect model behavior.

Birch (2006) compared a hexagonal tessellation with a modified square tessellation where diagonal interactions were given half the weight of orthogonal interactions, in an attempt to approximate the behavior of the equiprobable interactions in the hexagonal tessellation. Using a weed spread algorithm where the probability of spread was equal to the proportion of neighbor cells occupied minus the probability that external events (e.g., grazing) would occur, the modified square tessellation and hexagonal tessellation had similar behavior except when the grazing probability was in the range 0.25 to 0.3. (At 0.25 the square tessellation with only orthogonal interactions [i.e., using the von Neumann neighborhood] does not propagate occupancy to neighbor cells.) Bithell and Macmillan (2007) explored alternatives to regular tessellations with one individual per cell for cellular automata applications in population dynamics. They advocated for a “particle-in-cell” representation where more than one individual can occupy a cell.

Although hexagonal tessellations have been used in ecological modeling at least as far back as 1967 (Murray, 1967), the first comparison of tessellation properties for ecological research may have been that of Keller, Heimbuch, and Richmond (1979). These authors compared hexagonal and square tessellations for use in evaluating habitat edge effects, spatial trends in habitat distribution, and modeling territory size for terrestrial wildlife.

In this paper, the question is posed whether the topology of a network of ecological communities affects the dispersal statistics of populations in the communities. To do this we use a recently proposed theory that does, in some circumstances, appear to produce, when simulated or analyzed mathematically, observed empirical distribution patterns of species and their abundances. This theory has been called the neutral theory of community ecology (e.g., Bell, 2005) or, alternatively, the unified neutral theory of biodiversity and biogeography (Hubbell, 2001).

The theory is neutral in the sense that each species in a community of species that compete with one another is assumed to have the same per capita birth and death rates. This assumption contrasts with most accepted biological knowledge especially when carefully analyzed empirically (Chave, 2004). Furthermore, the theory has been developed with the assertion, although not specified as an assumption, of a uniform environment. This limitation, obvious to anyone, has been explicitly investigated by Bell (2005).

What, then, is striking about such a simplified model, having only a handful of parameters, that will be described shortly, is that both analytical results and simulated exper-

iments yield patterns that conform to many of the documented relationships about species, their abundances, and ranges. As a number of reviewers have noted (e.g., Brown, 2001; Chave, 2004), although the theory is almost surely incorrect in its assumptions, it is the most ambitious, creative, and successful attempt so far to account for many of the issues and assemblage data of community ecology. This theory has also, appropriately to its importance, generated substantial investigations both theoretical and empirical into its properties and validity (e.g., Adler, 2004; Bell, 2000, 2003; Chase, 2005; Chave, Muller-Landau, & Levin, 2002; Condit et al., 2002; Enquist, Sanderson, & Weiser, 2002; Etienne & Olf, 2004; Gilbert & Lechowicz, 2004; He, 2005; Hubbell, 2005; Magurran, 2005; McGill, 2003; McGill & Collins, 2003; McKane, Alonso, & Solé, 2004; Nee, 2005; Nee & Stone, 2003; Vallade & Houchmandzadeh, 2003; Volkov, Banavar, Hubbell, & Maritan, 2003; Yu, Terborgh, & Potts, 1998).

The present paper contributes to this literature by examining the extent that simulation models of the theory may depend upon, in addition to any other parameters, the geometric nature of the network in which the communities of species are presumed to inhabit.

2. Methods

The six parameters for the Bell (2001) version of neutral community ecology models are (1) the number of species in the species pool, (2) the (maximum) number of individuals in a community (a carrying capacity), (3) the probability that an individual of any species will give birth in each time step, (4) the probability that an individual of any species will die in each time step, (5) the probability that a newborn individual will disperse to an adjacent community, and (6) the probability that a new individual of each species will immigrate (from outside the meta-community) in each time step. It appears from Bell (2005, Fig. 1) that he used a square tessellation in his simulations, although this was not specified in his papers nor whether he used the von Neumann or Moore neighborhoods. (Hubbell (2001) used the square tessellation with the Moore neighborhood for simulation results.)

In this study, simulation runs were initialized by assigning to each community an initial population of half the carrying capacity randomly distributed to each species. The actions in each time step were immigration, birth and dispersal, death, and maintenance of carrying capacity. Each community was assigned immigrant individuals according to the immigration probability, distributed randomly to each species. Each existing individual of each species in each community produced a new individual with probability equal to the probability of birth. Each new individual moved to a random adjacent location with probability equal to the probability of dispersal and continued moving until the probability of dispersal was not met (Bell, 2001). Each existing individual died with probability equal to the probability of death. Finally, if the number of

individuals in a community exceeded the carrying capacity, the excess were deleted randomly. The algorithm for the neutral model represented in pseudo-code is

```

for ( $t \in 1:nT$ )
  for ( $c \in 1:nC$ )
    Immigration
    for ( $s \in 1:nS$ )
      if  $x \sim U[0,1) < P(m)$  then  $N\{c,s\} ++$ ;
    end ( $s$ );
    for ( $s \in 1:nS$ )
      Birth
      if  $x \sim U[0,1) < P(b)$  then
        Dispersal
         $i = c$ ;
        while  $x \sim U[0,1) < P(u)$  do  $i = a$ 
           $\{i,y \sim V[1,m\{i\}]\}$ ;
           $N\{i,s\} ++$ ;
        end birth & dispersal;
        Death
        if  $x \sim U[0,1) < P(d)$  then  $N\{c,s\} --$ ;
      end ( $s$ );
      Carrying Capacity
       $E = N\{c\} - K$ ;
      for ( $e \in 1:E$ )
         $j = x \sim U[s \in (S | N\{c,s\} > 0)]$ ;
         $N\{c,j\} --$ ;
      end ( $e$ );
    end ( $c$ );
  end ( $t$ );
  
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where t indexes time steps, nT is the total number of time steps, $:$ is the range operator ($a:b$ means integers between a and b), c indexes communities, nC is the total number of communities, s indexes species, nS is the number of species, x is a random number, $U[a,b)$ is the uniform continuous distribution from the closed lower bound a to the open upper bound b , $P(m)$ is the probability of immigration, $N\{c,s\}$ is the population of species s in community c , $++$ is the increment operator (by one unit), $P(b)$ is the probability of birth, i indexes community location, $P(u)$ is the probability of dispersal, $a\{i,\}$ is the adjacency table of adjacent communities for community i , y is a random variable, $V[a,b]$ is the uniform discrete distribution for integers between a and b , $m\{i\}$ is the number of adjacent communities to community i , $P(d)$ is the probability of death, $--$ is the decrement operator (by one unit), E is the excess number of individuals in a community, K is the carrying capacity, e indexes the excess amount, j is a random species with population greater than zero.

The simulations used a set of 121 communities arranged either as an 11 by 11 tessellation of squares or as an 11 by 11 tessellation of hexagons. These tessellations were not connected across edges with toroidal topology but were considered as planar bounded spaces. Adjacency for square

tessellations was defined by both the von Neumann neighborhood, meaning the side adjacent four neighbors, as well as the Moore neighborhood of those four plus the corner four neighbors.

The number of species was set to 15, the number of individuals to 1000, and the probability of immigration to 0.001, for all simulation runs. The probability of birth and death was set to 0.3; and the probability of dispersal varied between 0.0 and 0.4. There were 400 replicates, each having 2000 time steps, for each topology for each change in parameter settings.

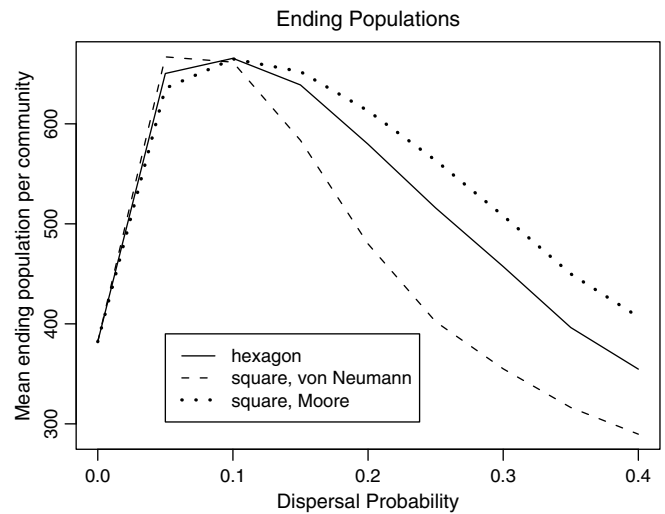


Fig. 2. Mean for all simulations of total populations per community across all species at the end of the 2000 step replicates, for each dispersal probability, by topology. Dispersal probabilities were from 0.00 to 0.40 by increments of 0.05.

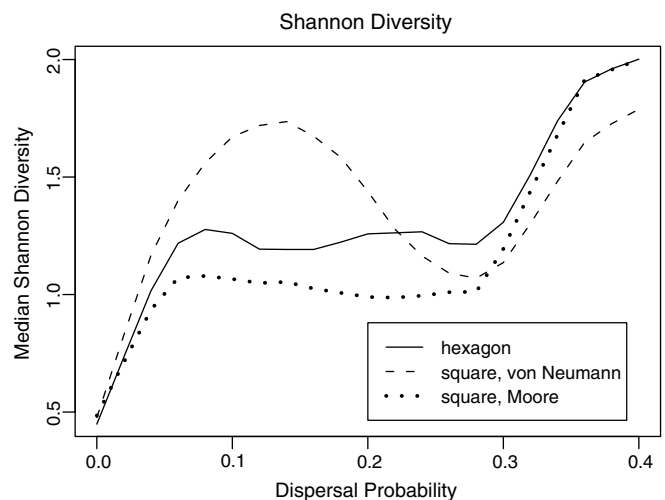


Fig. 3. Median values of Shannon diversity across all simulations and communities, for each dispersal probability, by topology. Dispersal probabilities were from 0.00 to 0.40 by increments of 0.02. The graphs are less smoothed versions of the point by point trajectories, where the proportion of points used for each smoothed value was 0.3 of the total.

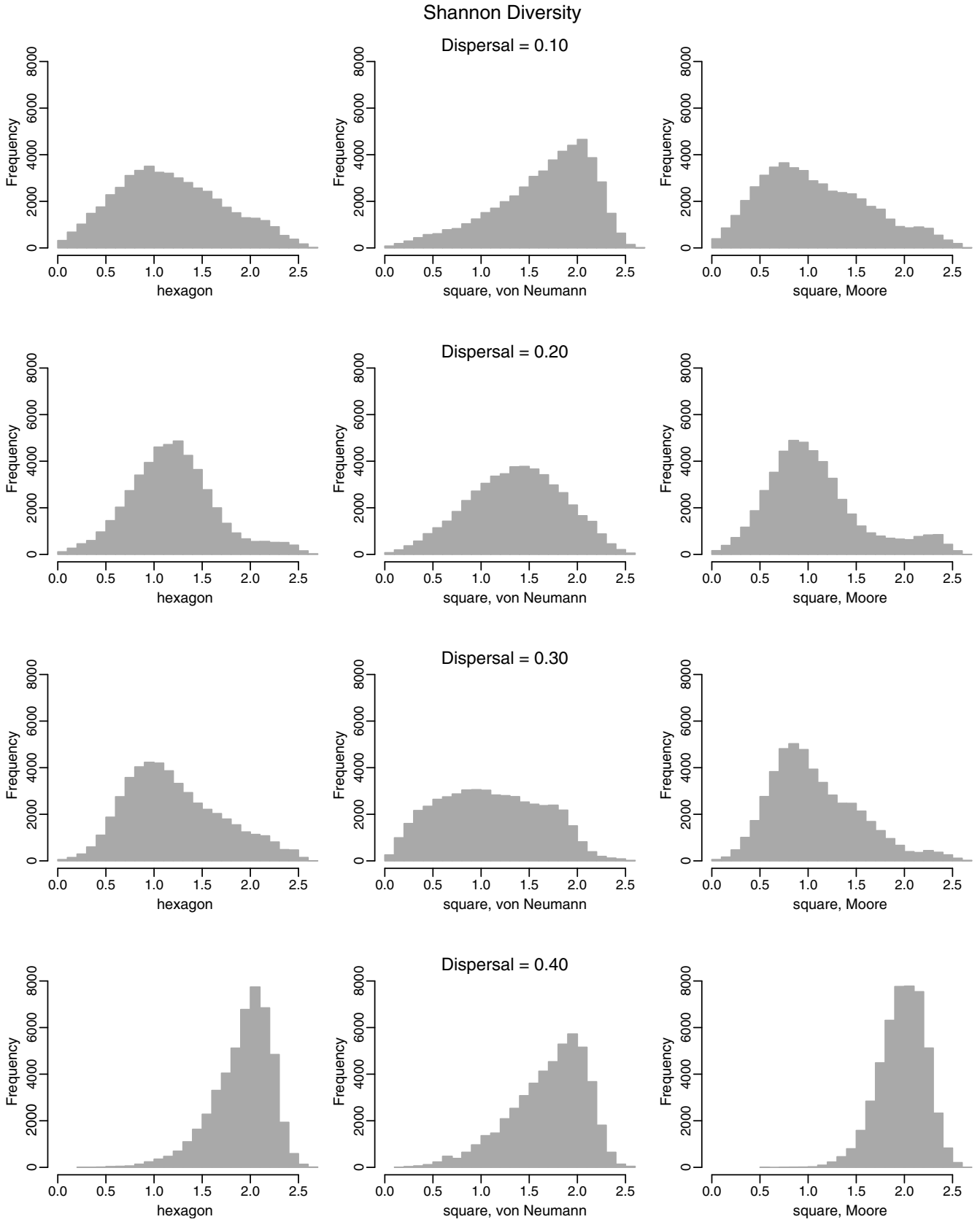


Fig. 4. Histograms of the distribution of Shannon diversity values for each combination of dispersal probability and topology. Each histogram includes 48,400 values.

Community outcomes were measured as the mean values of total community population at the end of each simulation, plus the community diversity measures of species richness, Shannon diversity, and Simpson diversity (the negative of the original measure, see Magurran, 1988 for Shannon and Simpson measures and variants, and Lande, 1996 for analysis of Simpson's measure). The formulas of the diversity measures, for one community, are

$$\text{Species richness: } S = \sum_{i=1}^{\#\text{species}} I_i$$

$$\text{Shannon diversity: } H' = - \sum_{i=1}^{\#\text{species}} \frac{n_i}{N} \ln \frac{n_i}{N}$$

$$\text{Simpson diversity: } D = 1 - \frac{\sum_{i=1}^{\#\text{species}} n_i(n_i - 1)}{N(N - 1)}$$

where I_i is the indicator variable having the value of 1 if there is at least one individual of species i , otherwise zero; n_i is the number of individuals for species i , N is the total number of individuals, and \ln is the natural logarithm.

3. Results

For the three topologies in the configurations studied here, the mean number of adjacent communities was 5.29 for the hexagonal tessellation (“hexagon”), 3.64 for the square tessellation with the von Neumann neighborhood (“square-von Neumann”), and 6.942 for the square tessellation with the Moore neighborhood (“square-Moore”).

Total populations at the end of the simulations had several characteristics (Fig. 2). From relatively low ending populations at no dispersal all topologies reached a peak by a dispersal probability of 0.10 and then declined. Before 0.10 the ranking of values was square-von Neumann, hexagon, square-Moore. After 0.10, the ranking was square-Moore, hexagon, square-von Neumann. At 0.40 ending populations declined to between 40% and 60% of the highest values.

Median values of Shannon diversity had a less consistent pattern (Fig. 3). Between minimum values for no dispersal and a probability of dispersal of about 0.20, square-von Neumann had the highest diversity and hexagon was higher than square-Moore. Between dispersal probabilities of about 0.20 to 0.40, hexagon had the highest values, although square-Moore was essentially the same from 0.36 to 0.40. Median values of species richness and Simpson diversity had the same patterns.

Medians of Shannon diversity revealed one story but the distributions of these values revealed another aspect (Fig. 4). Distributions of Shannon values for hexagon and square-Moore were generally similar whereas square-von Neumann was either skewed in the opposite direction (dispersals of 0.10 and 0.20) or broader in shape (dispersal of 0.30). All distributions had a strong negative skew at a

dispersal probability of 0.40, contrasting with more symmetric or positive skews at lower values of dispersal.

4. Discussion

Topological differences clearly show in the results in Figs. 2–4, but the patterns are complex. Ending populations have the simplest pattern, however even there the ranks of the topologies flipped at a low value of dispersal. As dispersal increased, the topologies with higher degrees of adjacency were less impacted by decline in population, possibly because of more even spread of populations.

It might be expected that topologies with more neighbors would lead to more evenly spread populations for each species also. The results for Shannon diversity only support this hypothesis for species diversity within communities at higher values of dispersal. At lower values, below the range 0.22–0.28, the reverse was the case.

Behavior reversals were also evident in the distribution of Shannon diversity values. The hexagon topology had positively skewed histograms at dispersals of 0.10 and 0.30 but a nearly symmetric histogram at 0.20. The square-von Neumann topology changed from strong negative skew at 0.10, to a slight negative skew at 0.20, to a broad distribution with slight positive skew at 0.30, and then back to a strong negative skew at 0.40. The square-Moore topology had positive skews between 0.10 and 0.30, and then negative skew at 0.40.

Although the results beg for further exploration and explanation, the dynamics of topological effects on properties of networks of ecological communities are complex and suggest potentially important issues. These impacts of topology on models of ecological processes have been little studied, and there is little awareness of the possibility of important effects. Because the large majority of modeling applications that use regular tessellations do use square tessellations, and because the two main topologies for implementing models using squares have drawbacks—von Neumann neighborhoods ignoring the diagonal neighbors, Moore neighborhoods implicitly assuming a non-tiling cell shape—greater attention to topological structures for process modeling is certainly called for.

Computer code in the R or C languages implementing the neutral model simulations are available from the first author.

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