



Analysing tree species and size diversity patterns in multi-species uneven-aged forests of Northern China



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ABSTRACT

The diversity of complex multi-species uneven-aged forests is not easy to describe efficiently and meaningfully. In the past, most importance has been assigned to species diversity and there is a wide range of approaches to quantifying this aspect of diversity. In woodlands, size diversity is another important dimension of biodiversity, as trees can be small or large and depending on their size play different ecological roles. Traditionally size diversity has often been neglected in diversity surveys of woody vegetation or considered as difficult to handle. We investigated the size and species diversity of two multi-species uneven-aged forests from monsoon- and subtropical/warm-temperate climate zones in northern China using non-spatial and spatially explicit forestry and diversity characteristics. We found that the analysis of both species and size diversity provided a much better understanding of diversity patterns in complex multi-species forests. Interestingly the relationship between size- and individual-based relative abundances follows a saturation curve. The analysis using non-spatial forestry and biodiversity characteristics led to approximately similar results in all four plots despite the very different woodland communities involved. However, with spatial measures we gained a deeper insight concerning the deviation from random distributions of species and size as well as interaction ranges of trees. We also found an aggregation of similar species and sizes at small inter-tree distances in the monsoon influenced climate and an aggregation of different sizes in the subtropical/warm-temperate climate zone. The use of second-order characteristics was instrumental in elaborating the subtle differences between the diversity of the two study areas and thus made an important contribution to this study.

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1. Introduction

Species diversity, a combination of species richness and relative abundance (Newton, 2007), is not the only aspect of biodiversity, but a rather important and the most commonly considered one (Kimmins, 2004, p. 429). Much research has already been dedicated to this topic and many different quantitative species diversity measures have been proposed. They provide important information on the distribution of species in plant communities. This information is crucial for understanding the structure and ecological processes involved in plant communities and for monitoring biodiversity. Species richness, an important aspect of species diversity, is often interpreted as a surrogate measure for other kinds of biodiversity: More species usually lead to greater genetic variation, i.e. there is a greater diversity of genes in the population.

This implies greater ecological variation and a better exploitation of niches and habitats (Magurran, 2004; Gaston and Spicer, 2004, p. 13; Krebs, 1999, p. 17).

A common assumption in diversity surveys and analyses is that all individuals of a population are equal (Magurran, 2004, p. 11f.). In contrast to many other vascular plants tree sizes can range from those of small seedlings to those of mature giants of up to a total height of 40 m or in some ecosystems even up to 100 m. Size diversity hugely contributes to structural diversity of woodlands and it is widely acknowledged that structural diversity largely affects the number and quality of habitats and niches a forest can offer (Kimmins, 2004). Size obviously does matter in diversity surveys of woody vegetation, as the individuals involved occupy different niches and fulfil different ecological roles (Newton, 2007). Also there is a clear relationship between size and abundance – species involving large body sizes are rarer than many species with smaller body sizes (Gaston and Spicer, 2004, p. 10).

Only comparatively recently the interplay between species and size has been addressed in functional diversity (Botta-Dukát, 2005; Mason et al., 2005; Lavorel et al., 2008). Functional diversity is

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generally defined as the distribution of *traits* in a community (Díaz and Cabido, 2001; Tilman, 2001). Species abundance can be combined with these traits to result in a *community weighted mean* (CWM), where traits can for example be different measures of tree size although they are not limited to quantitative information. Also a number of different traits can be simultaneously included in multivariate analyses (Laliberté and Legendre, 2010; Clark et al., 2012).

At another level, spatial measures of species and size of trees provide even more information on biodiversity patterns in forests than non-spatial diversity indices (Pommerening, 2002). They explain how diversity changes with different scales (Dale, 1999) and extend information derived from non-spatial measures. In addition we learn for example about minimum and maximum interaction ranges between trees. Also we can study whether species and size variables form specific spatial patterns that deviate from random assignment. If so we can continue and find out whether there is an aggregation of similar or different species and sizes at close proximity (Diggle, 2003; Illian et al., 2008). Spatial measures involving species and size have, however, been rarely used so far in biodiversity analyses (Krebs, 1999; Magurran, 2004). These few examples clearly highlight the usefulness of spatially explicit diversity analyses.

In this context, mixed species forests are particularly interesting for diversity research as much variety of tree species and sizes can be expected in this forest type. Pretzsch et al. (2010, 2013) for example were able to demonstrate a number of benefits of mixed-species forests in Central Europe, including increased biomass production, niche complementarity on poor sites and greater resilience to impacts.

Analysing species and size diversity of woodland communities that comprise many different species is challenging (Bagchi et al., 2011). Large numbers of species can often be found in tropical and subtropical forests (Wright, 2002; Wiegand et al., 2007), but occasionally also in temperate climates. These challenges are also addressed in this paper.

To study tree diversity at different levels we have analysed spatially explicit tree data from semi-natural woodlands in the monsoon- and subtropical/warm-temperate climate zones of northern China.

The objective of this paper is to identify similarities and dissimilarities between patterns of species and size diversity in multi-species uneven-aged forests. For this purpose we (1) analyse the data using non-spatial diversity characteristics. (2) In addition we employ two new second-order characteristics, the mark mingling and mark differentiation functions (Pommerening et al., 2011), as spatial measures of tree diversity for a more detailed analysis. (3) Finally we interpret all results for the benefit of a holistic description of the tree diversity of the analysed forest types and we compare and discuss the performance of and information produced by the different tree diversity metrics.

2. Materials and methods

2.1. Data

For this study we have selected four large replicated monitoring plots from semi-natural forests, which have been taken out of forest management 50 years ago and can now be considered as biodiversity hotspots in northern China. The observed tree patterns are now increasingly the consequence of natural processes without human disturbances and therefore also represent typical zonal plant communities in this part of China.

The first set of two monitoring plots (B and F) is located in the Dongdapo Natural Reserve (43°51'–44°05'N and 127°35'–127°51'E), which has a size of 16,660 ha and is part of the Zhangguangcai mountain range extending from north of the Songhua river

to south of the Changbaishan mountains (see Fig. 1, bottom left and Fig. 2, top).

This area is approximately 45 km from Jiaohe in Jilin Province, China, and has a monsoon climate with dry, windy springs and warm, wet summers. The tree vegetation primarily consists of 19 tree species, among which *Juglans mandshurica* MAXIM., *Fraxinus mandshurica* RUPR. and *Phellodendron amurense* Rupr. are used to define forest stand types and are known as the “three great hardwoods” in north-eastern China because of their economic importance and increasing value in forest conservation. The two monitoring sites in this area are both 1 ha in size.

The second set of monitoring plots (H and I) is located in mixed pine-oak forest on the north-facing slopes of the Qinling Mountain Range (see Fig. 1, right and Fig. 2, bottom). This area in the transition zone between the subtropical and the warm-temperate region also forms a natural reserve and contains 432,914.0 ha of forest land. The plots were located in the 57th compartment of the Baihua forest farm (33°30'–34°49'N, 104°22'–105°43'E) on Xiaolong Mountain, Gansu Province. The forest contains more than 30 species including *Quercus liaotungensis* KOIDZ., *Carya cathayensis* SARG. and *Pinus armandii* FRANCH. The dominant species is *Quercus aliena* var. *acuteserrata* MAXIM., which accounts for about 20% of the total number of trees in the plots. The forest is highly natural and its spatial structure is complex. The monitoring plots have a size of 0.49 ha each.

Compared to temperate forests in other parts of the world the study woodlands show a high species diversity and are therefore a challenge to any characterisation of tree diversity. This makes them an ideal object for comparative studies using different measures of tree diversity.

2.2. Non-spatial diversity measures

2.2.1. Species diversity measures

For quantifying tree species diversity we used the evenness measure of the Shannon index (Shannon and Weaver, 1949, Eq. (1)), an information theory index. The Shannon index was originally proposed to quantify the entropy, i.e. the uncertainty of information, in strings of text (Krebs, 1999, p. 444). By contrast, the Simpson index (Simpson, 1949, Eq. (2)) is a dominance or concentration measure.

$$E'_H = \frac{H'}{\ln s} \quad \text{with } H' = -\sum_{i=1}^s p_i \ln(p_i) \quad (1)$$

$$E_D = \frac{D}{s} \quad \text{with } D = \frac{1}{\sum_{i=1}^s p_i^2} \quad (2)$$

p_i is the proportion of individuals found in the i th species and s is the number of species. The Simpson index has been calculated in various ways and we have followed Magurran's (2004, p. 116) recommendation to adopt the reciprocal as opposed to the complement form for calculating the evenness measure. Whilst the Shannon evenness measure emphasizes the species richness component of diversity the Simpson evenness index is weighted by abundances of the commonest species. Both Shannon and Simpson measures are among the most meaningful and robust diversity measures available (Krebs, 1999, p. 444ff.; Magurran, 2004, p. 114ff.).

The evenness forms (Eqs. (1) and (2)) are often used as standardisation to allow for comparisons between different monitoring sites (Pretzsch, 2009, p. 280). Both species diversity measures can be calculated based on tree number proportions and basal area proportions. Basal area, g (measured in m^2), relates to stem diameter, dbh (measured in cm), through $g = \pi(dbh/200)^2$. In the case of

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