



# Multi-scale analysis on species diversity within a 40-ha old-growth temperate forest

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## ARTICLE INFO

### Article history:

Received 7 October 2017  
Received in revised form  
5 December 2017  
Accepted 18 December 2017  
Available online 4 January 2018

(Editor: Gil Bohrer)

### Keywords:

Species richness  
Species abundance  
Spatial scales  
Niche theory  
Neutral theory

## ABSTRACT

In order to better explore the maintenance mechanisms of biodiversity, data collected from a 40-ha undisturbed *Pinus* forest were applied to the Individual Species–Area Relationship model (ISAR) to determine distribution patterns for species richness. The ecological processes influencing species abundance distribution patterns were assessed by applying the same data set to five models: a Log-Normal Model (LNM), a Broken Stick Model (BSM), a Zipf Model (ZM), a Niche Preemption Model (NPM), and a Neutral Model (NM). Each of the five models was used at six different sampling scales (10 m × 10 m, 20 m × 20 m, 40 m × 40 m, 60 m × 60 m, 80 m × 80 m, and 100 m × 100 m). Model outputs showed that: (1) Accumulators and neutral species strongly influenced species diversity, but the relative importance of the two types of species varied across spatial scales. (2) Distribution patterns of species abundance were best explained by the NPM at small scales (10 m–20 m), whereas the NM was the best fit model at large spatial scales. (3) Species richness and abundance distribution patterns appeared to be driven by similar ecological processes. At small scales, the niche theory could be applied to describe species richness and abundance, while at larger scales the neutral theory was more applicable.

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## 1. Introduction

Interactions between forest communities and ecosystems are reflected in species richness and abundance patterns (Wright, 2002). Distribution patterns of species richness and abundance are representative of community biodiversity and the structural characteristics and organization patterns of communities, which are important considerations in community ecology research (He and Gaston, 2000). Biodiversity has been shown to exert significant positive effects on ecosystem productivity. Species richness and abundance estimates vary significantly at different spatial scales, likely due to scale-dependent changes in ecological processes (Collins and Glenn, 1997; He et al., 2002; Giladi et al., 2011).

Although many theories have been proposed to explain variation in species diversity and species richness distribution patterns at different spatial scales (Silvertown and Law, 1987; Hacker and Gaines, 1997; Adler et al., 2007), it is still difficult to quantify

their relative application. Many studies have found that neutral theory or niche theory best explains species richness and abundance patterns (MacArthur, 1957; Whittaker, 1972; Hubbell et al., 2001; Chase, 2003; Hubbell, 2005, 2006). Neutral theory proposes that the niche of each individual is equivalent (Hubbell et al., 2001; Chase, 2003), and has a certain scale effect. However, the simplicity of the neutral theory (e.g. the symmetric assumption) makes it vulnerable to criticism because it commonly contradicts reality (Lin et al., 2009). Niche theory proposes that niche differentiation, which is affected by available resources and environmental factors, is a necessary condition for species coexistence (Chase, 2003). A current goal of ecological studies is to reconcile neutral and niche theories by either incorporating neutral theory drift into niche theory or niche into the neutral theory framework (Hubbell, 2005, 2006).

Several models have been developed to assess the spatial distribution patterns of species richness and diversity. The Species Area Relationship Model (SAR) has been widely used to describe species richness distribution patterns (He et al., 2002; Fridley et al., 2006; Harte et al., 2009). However, SAR cannot be used to quantify

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Peer review under responsibility of Editorial Office of Plant Diversity.

the contributions of individual species to community species diversity. The Individual Species–Area Relationship model (ISAR) analyzes species richness and spatial patterns at the individual species level, and classifies species as accumulators, repellers, and neutral species (Wiegand et al., 2007). The Broken Stick Model and the Overlapping Niche Model are based on niche theory (Williams, 1964; Walker and Cyr, 2007). The Zero-sum Multinomial Model is derived from neutral theory. Statistical distributions that have been applied to these models, including lognormal and negative binomial distribution, have verified species richness and abundance patterns.

In this study, we used the Beijing Songshan Nature Reserve as a model system to identify mechanisms that influence the maintenance of species richness and abundance in an undisturbed forest. For this purpose, we used five models (a Log-Normal Model, a Broken Stick Model, a Zipf Model, a Niche Preemption Model, and a Neutral Model) to test which ecological processes best explained diversity and abundance patterns at six spatial scales. These models may also provide feasible suggestions for forest management.

## 2. Materials and methods

### 2.1. Study area

This research was carried out in a 40-ha undisturbed pine forest in the Songshan Nature Reserve in northern China. The average annual temperature of the region is 8.5 °C, with average daily temperatures ranging between 39 °C and –27.3 °C. The mean duration of annual sunshine, cumulative rainfall, and evaporation are 2836.3 h, 493 mm, and 1770 mm respectively. The highest elevation of the Songshan Nature Reserve is 2198.39 m. Songshan Nature Reserve is home to 713 vascular plant species, 300 of which are medicinal plants; and 216 species of vertebrates, including 158 bird species. The dominant tree species within the study forest are *Pinus tabulaeformis* Carrière, *Fraxinus chinensis* Roxb, *Synga reticulata* var. *Mandshurica*, *Quercus mongolica*, *Ulmus macrocarpa* Hance and *Juglans mandshurica*.

### 2.2. Data collection

In 2014, the 40-ha (400 m × 1000 m) study forest was established and divided into 1000 continuous 20 m × 20 m plots. The number of individual standing trees ≥1 cm diameter at breast height (dbh) were physically counted and measured at a height of 1.3 m above ground level. We recorded the spatial locations (GPS coordinates) of each plot and measured dbh and height of all free-standing trees at least 1 cm in diameter.

### 2.3. Data analysis

#### 2.3.1. ISAR model

We used an ISAR model to verify the effects of each individual species on species diversity at different spatial scales (0–50 m). ISAR is the expected number of species within a circular area of radius  $r$  around a randomly chosen individual of the target species  $i$ . The model is defined as:

$$ISAR(r) = \sum_{j=1}^N [1 - P_{ij}(0, r)]$$

where  $P_{ij}(0, r)$  is the probability that species  $j$  is not present within  $r$  meters around any individual of the target species  $i$  (Wiegand et al., 2007). In order to quantify the significance of the effects of target species on species diversity, 95% confidence intervals were

calculated by Complete Spatial Randomness (CSR). We used the null model to test the ISAR. When the empirically-determined  $ISAR(r)$  was larger than the second highest  $ISAR(r)$  of the 99 simulations of the null model at scale  $r$ , the species was regarded as a diversity accumulator (positive effect on species diversity) with an approximate significance level of 0.05. When the empirical  $ISAR(r)$  was smaller than the second smallest  $ISAR(r)$  of the 99 simulations at scale  $r$ , the species was classified as a diversity repeller (negative effect on species diversity) at scale  $r$ . Species were classified as neutral (no significant effect on species diversity) at scale  $r$  when the empirically-determined  $ISAR(r)$  was not outside of the null model range.

#### 2.3.2. Species abundance sampling across spatial scales

In order to quantify the ecological processes influencing species abundance distribution patterns at different spatial scales, we sampled species abundance within six area dimensions (10 m × 10 m; 0.01 ha, 20 m × 20 m; 0.04 ha, 40 m × 40 m; 0.16 ha, 60 m × 60 m; 0.36 ha, 80 m × 80 m; 0.64 ha, and 100 m × 100 m; 1 ha) or spatial scales. For each spatial scale, 600 randomly selected replicate areas were assessed.

#### 2.3.3. Species abundance distribution models

##### 2.3.3.1. Log-Normal Model.

The Log-Normal Model (LNM), based on niche theory, was first proposed by Preston (1948). The model assumes that the logarithmic form of species abundance is normally distributed. The model is defined as:

$$S_{(R)} = S_0 e^{-(a^2 R^2)} \quad (1)$$

where  $S_{(R)}$  is the number of species within the  $R$ th octave to the left and right of the symmetrical curve;  $S_0$  is the number of species within the modal abundance octave and  $1/a$  is the distribution width (Kevan and Belaousoff, 1997).

##### 2.3.3.2. Broken Stick Model.

The Broken Stick Model (BSM) was first proposed by MacArthur (1957). The sampled area is compared with a stick of unit length,  $S-1$  points are placed at random, where  $S$  is area. The stick is broken at each point and the lengths of the  $S$  resulting segments are proportional to the abundances of  $S$  species. Assuming all species within the community share close taxonomic statuses and possess similar competitive capacities, the expected abundance of the  $i$ th rarest species among  $S$  species and  $N$  individual trees are:

$$N_i = \frac{N}{S} \sum_{k=i}^S \frac{1}{k}, \quad (2)$$

where  $k$  equals  $i$ . The model assumes that resource allocation among competitive species follows a one-dimensional gradient (Purves et al., 2005).

##### 2.3.3.3. Zipf Model.

The Zipf Model (ZM) was first introduced by Frontier (1985), who assumed that species occupancy is dependent on the environmental and physical conditions and the species present. Cost of living is much higher for late successional species than for pioneer species. The abundance of the  $i$ th species is:

$$N_i = Nq_i^\gamma, \quad (3)$$

where  $N$  is the number of individual trees,  $q$  is the predicted relative abundance of the species with the highest frequency within the community, and  $\gamma$  is a constant representing the average probability of species occupancy (Frontier, 1985).

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