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Species turnover of wetland vegetation in northeastern China: Disentangling the relative effects of geographic distance, climate, and hydro-geomorphology

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ABSTRACT

Species turnover is a central issue in plant ecology and has a high significance in conservation of biodiversity and ecosystem management. Niche differentiation and dispersal limitation are the two main processes controlling species turnover of upland vegetation. However, our understanding of the drivers of plant species turnover in wetlands remains poor. To comprehensively disentangle the influences of niche differentiation and dispersal limitation on the plant species turnover in wetlands of the Great Hing'an Mountain valleys, we not only considered two plant functional groups (herbs and shrubs), but also took hydro-geomorphological variables into account when quantifying the effect of environmental differences on species turnover. We found that species similarity, measured by the Jaccard similarity index, decreased with geographic distance for both herbs and shrubs with a decay rate being −0.39 and −0.49, respectively. We then partitioned the variance of species similarity based on type III sums of squares in partial correlations. Results showed that geographic distance and the joint effect were the most important factor explaining the species turnover of herbs and shrubs respectively when representing environmental constraints with climatic variables only. The total explained variances were improved by 15.93% for herbs and 24.69% for shrubs after including hydro-geomorphologic measurements. Our study showed that both dispersal limitation (represented by geographic distance effects) and niche differentiation (represented by climate and hydro-geomorphology) played important roles in shaping wetland species turnover, but their relative effects differed by plant functional groups. Considering hydro-geomorphological characteristics can better elucidate the role of the environment in shaping species turnover in wetland systems than using climatic variables alone.

1. Introduction

Wetland is regarded as one of the three major global-scale ecosystems (Zhou et al., 2006) and supports a distinctive flora that differs in composition, structure, and function from adjacent upland vegetation partly due to the close relationship between vegetation and hydrology in this ecosystem (Coops et al., 1996; Zhou et al., 2008). Plant diversity of wetlands plays a key role in sustaining the ecological function (e.g., nutrient traps) (Hansson et al., 2005) and stability (resistant to invasive species) (Moss, 2000) of wetland ecosystem (Cheng et al., 2010; Freestone and Inouye, 2006). Understanding the plant diversity pattern in wetland ecosystem and driving mechanisms is therefore an important building block to achieve wetland conservation and protection (Li et al., 2014).

Previous studies of wetland vegetation diversity have primarily focused on its alpha diversity (Minggagud and Yang, 2013; Todd et al., 2010). In contrast, species turnover has received far less attention. Such scarcity is even more pronounced when compared with the numerous studies that examined spatial turnover in species composition and its association with environment for upland vegetation (Condit et al., 2002; Gilbert and Lechowicz, 2004; Myers et al., 2013; Qian et al., 2005). Those upland vegetation studies primarily used climatic variables to represent environmental conditions

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(Qian and Ricklefs, 2012; Wilson and Meurk, 2011). Because of the unique contributions of hydrological processes in wetland ecosystems (Pollock et al., 1998), traditional methods may be insufficient for representing environmental differences in those wetland areas. However, no previous studies have simultaneously incorporated climate and hydrologic processes to explain the patterns of species turnover in wetland ecosystems.

Two main processes explain species turnover: dispersal limitation and niche differentiation (Harrison et al., 1992; Qian and Ricklefs, 2007; Smith and Lundholm, 2010). Variation in species turnover with respect to geographic distance supports dispersal limitation (Condit et al., 2002; Linares-Palomino and Kessler, 2009; Svenning and Skov, 2004), whereas variation in species turnover with respect to environmental differences provides evidence for niche differentiation. Dispersal limitation (Bell, 2001; Gotellia et al., 2010; Kristiansen et al., 2012) assumes that species are competitively equal; differences of species composition between different areas is thus created through random processes that are purely limited by dispersal ability. In contrast, niche differentiation (Gilbert and Lechowicz, 2004; Soininen et al., 2007; Tuomisto et al., 2003) assumes sites with different environments should host different sets of species; a more heterogeneous environment therefore leads to greater species turnover. There is a growing interest to determine the relative importance of these two processes on species turnover by variance partitioning. However, a large body of research has employed only climatic variables to represent environmental dissimilarity (Qian et al., 2005; Qian and Ricklefs, 2012; Wilson and Meurk, 2011), which could result in magnifying the assessed importance of dispersal limitation. Recent studies of upland vegetation have begun to include other environmental factors such as land cover (Keil et al., 2012), land use (Pompe et al., 2012), topography (Qian et al., 2009), and soil characteristics (Fernandez-Going et al., 2013; Kitayama, 2012); but few have incorporated variables describing hydro-geomorphology when studying species turnover in wetland systems.

Hydrologic processes affect wetland plant species and distribution by influencing groundwater level, soil characteristics and drainage characteristics (Carter, 1986; Doyle et al., 2003; Magee and Kentula, 2005). Hydro-geomorphology is proved to be a significant indicator for characterizing the hydrology of wetlands (Cole et al., 1997; Franklin et al., 2009; Kupfer et al., 2010; Steiger et al., 2005). Therefore, differences in hydro-geomorphology can result in changes to wetland vegetation composition and distribution. Research has shown that the distribution of vegetation types follows a specific pattern along a hydro-geomorphological gradient (Cole et al., 1997; Franklin et al., 2009; Kupfer et al., 2010) considering watershed area, length, relief, ruggedness, and stream power. Small, steep and rugged watersheds often promote rapid run-off (Germanoski and Miller, 2004; Howard, 1990) and provide a more suitable habitat for shrubs (Engelhardt et al., 2012). In contrast, herbaceous vegetation prefers to watersheds characterized with large size and less relief, which has a high water Table (Carter, 1986; Engelhardt et al., 2012; Miller et al., 2001). Taking hydro-geomorphologic variables into account when quantifying environmental differences can better elucidate the role of the environment in species turnover of wetland vegetation and improve our understanding of the relative importance of niche differentiation and dispersal limitation.

The objective of this study is to disentangle the relative influences of geographic distance, climate, and hydro-geomorphology on species turnover in the wetlands of the Great Hing'an Mountain valleys, China. We investigated two distinct plant functional groups: herbs and shrubs. These two groups have different dispersal abilities due to their different dispersed modes. Many herbaceous species (e.g., horsetails, ferns, mosses) are spore-bearing plants with light and effectively dispersed diaspores. In contrast, shrub species tends to be seed-bearing plants that have heavier and less well-dispersed diaspores (Lenoir et al., 2012; Nekola and White, 1999). Previous upland vegetation studies have suggested that dispersal ability is negatively related to the rate of species turnover (Harrison et al., 1992; Lenoir et al., 2012; Linares-Palomino and Kessler, 2009). By focusing on wetland species that also possess different dispersal traits, we attempted to evaluate the relative effects of environmental differences and geographic distance on species spatial turnover. Moreover, compared to many previous studies that only employed climatic variables at the regional scale to represent environmental dissimilarity (e.g., Qian et al., 2005; Qian and Ricklefs, 2012; Wilson and Meurk, 2011), we considered a more comprehensive set of environmental factors by incorporating hydro-geomorphologic variables at local scale into the measurement of environmental differences in wetland ecosystems. Specifically, we tested the following hypotheses:

1. The decay rate of species similarity with geographical distance is shaped by dispersal ability of the species. Specifically, shrubs should show a steeper decay rate than herbs.
2. The relative effect of niche differentiation and dispersal limitation varied in these two plant functional groups (herbs and shrubs).
3. Hydro-geomorphology plays an important role in shaping the distribution of wetland plant species and affects the relative importance of dispersal limitation and niche differentiation in herbs and shrubs.

2. Material and methods

2.1. Study area

The study sites were located in the wetlands of the valleys along the west slopes of the Great Hing'an Mountains (Fig. 1), ranging from 48°49′36″N to 53°12′10″N and from 120°47′59″E to 122°59′59″E. The altitude ranges between 463 and 787 m. The study area is characterized by the terrestrial monsoon climate of the Cool Temperate Zone, with a long and severe winter. Average annual temperature is approximately −3 to 0 °C, and average annual precipitation is approximately 300–500 mm, of which more than 80% occurs between June and August. The average annual frost-free period varies between 90 and 110 days. The 11 study sites were established in the wetlands of the mountain valleys. These natural valleys are broad and plain, underneath with the meadow and marsh soils, which are loose and rich in organic matter and water. The studied wetland species, distinguished mainly by their hygrophilous nature and cold resistance, included *Larix. gmelinii*, *Betula platyphylla*, *B. fruticosa*, *Rhododendron parvifolium*, *Ledum palustre* var. *angustum*, *Salix rosmarinifolia*, *Vaccinium uliginosum*, *Carex* spp., and *Sphagnum* spp.

2.2. Field sampling

Ecological surveys were performed during three weeks in August 2007 and 2008, when every species was most conspicuous. We established 11 sites along the western slopes of the Great Hing'an Mountains. These sites, from north to south, are Tuqiang upper reach, Tuqiang lower reach, Chaoman, Mangui, A Longshan, Jinhe, Genhe, Tu Lihe, Yuanlin, Ya Keshi, and Wu Nuer. The latitude, the longitude, and the altitude of each site were recorded using GPS. We sampled 13–18 plots of 2 m × 2 m to count herbs and 10 plots of 4 m × 4 m to count shrubs. The number of plots was determined as that necessary to capture at least 90% of the species at each site. The species identity, density, height, crown width, and frequency of the plant species in each plot were recorded. Our analyses included