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Original Research Article

Multi-scale comparison of topographic complexity indices in relation to plant species richness

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ABSTRACT

Topographic complexity is a key component of habitat, which has been linked to increased species richness in many ecological communities. It can be measured in various ways and it is unclear whether these different measurements are mutually comparable when they relate to plant species richness at different spatial scales. Using a densely sampled set of observations for Rhododendrons (406 species and 13,126 georeferenced records) as a test case, we calculated eight topographic complexity indices from a 250-m resolution digital elevation model and examined their correlations with Rhododendron species richness in China at seven spatial scales: grain sizes 0.05°, 0.1°, 0.25°, 0.5°, 1.0°, 1.5°, and 2.0°. Our results showed that the eight topographic complexity indices were moderately to highly correlated with each other, and the relations between each pair of indices decreased with increasing grain size. However, with an increase in grain size, there was a higher correlation between topographic complexity indices and Rhododendron species richness. At finer scales (i.e. grain size $\leq 1°$), the standard deviation of elevation and range of elevation had significantly stronger correlations with Rhododendron species richness than other topographic complexity indices. Our findings indicate that different topographic complexity indices may have positive correlations with plant species richness. Moreover, the topographic complexity–species richness associations could be scale-dependent. In our case, the correlations between topographic complexity and Rhododendron species richness tended to be stronger at coarse-grained macro-habitat scales. We therefore suggest that topographic complexity index may serve as good proxy for studying the pattern of plant species richness at continental to global levels. However, choosing among topographic complexity indices must be undertaken with caution because these indices respond differently to grain sizes.

1. Introduction

Topographic complexity is a key component of habitat that has been linked to species richness in many ecological communities, including terrestrial plants (Simpson, 1964; Bruun et al., 2006; Moeslund et al., 2013a; Stein et al., 2014). From the geomorphometric perspective, topography is always associated with elevation, slope, aspect, and curvature, which in turn affect the water and energy budgets of a location. This influences plant species distribution and richness indirectly. Specifically, air temperature, atmospheric pressure, wind speed, season length, snow drift, snow depth (Litaor et al., 2008), fog frequency (Svenning, 2001; Eiserhardt et al., 2011), and even human land use change with elevation (Franklin, 1998; Körner, 2007). Slope (gradient) affects the overland and subsurface flow velocity and runoff rate as well as the soil water content (Gosz and Sharpe, 1989; Bispo et al., 2012), while terrain curvature is related to soil migration processes, water accumulation, and the movement of minerals and organic substances through the soil.

Many studies have used "topographic complexity" as a measure of topographic heterogeneity or even habitat heterogeneity, which in turn have served as a proxy when exploring the determinants of plant distribution and diversity patterns (Nichols et al., 1998; Kreft et al., 2006, 2010; Stein et al., 2014). The elevation range has frequently been used to express topographic complexity. For example, its effect has been demonstrated on palm species richness (Kreft et al., 2006), mainland pteridophyte and seed

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plant richness (Kreft et al., 2010), and vascular plant diversity (Kreft and Jetz, 2007). Other topographic complexity indices have also been used in studies. Standard deviation of elevation as a proxy for topographic heterogeneity showed a positive relationship with plant species richness in California (Richerson and Lum, 1980), South Africa (Thuiller et al., 2006), and southwestern Finland (Luoto and Heikkinen, 2008). Everson and Boucher (1998) reported a significant positive relationship between tree species richness and standard deviation of slope along the riparian edge of the Potomac River in the United States. Hofer et al. (2008) indicated that topographic complexity had strong effects on niche or microsite diversity. They found standard deviation of elevation and standard deviation of slope as proxies for topographic complexity to be appropriate estimators of plant species richness. In recent years, rugosity, which is the ratio of the actual area measured along the undulating terrain to the planar area, has been introduced as a proxy for topographic complexity in several studies (Jenness, 2004; Walker et al., 2009; Zawada et al., 2010). The standard deviation of terrain curvature has also been applied to examine the effect of topographic complexity on species richness (Bispo et al., 2012; Stein et al., 2014). Despite the important link between topographic complexity and plant species richness, there is no consensus about which index can best represent topographic complexity when exploring the relationship with plant species richness.

Different studies selected various topographic complexity indices, and most of them were conducted at a single spatial scale. However, different mechanisms act at different scales, the importance of scale in ecology has been widely emphasized (Hutchinson, 1953; Rosenzweig, 1995; Crawley and Harral, 2001; Rahbek and Graves, 2001; Rahbek, 2005). In studies of geographical variation in species richness, two particularly interesting attributes of scale are the unit of sampling and the geographic space covered. The first attribute is defined by 'grain', being the size of the common analytical unit and focus, the area or inference space represented by each data point. The second attribute is 'extent', and refers to the inference space to which the entire set of sample unit applies, describing the geographic space over which comparisons are made (Wiens, 1989b; Willig et al., 2003; Rahbek, 2005). Previous studies showed that topographic complexity influences plant species richness at local and landscape extents with fine grain sizes (Pearson and Dawson, 2003; Pe'er et al., 2006). But this relationship remains underexplored at other spatial scales, especially at multiple coarse-grained large spatial extents such as continental and global levels.

Quantifying topographic complexity by using different proxies over multiple spatial scales (i.e. grain sizes) would enable us to make recommendations for ecologists to choose the most suitable topographic complexity indices. We note at the outset that we are not proposing that plant species richness can be explained by topographic complexity alone, but rather we seek (1) to assess if high correlations exist among various topographic complexity indices at multiple scales, (2) to investigate how the correlations between topographic complexity indices and plant species richness change across scales, and (3) to examine differences in the relationships between various topographic complexity indices and plant species richness at different scales.

2. Materials and methods

2.1. Study area

The study area (i.e. extent) is the whole of China. The topography of China varies from highly mountainous regions to desert zones, and flat, fertile plains. Mountainous areas make up about two-thirds of the country's area. The Himalaya is the highest mountain range on Earth and the Tibetan Plateau's average elevation is over 4000 m, while the lowest spot in China is the Turpan Basin in Xinjiang, at 154 m below sea level. With its vast territory, wide latitudinal range, complex terrain, and diverse climate, China provides a "natural laboratory" in which to explore the relationship between topographic complexity and macro-scale patterns of plant diversity.

2.2. Rhododendron species data

Rhododendron, the largest and most diverse genus in the plant kingdom, can be found in many habitats of Asia, North America, Europe, and Oceania, such as forest floors, stream sides, marshes, ridges, glades, cliffs, rocks and boulders, open meadows and thickets, scree, and mountain tops (Gibbs et al., 2011). With 1157 species, Rhododendron exhibits an amazing geographic variation in phylogeny and life forms. Mainland Southeast Asia harbors more than 90% of all known Rhododendron species (Kumar, 2012). According to the latest study by Wu et al. (2005), about 542 species of Rhododendrons have been found in China, and Northwestern Yunnan Province in China is considered as the center of origin of the genus. Given the variation in geographical distribution and life forms, Rhododendron is an ideal model genus for studying the relationship between plant species richness and topographic complexity. In this study, Rhododendron distributional records were collected from seven main herbaria and botanical museums in China: Herbarium, Institute of Botany, Chinese Academy of Sciences (CAS); Herbarium, Kunming Institute of Botany, CAS; South China Botanical Garden, CAS; Wuhan Botanical Garden, CAS; Sichuan University of Botany; Sichuan Forest School; and Lushan Botanical Garden. The spatial information, taxonomy and all specimens were verified by a number of Rhododendron experts in China. Because a high locational accuracy is required for studying species distributions of plants, all records with inadequate descriptions of the location (e.g. only mentioning a county or a mountain) were excluded. The resulting dataset comprised 13,126 georeferenced records with a spatial uncertainty of less than 1 km, referring to 406 species (Fig. 1).

2.3. Selection and calculation of topographic complexity indices

We began by selecting the five most commonly used topographic complexity indices: standard deviation of elevation (SE), elevation range (RE), standard deviation of slope (SS), rugosity

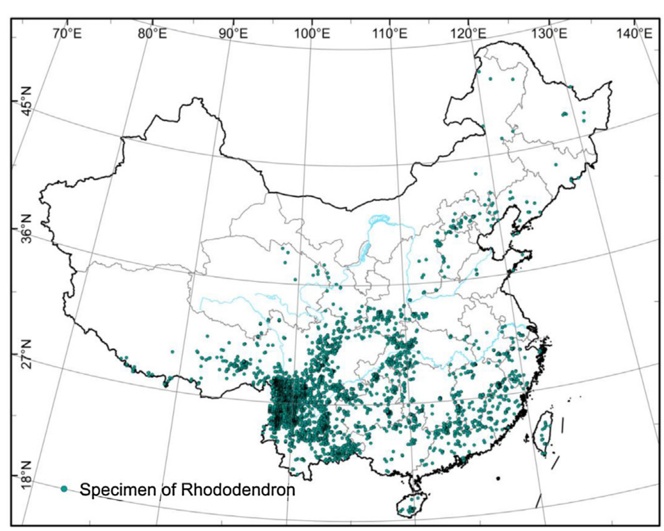

Fig. 1. Map of study area and the location of Rhododendron species observations.