CONSERVATION BIOGEOGRAPHY OF RHODODENDRONS IN CHINA

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DISSERTATION

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In Xinjiang, China

This thesis is approved by

Prof. dr. A.K. Skidmore, supervisor
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Dr. T.A. Groen, co-supervisor

To my family

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Chapter 1

General introduction

1.1 Background

Conservation biogeography is defined as 'the application of biogeographical principles, theories, and analyses, being those concerned with the distributional dynamics of taxa individually and collectively, to problems concerning the conservation of biodiversity' (Whittaker et al., 2005). Conservation biogeography is a newly emerging sub-discipline of both biogeography and conservation biology (Richardson, 2005). Biogeography is the study of the distribution of species and ecosystems across geographic space at all possible scales (Lomolino et al., 2010). Compared to conservation biology, which is primarily concerned with conservation through the application of population biology, taxonomy, and genetics (Caughley, 1994), conservation biogeography tends to explore the sensitivity of the assumptions concerning data quality, scale dependency (both spatial and temporal), range restricted species, and effects of model structure, and parameterisation on hotspots and reserve design, etc., (Whittaker et al., 2005).

One of the preliminary tasks of conservation biogeography is to explore the geographic patterns of species to gain information for conservation and management actions (Richardson & Whittaker, 2010). Species are not distributed evenly across this planet. To conserve species, knowledge about the geographic variation of species is essential to biogeographical studies (Lomolino et al., 2010). In exploring the patterns and process of species distribution, the fundamental unit is the geographical range. Species' range size - reflecting interspecific differences of ecological tolerance, dispersal ability, and evolutionary history - can be considered to be a species trait (Thompson et al., 1999; Olalla-Tarraga et al., 2011). Even closely related species can have dramatically differing range sizes (Brown et al., 1996). Combined with population size, species' range size has been used as a proxy for extinction risk as well as to prioritize species that need conservation action in the face of rapid global change (Thuiller et al., 2005; Pompe et al., 2008; Gallagher, 2016). Consequently, understanding why some species have highly restricted geographical ranges, while closely related species might have a widespread distribution, can provide valuable insights for conservation.

Protected area planning - frameworks and their resulting map outputs are amongst the most powerful and influential applications within conservation biogeography (Whittaker et al., 2005). A major concern in biogeography has been the distribution and the dynamics of diversity over time. To manage biodiversity, we need to know where species diversity are, how they are distributed, and how the different aspects of diversity co-vary in space and time (Richardson & Whittaker, 2010). The standard approach to select priority areas for conservation is identifying biodiversity hotspot and performing gap analysis. Various metrics have been used to quantify species diversity and hotspots, which are generally defined either as the top sites in terms of species diversity or as the sites where most threatened or most endemic species occur (Prendergast et al., 1993; Myers et al., 2000; Orme et al., 2005).

One of the greatest challenges in conservation biogeography is putting forward sensible strategies for adaption to anticipated global environmental change, which is based on the prediction of future changes in the distribution of species and ecosystems (Ackerly et al., 2010; Franklin, 2010; Richardson & Whittaker, 2010). The cumulative or synergistic interactions between climate change and human land use change are believed to have a great impact on biodiversity and species distribution over the coming century (Sala et al., 2000; Brook et al., 2008). Rapid climate change has resulted in distributional changes for a wide range of taxa (Parmesan, 2006; Chen et al., 2011). The general trend is for species distributions to shift poleward and upslope (Parmesan & Yohe, 2003; Lenoir et al., 2008). If climate change continues, many species, especially the narrowly distributed species with small population sizes, may become extinct over the next century (Pearson et al., 2014). In addition, human-caused habitat loss and fragmentation (mainly through land use change) has long been considered a primary cause for biodiversity loss and ecosystem degradation worldwide (Foley et al., 2005; Oliver & Morecroft, 2014). Land use change includes deforestation, road construction, agricultural encroachment, dam building, irrigation, mining, expansion of urban environments, and other activities. Key questions for the management of sustainable landscapes are whether a species is likely to be able to persist in a landscape that is undergoing a certain degree of land use change in combination with changing climatic conditions, or whether this species will be able to migrate to new regions as they become climatically suitable (Travis, 2003).

Species distribution models (SDMs, sometimes also called environmental or bioclimatic niche models), linking species occurrence with multiple environmental predictors, and employing a wide variety of statistical and machine-learning methods, are increasingly used in conservation biogeography (Elith & Leathwick, 2009; Franklin, 2010). SDMs have been widely used in reserve design, ecological restoration, and predicting the effect of global change on species distribution and biodiversity (Franklin, 2010; Franklin, 2013). As essential input in SDMs, species occurrence is the most widely collected piece of biodiversity information (Walters, 2013). With the ongoing digitization of natural history museum collections and herbarium specimens, more data are becoming available, providing an opportunity to analyse ensuing species occurrence data in support of conservation efforts. However, observations of species distributions remain sparse and incomplete, and 'interpolation' using SDMs based on the relationship between species and environmental gradients can aid the filling in geographical gaps in our knowledge of species distribution. 'Extrapolation' using SDMs based on the empirical equilibrium assumption has also been an important approach to forecast species distribution and biodiversity in the face of global environmental change and in support of conservation biogeography (Pearson et al., 2004; Pompe et al., 2008).

The aim of conservation biogeography is to link biogeographical theory and practice to improve conservation and the sustainable and equitable use of biodiversity - the main objectives of the Convention on Biological Diversity (CBD) (Whittaker et al., 2005). Despite years of international cooperation to tackle the loss of biodiversity, species and their habitats are still being lost at a very rapid rate (Pettorelli et al., 2016a). Under the CBD 190 parties pledged to reduce biodiversity loss at the level of genes, populations, species, and ecosystems by 2020 in a shared mission and with 20 targets, known as the Aichi Biodiversity Targets (https://www.cbd.int/sp/targets/). As a scientific discipline, conservation biogeography cannot provide all the solutions to the problems of biodiversity loss, but it can provide many tools and concepts to assist in making scientifically informed choices about what to protect where, as well as insight into the potential consequences of future environmental change (Cox et al., 2016).

1.2 Rhododendrons and research gaps

1.2.1 Distribution and importance of Rhododendrons in the world

The genus Rhododendron, containing about 1,025 species, occurs in Asia, Europe, North America, and Oceania (Island of New Guinea) (Figure 1.1) (Chamberlain, 1996). Rhododendron is a genus well-known for its stunning variety and beauty, and long and rich horticultural history (Brown, 2004).

The centres of origin of Rhododendrons are located in the Himalayas and south-eastern Asia, with more than 90 % of the world's natural population of Rhododendrons originating from this region (Kumar, 2012). Rhododendrons are found in ecological zones ranging from lowland to high altitude forest, scrub and grasslands at various altitude, bogs and swamps, as well as montane and alpine zones (Cox & Cox, 1997; MacKay & Gardiner, 2016). Life forms of Rhododendrons include trees, shrubs, groundcovers, and even epiphytes (MacKay & Gardiner, 2016).

Rhododendrons form a major component of the montane ecosystem in the Himalayan subalpine and alpine zone (Kumar, 2012). Rhododendrons also play a vital role in slope stabilization and watershed protection in the Himalayas, where many of Asia's major rivers originate (Gibbs et al., 2011). In addition, certain Rhododendrons serve as antibiotics, anti-inflammatories or as treatment of diarrhoea, and are thus valued for their medicinal properties. In some communities, Rhododendrons are used for firewood and timber, or for non-timber products such as tea, honey, wine and jam. Some species have being valued for their narcotic potential, and others even as source of insecticide (Singh et al., 2003; Gibbs et al., 2011).

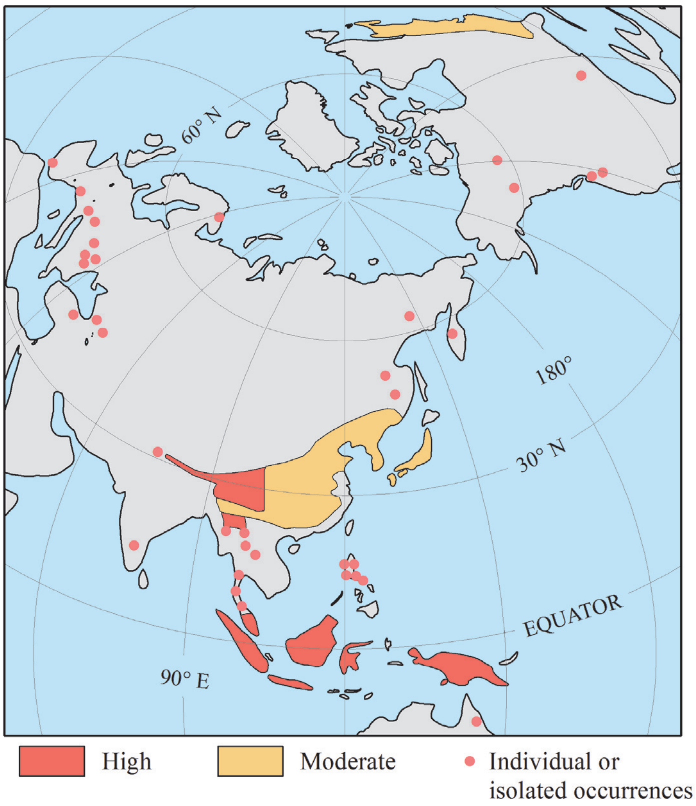

Figure 1.1 Natural distribution of Rhododendrons in the world, figure adapted and modified from Irving and Hebda (1993)

1.2.2 Current status and major threats to Rhododendrons

In times of rapid global climate and land use change, Rhododendrons also experience the impact of disturbance to ecosystems (Singh et al., 2003). The Himalayan region, which has been recognized as one of the most fragile zones in the world, is experiencing great change (Xu et al., 2009; Kumar, 2012). Various studies suggest that warming in the Himalayas, including the Tibetan plateau, has been much greater than the global average of 0.74 ℃ over the last 100 years (Hijioka, 2014). Increased temperature will have a direct bearing on snowfall, snowmelt, and rainfall regimes, affecting soil moisture and habitat conditions, which in turn affects species regeneration and establishment (Kumar, 2012). Many alpine plant species are in the process of shifting uphill, and some species on mountain ranges with restricted habitats will experience habitat loss, or even extinction if they cannot move to higher elevations. Certain Rhododendrons belong to this category (Kumar, 2012). In addition, rapid population growth, and the ever-increasing demands for natural resources have collectively placed considerable pressure on Rhododendrons in their natural habitat (Kumar, 2012; Ma et al., 2014). Rhododendrons that grow at higher altitudes are sensitive to disturbances due to natural factors, such as landslides and forest fires. Rhododendrons that grow at lower altitudes are exposed to threats from human activity, such as deforestation, firewood harvesting (Singh et al., 2003), the rising demand for agricultural land, road construction, walnut planting, coal mine construction, and the growing tourism industry (Ma et al., 2014).

1.2.3 Distribution and diversity of Rhododendrons in China

China has approximately 571 Rhododendron species, accounting for nearly 55% of the world's total (Ma et al., 2014). Rhododendrons occur in most of China's provinces (except Xinjiang and Ningxia), and are found across 60% of China's land area. Over 74% of the Rhododendrons occurring in China are endemic species (Wu, 2005; Ma et al., 2014). Yunnan province has been recognized as the centre of origin of Rhododendrons (Krüssmann, 1970; Fang & Ming, 1995). Rhododendrons exhibit a great diversity in China. The Red List of Rhododendrons has been published to promote action regarding the protection of threatened Rhododendron species in their natural habitats around the world (Gibbs et al., 2011). In China 31 Rhododendron species have been ranked endangered or critically endangered, accounting for 41% of the globally endangered Rhododendron species (Ma et al., 2014).

1.2.4 Research and knowledge gaps for the conservation of Rhododendrons

The CBD identifies nations as the main actors regarding implementation of the 20 'Aichi Biodiversity Targets'. National-level analyses of conservation priority might provide the most useful information for designing national action plans (Kullberg & Moilanen, 2014). In China, however, information on native flora, including Rhododendrons, was lacking (Young et al., 1980). Of the few studies on Rhododendrons undertaken in China, most either considered only limited locations (Zha & Feng, 2008; Zhao et al., 2013), or were mainly taxonomically oriented (Ma et al., 2012). Only Ma et al. (2014) conducted a field investigation in China concerning ten Rhododendron species, covering seven provinces, and comprising 95 days in 2011 to 2013. They concluded that conservation of Rhododendrons in China is of greater urgency than has previously been acknowledged. However, classic questions on Rhododendron conservation in China have yet to be answered. More specifically: what is the diversity pattern of Rhododendrons? And where are the hotspot and priority areas for the conservation of Rhododendrons? These questions will need to be answered to form a sound basis for the conservation of Rhododendrons in China.

The genus Rhododendron is considered to be one of the 'big plant genera' (using '500 known species' as a threshold, Frodin, 2004). The 'big plant genera' have aroused great interest among systematic botanists, because they generally cover broad geographical and ecological ranges, or contain important horticultural values (Frodin, 2004). Nevertheless, Rhododendrons form one of the most neglected groups of plants in terms of scientific inquiry (Kumar, 2012). This while, as a 'big plant genus', Rhododendron forms an excellent candidate for expanding our knowledge of biogeography for plant conservation (MacKay & Gardiner, 2016).

Rhododendrons display a great variation in range size (Kumar, 2012). Some Rhododendron species occur throughout most of the northern hemisphere, while others are highly restricted to small regions. A variety of hypotheses and paradigms have been proposed to explain the variation seen in geographical range sizes between species, including climatic variability (Stevens, 1989), evolution (Gaston, 1996), complex interactions (Brown et al., 1996), niche breadth (Gaston et al., 1997; Gaston & Spicer, 2001), energy availability (Morin & Chuine, 2006), climate tolerance (Pither, 2003), glacial history (Jansson, 2003), colonization ability (Lowry

& Lester, 2006), and a combination of habitat area and climate stability (Morueta-Holme et al., 2013). Among these hypotheses, the niche breadth hypothesis, which has recently gained more support, suggests a positive correlation between the niche breadth and geographical range size of a species (Boulangeat et al., 2012; Botts et al., 2013). However, the relative importance of the basic factors that define niche breadth (i.e. climate, topography, and soil) in shaping the distribution of plant species with different range sizes is unclear. Are these basic factors to a large extent equally important in explaining the distribution of narrow- and wide-ranging species? Or is climate more important than topography and soil for narrow-ranging species that are expected to be more sensitive to climate change? Additionally, the term 'climate' itself refers to a diverse set of measurable variables. It is important to know which of these variables (highly) affect the distribution of a species if we want to determine the impact of projected trajectories of climatic change on species' shifts in ranges.

Species that share the same ecological trait might respond to environmental changes in the same way (Thuiller et al., 2005). Species with a small geographical range size, as is the case with many endemic species, could be more sensitive or vulnerable to climate change due to lack of plasticity and insufficient genetic variation to respond to novel selection pressure (Sheth & Angert, 2014). While broadly distributed species with large population sizes, which usually have wide climatological niches, may be buffered against extinction due to their evolved tolerance to a broad range of climatic conditions (Pearson et al., 2014). Meanwhile, narrowly distributed species are more likely to be threatened by land use change if they are restricted to a single habitat type, and thus at higher risk of experiencing habitat loss (Köster et al., 2013). The relatively low effect of land use change on widely spread species may also be due to their ability to exploit a wide range of ecological niches (Harcourt et al., 2002; Cleary & Mooers, 2006). Biodiversity loss and variation in species response to environmental change is seen in many different taxonomic groups (Hickling et al., 2006; Pompe et al., 2008), but what is known about the response within taxonomic groups? Is there any interspecific variation in response to environmental change? Will narrow-ranging and wide-ranging species of the same taxonomic group respond differently to change in climate and land use? And if they do respond differently, what is the difference? Predicting the distribution of narrow- and wide-ranging Rhododendron species under climate and land use change would, therefore, help us understand the evolution and diversification of flora in the light of global change, as well as provide insights for conservation planning in the strategies required to sustainably maintain alpine and subalpine ecosystems in the future.

1.3 Research objectives

Taking the genus Rhododendron (406 species in total) as our focal species, the general objective of this thesis is to investigate the biogeographical patterns and the underlying mechanisms of distribution and diversity of Rhododendrons in aid of their conservation in a changing world. To achieve this, four specific objectives are formulated as follows:

- To examine the relationship between topographic complexity and Rhododendron species richness in China
- To explore and understand the role of climatic, topographic and edaphic variables in determining the distribution of Rhododendron species with different range sizes in China
- To predict Rhododendron diversity patterns, and identify Rhododendron hotspots and priority areas for conservation in China
- To predict the distribution of narrow- and wide-ranging Rhododendron species in the face of climate and land use change in China

1.4 Study area and species data

1.4.1 Study area

The study area comprises 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 Himalayas form the highest mountain range on Earth and the Tibetan Plateau's average elevation is over 4,000 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 for exploring the relationship between environmental factors and macro-scale patterns of plant distribution and diversity.

China is one the Earth's megadiverse countries (Xu et al., 2009a). China is also considered one of the main centres of origin of diversification for seed plants in the world (Lopez-Pujol et al., 2006). However, biodiversity in China is facing severe threats, including rapid climate and land use changes (Lopez-Pujol et al., 2006), even within Chinese nature reserves (Wang et al., 2016).

1.4.2 Herbarium data

In this thesis, 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 an inadequate description 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 (Figure 1.2).

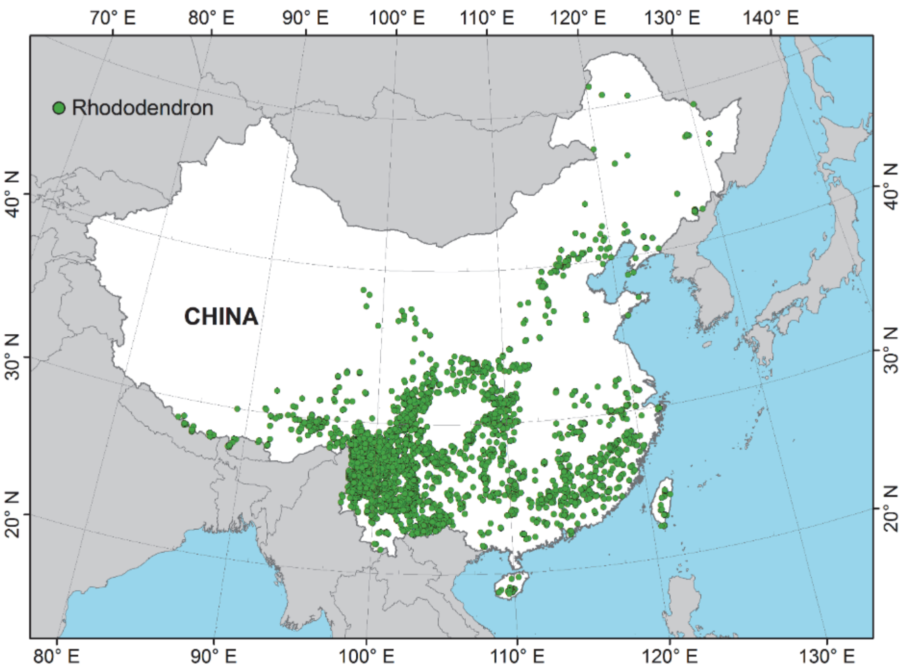

Figure 1.2 Study area and the locations of Rhododendron species' observations

1.5 Outline of the thesis

This thesis consists of six chapters, a general introduction, four core chapters and a synthesis. Each core chapter has been prepared as a stand-alone research paper that has been published in or submitted to a peer-reviewed, international journal. The six chapters are arranged as follows:

Chapter 1 presents the research background, research gaps, research objectives, study area, and the structure of the thesis.

Chapter 2 examines the correlations between eight topographic complexity indices and Rhododendron species richness in China at seven spatial scales: grain sizes of 0.05°, 0.1°, 0.25°, 0.5°, 1.0°, 1.5°, and 2.0°.

Chapter 3 examines the relationship between geographical and elevational range sizes for 80 endemic Rhododendron species in China, and investigates the importance of basic factors of 'niche breadth' (i.e.

climate, topography, and soil) in shaping the distribution of Rhododendrons with various geographical and elevational range sizes.

Chapter 4 predicts Rhododendron diversity patterns, and identifies Rhododendron hotspots and priority areas for their conservation in China.

Chapter 5 predicts the potential impact of climate and land use change on the distribution of narrow- and wide-ranging Rhododendron species in China.

Chapter 6 provides an overview of the research findings from the previous chapters relevant to specific research objectives. It elaborates on the implications of these results for the conservation of Rhododendrons and biodiversity.

Chapter 2

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

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This chapter is based on: Yu, F.Y., Wang, T.J., Groen, T.A., Skidmore, A.K., Yang, X.F., Geng, Y.Y., and Ma, K.P. 2015. Multi-scale comparison of topographic complexity indices in relation to plant species richness. *Ecological Complexity*, 22: 93-101.

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 ≤ 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.

2.1 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., 2013b; 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 & 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; Kreft et al., 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 plant richness (Kreft et al., 2010), and vascular plant diversity (Kreft & 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 & Lum, 1980), South Africa (Thuiller et al., 2006), and south-western Finland (Luoto & 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 & Harral, 2001; Rahbek & 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 & 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.

2.2 Materials and methods

2.2.1 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 4,000 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.

2.2.2 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 1,025 species, Rhododendron exhibits an amazing geographic variation in phylogeny and life forms. Mainland Southeast Asia harbour is more than 90% of all known Rhododendron species (Kumar, 2012). According to the latest study by Wu (2005), about 571 species of Rhododendrons have been found in China, and North-western Yunnan Province in China is considered as the centre 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 (Figure 2.1).

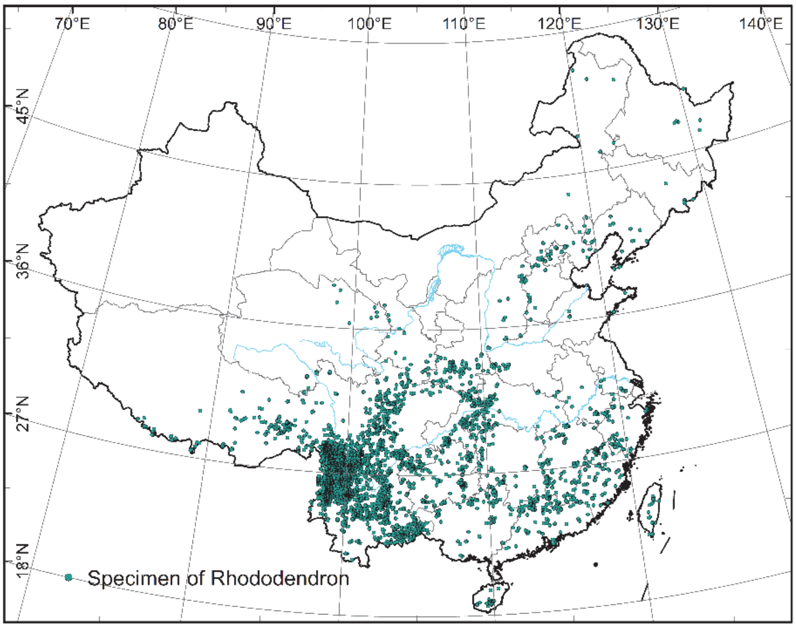

Figure 2.1 Map of study area and the locations of Rhododendron species observations

2.2.3 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 (RU), and standard deviation of curvature (SC). These five indices depict topography from different perspectives and have been used as proxies for topographic complexity in previous studies exploring the underlying mechanisms of plant species richness. In addition to these indices, we included two less studied but potentially important topographic complexity indices: slope range (SR) and the compound terrain complexity index (CTCI). SR expresses the variability of slope, which affects the velocity of both surface and subsurface flow and hence soil water content, erosion potential, soil formation, and many other important processes (Gallant, 2000). CTCI, deduced from four indices (standard deviation of elevation, elevation range, total curvature, and rugosity) is a synthetic index that comprises different features of topography and so can be used to evaluate several aspects of topographic complexity simultaneously (Lu et al., 2007). Our study is the first to test the relationship between CTCI and plant species richness.

Principal component analysis (PCA) is one of the most common methods for detecting multi-collinearity in a variable set and to reduce the number of variables in data analysis (Austin, 2002; Svenning et al., 2010; Wang et al., 2012b; Barbosa et al., 2014). It can be used to select the variables that contain the most information. Based on the results of a principal component analysis of the six fundamental topographic complexity indices (i.e. SE, RE, SS, RS, SC, and RU), we adopted the first principal component which accounts for over 80% of the variance in the data as a new topographic complexity index (i.e. PCA) in our study. The definition and equations of all above mentioned eight indices are given in Table 2.1.

Table 2.1 Description of topographic complexity indices

Index	Unit	Abbr	Definition	Equation	Source
Standard deviation of elevation	m	SE	A measure of the variability of elevation within the circular window. It measures the roughness of the landscape at the coarser scale	$\mathrm{SE} = \sqrt{\frac{1}{N}\sum_{i=1}^{N}(elevation_i - \overline{elevation})^2}$	-
Range of elevation	m	RE	Arithmetic difference between the maximum and minimum elevations	$\mathrm{RE} = \mathrm{Maximum}_{elevaiton}\text{-}\mathrm{Minimum}_{elevaiton}$	-
Standard deviation of slope	degree	SS	Standard deviation of slope	$\mathrm{SS} = \sqrt{\frac{1}{N}\sum_{i=1}^{N}(\ Slope_i - \overline{Slope})^2}$	-
Range of slope	degree	RS	A measure of the "relief of slope" of a landscape	$\mathrm{RS} = \mathrm{Maximum}_{slope}\text{-}\mathrm{Minimum}_{slope}$	-

(Continued) Table 2.1 Description of topographic complexity indices

Index	Unit	Abbr	Definition	Equation	Source
Standard deviation of curvature	in radians per square meter	SC	Description the variation of the land surface, if that surface is merely flat or hilly	$\mathrm{SC} = \sqrt{\frac{1}{N}\sum_{i=1}^{N}(\mathrm{Cur}_i - \overline{\mathrm{Cur}})^2}$ $\mathrm{Cur} = -\frac{p^2r + 2pqs + q^2t}{(p^2+q^2)(\sqrt{1+p^2+q^2}^3)}$	Jenness (2013)
Rugosity	-	RU	The ratio of surface area (As) to planar area (Ap); describes how wrinkled a surface is	$RU = \frac{As}{Ap}, As = \frac{c^2}{Cos(S(\frac{\pi}{180}))}$ Where: c = cell size, S = slope in degree	Jenness (2013)
Compound terrain complexity index	-	CTCI	Weights four indices that depict terrain complexity from different perspectives	$\mathrm{CTCI} = (N_{SE} + N_{RE} + N_{SC} + N_{RU})\ /4$, where $N_{Index} = \frac{Index - min_{Index}}{max_{Index} - min_{Index}}$	Lu et al. (2007)
Principal component analysis	-	PCA	The first principal component of the six fundamental topographic complexity indices (i.e. SE, RE, SS, RS, SC and RU)	$\mathrm{var(PX)} = \mathrm{Pcov(X)P^{-1}}$	-

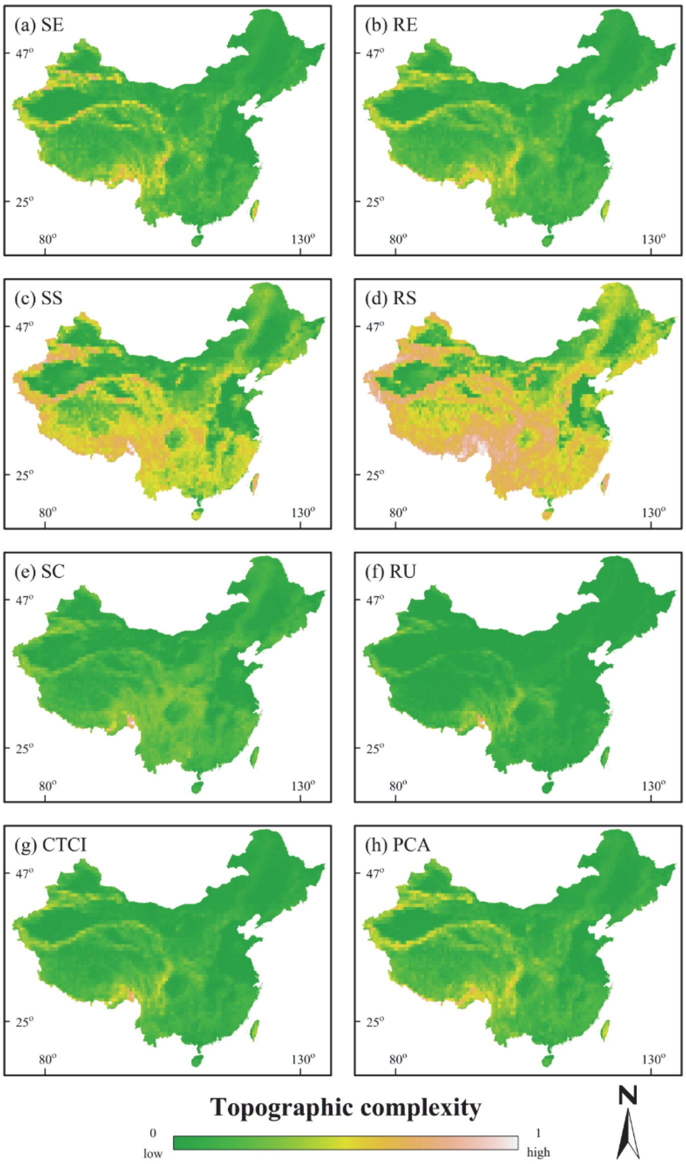

Figure 2.2 Maps of the topographic complexity indices in China with a grain size of 0.5°. (a) Standard deviation of Elevation (SE); (b) Range of Elevation (RE); (c) Standard deviation of Slope (SS); (d) Range of Slope (RS); (e) Standard deviation of Curvature (SC); (f) Rugosity (RU); (g) Compound Terrain Complexity Index (CTCI); and (h) The first principal component of the six fundamental topographic complexity indices (PCA)

The Digital Elevation Model (DEM) used to calculate the topographic complexity indices was derived from the USGS Global Multi-Resolution Terrain Elevation Data 2010 (http://topotools.cr.usgs.gov/gmted_viewer/), with a spatial resolution of 250 m. Slope was computed using the Slope Tool in the spatial analysis module of ArcGIS 10.0 (ESRI, Inc., Redlands, California, USA). The terrain curvature (hereafter referred to as "curvature"), total curvature, and rugosity were calculated with the DEM Surface Tool, an extension for ArcGIS10.0 (http://www.jennessent.com /arcgis/surface_area.htm). Subsequently, using elevation, slope, and curvature as primary input data and the Zonal Statistics Tool in ArcGIS 10.0 we calculated the standard deviation of elevation, range of elevation, standard deviation of slope, range of slope, and standard deviation of curvature. Lastly, we calculated CTCI with the algorithm developed by Lu et al. (2007). Maps of topographic complexity indices in China with a grain size of 0.5° are displayed in Figure 2.2. In order to make indices comparable, the original topographic complexity indices were normalized to a range of 0-1 for all maps. From the figure it can be seen that the most topographically complex region of China is the southeast, including Yunnan, Sichuan, and Tibet provinces.

2.2.4 Multi-scale analysis

To examine the effect of spatial scale (grain size) on the correlation between topographic complexity indices and species richness, our analysis was initially centred on a grain size of 0.5°×0.5°, as used in previous studies carried out on China as a whole or at continental scale (Kreft et al., 2006; Wang et al., 2011). We continued the analysis in two directions: downscaling to 0.25°×0.25°, 0.1°×0.1°, and 0.05°×0.05° and upscaling to 1.0°×1.0°, 1.5°×1.5°, and 2.0°×2.0°. We selected these seven grain sizes because they were the most commonly used grain sizes in the area of biodiversity and distribution studies at regional, continental and global scales (Crawley & Harral, 2001; Friedman et al., 2001; Wang et al., 2009; Belmaker & Jetz, 2011). We used the Zonal Statistics Tool in ArcGIS 10.0 to calculate the topographic complexity indices at these grain sizes.

The grain size in Zonal Statistical Tool refers to the size of the zone data. Taking the topographic complexity index RE at the grain size of 2.0° as an example, RE was calculated from the difference in maximum and minimum elevation values with a spatial resolution of 250 m DEM at the grain size of 2.0°×2.0°. Descriptive statistics of topographic complexity indices and Rhododendron species richness across scales were produced to interpret the information on the data distributions (Table 2.2).

2.2.5 Spatial autocorrelation

Spatial autocorrelation exists in most ecological and environmental dataset (Legendre, 1993; Kreft et al., 2006). When spatial autocorrelation is high in explanatory variables, it violates the assumption of independent samples, and might lead to overestimating the significance of correlations (de Knegt et al., 2010). To assess whether this could also be a problem for the correlations between topographic complexity and species richness, we calculated the range of the semi-variogram of each topographic complexity index. This range was compared with the average distance between Rhododendron species richness points that were selected by the bootstrapping procedure (see below) at every scale.

2.2.6 Statistical analysis

Pearson's correlation coefficient (*r*) was calculated for every combination of topographic complexity indices and between topographic complexity indices and Rhododendron species richness. To increase the stability and reliability of the correlations, we applied a bootstrapping procedure to calculate an average correlation from 500 bootstrapped samples, each consisting of 100 sampling units (Pattengale et al., 2009). We fixed the sampling size at 100 because at the coarsest grain size (2.0°) this was the maximum number of pixels available, given the spatial extent (China) of the study. By fixing the sample size over all scales, possible changes observed between the bootstrapped correlations may be attributed to the scale rather than to the variation in sample size between scales.

Table 2.2 Summary of statistics (mean ± SD) of the eight topographic complexity indices and the species richness (SP) of Rhododendrons at grain sizes of 0.05°, 0.1°, 0.25°, 0.5°, 1.0°, 1.5°, and 2.0°

Scale Index	0.05°	0.1°	0.25°	0.5°	1.0°	1.5°	2.0°
SE	221.92±128.51	287.47±162.83	334.35±187.08	335.22±192.66	341.17±202.14	376.55±262.76	384.52±261.62
RE	981.28±524.80	1330.32±676.34	1702.65±830.76	1913.36±980.98	2148.86±1120.15	2443.87±1320.96	2636.32±1400.22
SS	8.52±2.44	8.97±2.21	9.23±2.20	9.15±2.35	8.98±2.56	9.02±2.72	8.85±2.86
RS	41.99±10.90	46.97±10.05	51.61±9.55	54.07±9.53	56.11±9.66	58.18±10.07	58.87±10.49
SC	0.08±0.03	0.08±0.03	0.08±0.03	0.07±0.03	0.07±0.03	0.06±0.03	0.06±0.03
RU	1.08±0.06	1.08±0.06	1.07±0.06	1.06±0.05	1.05±0.04	1.05±0.04	1.04±0.04
CTCI	0.11±0.06	0.14±0.07	0.15±0.09	0.16±0.10	0.17±0.11	0.17±0.11	0.19±0.12
PCA	2.96±2.20	2.91±2.12	2.48±2.04	1.89±2.00	1.26±1.91	1.05±1.98	0.72±2.00
SP	3.28±5.07	3.96±5.99	5.81±8.52	8.05±12.20	11.18±16.08	14.21±20.12	19.10±27.97

For abbreviations of topographic complexity indices see Table 2.1

To compare the correlations between all combinations of topographic complexity indices and between Rhododendron species richness and topographic complexity indices at different scales, a Games-Howell post hoc test after a one-way ANOVA was used. All statistical analyses were implemented in the R software environment (version 2.15.3, R Development Core Team).

2.3 Results

2.3.1 Spatial correlation of topographic complexity indices at multiple scales

The eight topographic complexity indices were moderately to highly correlated with each other (Figure 2.3). The correlations between each pair of indices decreased with increasing grain size. In general, higher correlations can be found between SE, RE, and CTCI. By contrast, RU and SC had lower correlations with other indices.

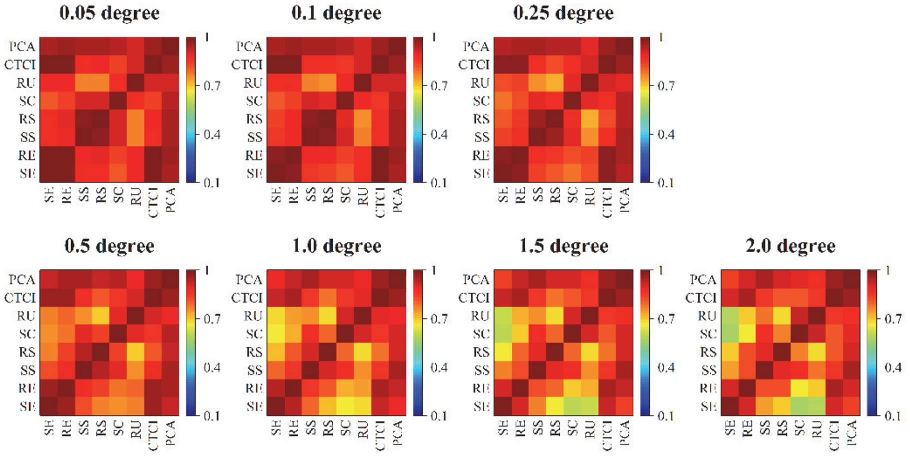

Figure 2.3 Cross-correlation matrix of eight topographic complexity indices at different scales. All correlations are significant at $p < 0.01$

2.3.2 Correlation between topographic complexity indices and Rhododendron species richness across scales

The average correlations from 500 repeated bootstrapping analyses showed that the eight topographic complexity indices had significantly positive correlations with Rhododendron species richness from 0.25° to 2.0°, but no significant correlations at scales of 0.05° and 0.1°. With an increase in grain size, the association between the eight topographic complexity indices and Rhododendron species richness changed (Table 2.3). Two groups of indices emerged. The first was the 'elevation group' (SE and RE): its correlations increased significantly from 0.05° ($r_{SE} = 0.202$, $r_{RE} = 0.182$) to 0.5° ($r_{SE} = 0.497$, $r_{RE} = 0.495$) and were more or less stable from 1.0° to 2.0°. The second group consisted of the remaining indices (SS, RS, SC, RU, CTCI, and PCA): these correlations showed significant increases over the whole range from 0.05° to 2.0°.

Table 2.3 Pearson's correlation coefficients between topographic complexity indices and Rhododendron species richness at grain sizes of 0.05°, 0.1°, 0.25°, 0.5°, 1.0°, 1.5°, and 2.0°

Scale Index	0.05°	0.1°	0.25°	0.5°	1.0°	1.5°	2.0°
SE	$0.202^{\text{n.s}}$	$0.279^{\text{n.s}}$	0.437^{*}	0.497^{*}	0.490^{*}	0.435^{*}	0.496^{*}
RE	$0.182^{\text{n.s}}$	$0.269^{\text{n.s}}$	0.431^{*}	0.495^{*}	0.519^{*}	0.494^{*}	0.506^{*}
SS	$0.176^{\text{n.s}}$	$0.209^{\text{n.s}}$	0.308^{*}	0.350^{*}	0.408^{*}	0.443^{*}	0.477^{*}
RS	$0.166^{\text{n.s}}$	$0.216^{\text{n.s}}$	0.317^{*}	0.395^{*}	0.449^{*}	0.479^{*}	0.432^{*}
SC	$0.080^{\text{n.s}}$	$0.123^{\text{n.s}}$	$0.183^{\text{n.s}}$	0.255^{*}	0.355^{*}	0.429^{*}	0.461^{*}
RU	$0.165^{\text{n.s}}$	$0.222^{\text{n.s}}$	0.312^{*}	0.386^{*}	0.471^{*}	0.549^{*}	0.592^{*}
CTCI	$0.194^{\text{n.s}}$	$0.279^{\text{n.s}}$	0.408^{*}	0.459^{*}	0.497^{*}	0.510^{*}	0.549^{*}
PCA	$0.181^{\text{n.s}}$	$0.252^{\text{n.s}}$	0.368^{*}	0.439^{*}	0.490^{*}	0.524^{*}	0.548^{*}

* indicates significant at $p < 0.05$, and n.s indicates not significant

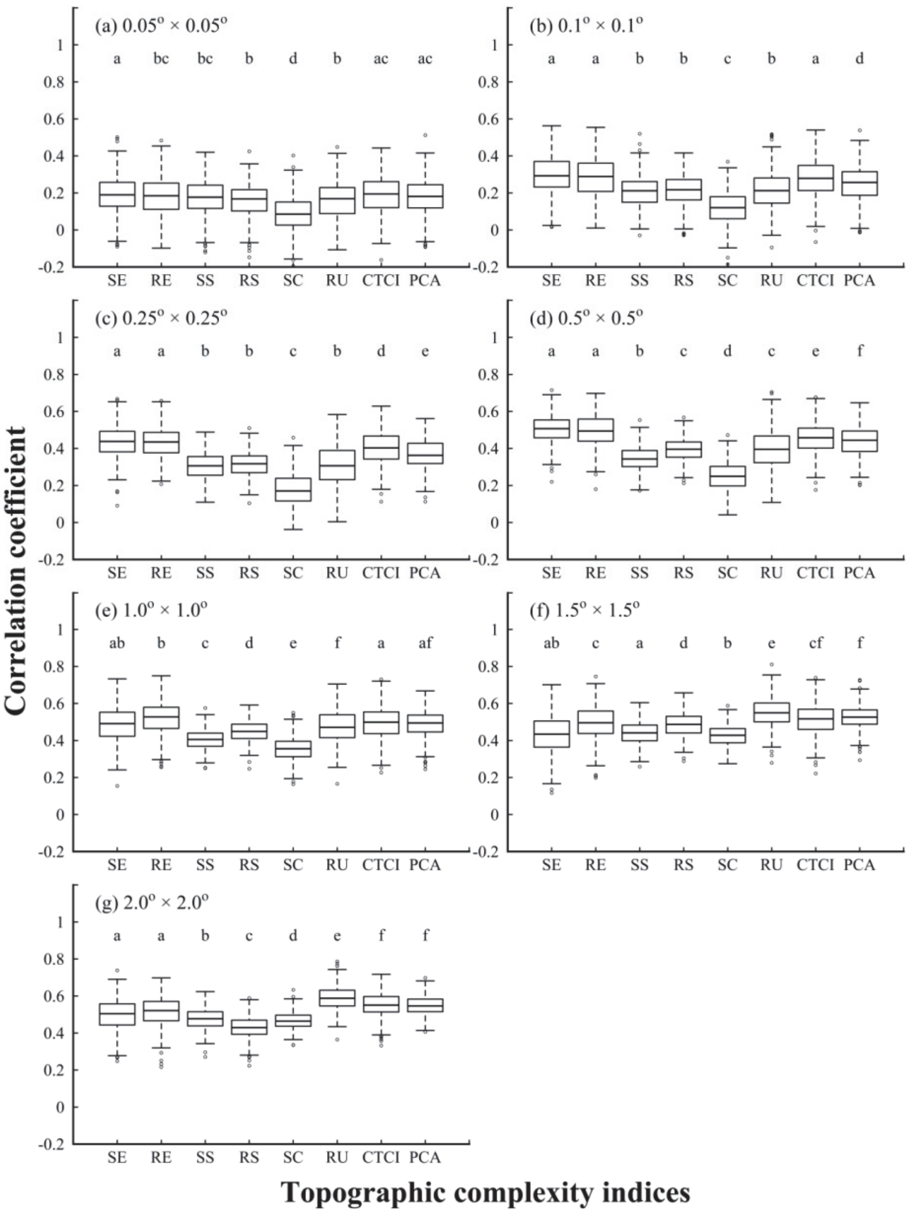

Figure 2.4 Comparison of correlation coefficients between various topographic complexity indices and Rhododendron species richness at every single scale. Different letters indicate statistically significant differences between topographic complexity indices. The same letter indicates no significant difference between indices ($p < 0.05$)

2.3.3 Difference in the correlations between various topographic complexity indices and Rhododendron species richness at different scales

We further compared correlations between the various topographic complexity indices and Rhododendron species richness at the same grain size. This revealed that at scales of 0.25°, 0.5°, and 1.0°, SE and RE had significantly stronger correlations with Rhododendron species richness than the other indices (Figure 2.4c-e), although there was no significant difference between SE and RE. RU had the highest correlation at scales of 1.5° and 2.0° (Figure 2.4f and g, $r_{RU} = 0.549$ at 1.5°, $r_{RU} = 0.592$ at 2.0°). At all scales up to 1.0°, the correlations of SC were significantly lower than those of the other indices.

2.3.4 Spatial autocorrelation and spatial scale

Among all the topographic complexity indices, rugosity showed positive spatial autocorrelation up to a distance of 1,200-1,500 km across all the scales (Figure 2.5), while the distance over which autocorrelation occurred for other indices decreased sharply at scales > 0.25°to distances of 500 km. The average distance between species richness points was within the range of spatial autocorrelation of topographic complexity indices at grain sizes of 0.05° to 0.25°, while it was larger for most complexity indices (except RU) between grain sizes of 0.5° to 2.0°. This indicates that spatial autocorrelation probably affects the correlation between topographic complexity and Rhododendron species richness at grain sizes of 0.05° to 0.25°. But this is not an issue at grain sizes from 0.5° to 2.0° for all indices except RU and at the grain size of 2.0°, for PCA and SS.

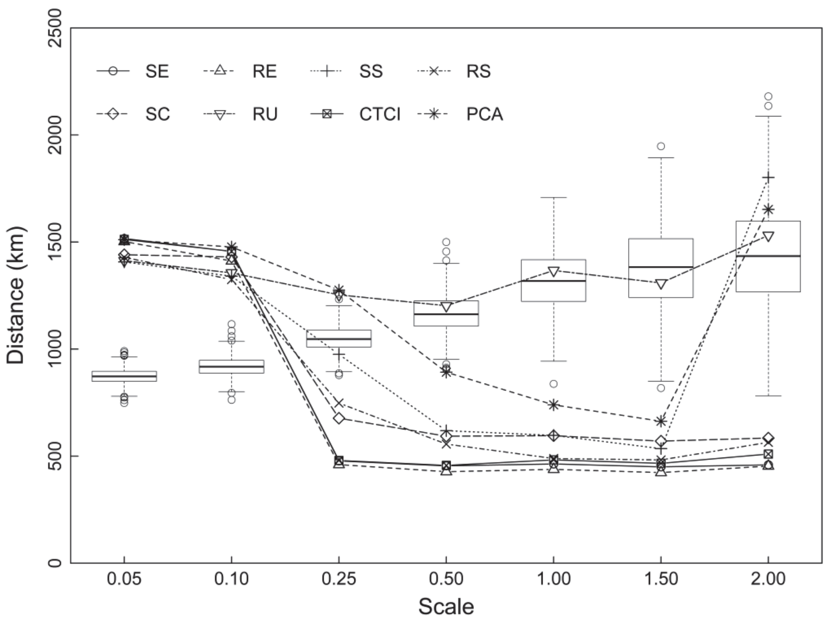

Figure 2.5 Range of the semi-variograms of the topographic complexity indices (lines) and the distribution of the average distance between the Rhododendron species richness points for all 500 bootstrapped samples (box and whiskers) across scales

2.4 Discussion

Species richness patterns are not solely shaped by topographic complexity, also by climatic heterogeneity, available water and energy, and human activities (Hawkins et al., 2003; Wang et al., 2011). Different factors may exert a dominant control in determining species richness at different scales. Most studies considered topographic complexity as an important element from plot to landscape scales for exploring the determinants of plant richness patterns (Svenning et al., 2009; Moeslund et al., 2013b; Moeslund et al., 2013a). In our study, taking spatial autocorrelation of topographic complexity indices into account, the positive and significant correlations between the eight topographic complexity indices and Rhododendron species richness in China across large grain sizes (i.e. 0.5°, 1.0°, 1.5°, and 2.0°) indicate that topographic complexity influences plant species richness at regional to continental scales as well, which is in accordance with previous studies (Coblentz & Riitters, 2004; Kreft et al., 2006; Eiserhardt et al., 2011). The positive correlations can be a consequence of the combined effect of different mechanisms, including promotion of species coexistence, persistence and diversification (Stein et al., 2014). Regions with more complex topographic conditions have steep climatic and habitat gradients promoting spatial turnover of species favoring different conditions. Moreover, topographic complex area could support more species by providing diverse habitats during glaciations and the consequent geographic isolation (Stein et al., 2014). The observation that mountainous areas harbor more species is a strong evidence for this (Körner, 2000). We found no significant correlations between the eight topographic complexity indices and Rhododendron species richness at the smaller grain sizes (0.05° and 0.1°), the dataset we used might inherently be a reason. The collection location of the specimens was accurate to 1 km (0.01°), and specimens were from seven different herbaria. Therefore positional inaccuracies are inevitable and 0.05° and 0.1° might be too small to average out the positional inaccuracies and to capture the Rhododendron species richness pattern. Besides, we noted that these correlations were affected by spatial autocorrelation in the topographical complexity indices.

Six topographic complexity indices (i.e. SS, RS, SC, RU, CTCI, and PCA) showed gradually stronger correlations with Rhododendron species richness at coarser grain sizes. This can be explained by that a larger unit (area) could potentially harbor more niches and, consequently, more species (i.e. species-area relationships) (Rosenzweig, 1995; Chown & Gaston, 2000; van Rensburg et al., 2002; Pausas et al., 2003). Our results highlight the importance of spatial grain in topographic complexity–plant species richness studies, which has been tested for various taxa and environmental factors. van Rensburg et al. (2002) emphasized that spatial grain and extent must be taken into account when investigating bird species richness-habitat heterogeneity relationships, while in another study, Tamme et al. (2010) suggested that grain is more important for species co-existence than other scale parameters during the meta-analysis.

Stein et al. (2014) investigated 1,148 points worldwide and concluded that spatial grain and spatial extent are the key factors influencing the strength of relationships between environmental heterogeneity and species richness of terrestrial plants and animals.

However, the correlations of SE and RE with Rhododendron species richness became asymptotically constant and even decreased above 1.0°. A possible cause could be the well-known hump-shaped relationship between species richness and elevation (i.e. with a peak in richness at intermediate elevations), which has been documented in a variety of habitats and taxa (see Rahbek 1995 for a detailed review). In our case, both SE and RE are fundamentally an expression of variation and range of the elevation, but also correlate with elevation. In this regard, we assumed the hump-shaped relationship between elevation and species may also influence the trend of correlation between SE and RE and species. Another probable cause is that RE and SE increased with increasing grain size, potentially covering more altitudinal zones. However, plant species, including Rhododendron, cannot grow above a certain altitude, causing for this effect to wear off after a certain altitudinal range is covered by a pixel.

A comparison of correlations between the eight topographic complexity indices and Rhododendron species richness suggests that SE and RE are the most appropriate proxies to study these correlations at finer scales (i.e. grain size ≤ 1.0°). SE and RE were derived from elevation, which is closely associated with climate. It has been shown that as the variation in elevation increases, the potential range of variability within a grid cell increases for all climate variables, therefore it can lead to a combined effect of topographic complexity and climatic heterogeneity on species diversity (Körner, 2007; Hofer et al., 2008). Specifically, Rhododendron species are dominant in the subalpine and alpine zone covering a vast tract of south-eastern Asia (Kumar, 2012), the environmental requirements for Rhododendron, such as an average annual precipitation above 800 mm and an average summer temperature below 28°(Geng, 2008) are parameters highly correlated with elevation.

Although Rhododendron species richness was most accurately explained by RU at large scales (i.e. with the grain sizes of 1.5° [$r = 0.549$] and 2.0° [$r = 0.592$]), we do not recommend to use it as index in topographic complexity-plant species richness studies. The high correlation coefficient can be the artificially high due to the high spatial autocorrelation across scales (Figure 2.5). Furthermore, our results showed that SC is a weaker index as a proxy for topographic complexity. It could be because that curvature is the second derivative from elevation and is extremely sensitive to noise in a DEM, and this sensitivity could be propagating into the output (Schmidt et al., 2003).

We expected to find stronger correlations between the two compound indices (CTCI and PCA) and Rhododendron species richness. However, our results demonstrated that the compound indices did not show stronger correlations compared to the other simple indices. This may be because of two reasons. Firstly, compound indices combine different information, including elevation, slope, aspect, and curvature. Although they are more comprehensive, it is also likely that they minimize the trait of topographic complexity. Secondly, the eight topographic complexity indices were moderately to highly correlated with each other as shown in Figure 2.3. Therefore, the collinearity among the indices can mean that there is no additional information in combining them.

2.5 Conclusions

We investigated the correlations between eight topographic complexity indices and Rhododendron species richness in China with grain sizes of 0.05°, 0.1°, 0.25°, 0.5°, 1.0°, 1.5°, and 2.0°. To the best of our knowledge, this is the first comprehensive and comparative study on the correlations between various topographic complexity indices and plant species richness at multiple coarse-grained macro-habitat scales. Our findings indicate that different topographic complexity indices may have positive correlations with plant species richness. The topographic complexity–plant species richness associations could be scale-dependent. In our case the correlations between topographic complexity and Rhododendron species richness in China tend to be stronger at a coarser grain size. We therefore suggest that a topographic complexity index may serve as good proxy for studying the pattern of plant species diversity at the continental to global levels. However, choosing among topographic complexity indices must be undertaken with caution because different topographic complexity indices respond differently to grain sizes. Nevertheless, further comparative research is needed to confirm or refute these findings in different taxonomic groups and different biogeographic regions.

Chapter 3

Climatic niche breadth can explain variation in geographical range size of alpine and subalpine plants

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Abstract

Understanding the environmental factors determining the distribution of species with different range sizes can provide valuable insights for evolutionary ecology and conservation biology in the face of expected climate change. However, little is known about what determines the variation in geographical and elevational ranges of alpine and subalpine plant species. Here, we examined the relationship between geographical and elevational range sizes for 80 endemic Rhododendron species in China using Spearman's rank-order correlation. We ran the species distribution model - maximum entropy modelling (MaxEnt) - with 27 environmental variables. The importance of each variable to the model prediction was compared for species groups with different geographical and elevational range sizes. Our results showed that the correlation between geographical and elevational range sizes of Rhododendron species was not significant. Climate-related variables were found to be the most important factors in shaping the distributional ranges of alpine and subalpine plant species across China. Species with geographically and elevationally narrow ranges had distinct niche requirements. For geographical ranges, the narrow-ranging species showed less tolerance to niche conditions than the wide-ranging species. For elevational ranges, compared to the wide-ranging species, the narrow-ranging species showed an equivalent niche breadth, but occurred at different niche position along the environmental gradient. Our findings suggest that over large spatial extents the elevational range size can be a complementary trait of alpine and subalpine plant species to geographical range size. Climatic niche breadth, especially the range of seasonal variability can explain species' geographical range sizes. Changes in climate may influence the distribution of Rhododendrons, with the effects likely being felt most by species with either a narrow geographical or narrow elevational range.

3.1 Introduction

Global climate change is expected to have an impact on the distribution of species (Thomas et al., 2004; Parmesan, 2006). Given the overall recorded rise in temperature, there are two likely consequences for species that are limited in their distribution by temperature constraints. Some species may shift their ranges to higher altitudes or higher latitudes, whereas others may experience a decrease or even extinction due to their slow migration rates or the limited availability of new habitat that results from the synergistic effects of a narrow niche and small range size (Ohlemuller et al., 2008; Chen et al., 2011; Lenoir & Svenning, 2015). Although individual species may have idiosyncratic responses to climate change, species that share the same ecological trait might respond in the same way (Thuiller et al., 2005). Range size - reflecting interspecific differences of ecological tolerance, dispersal ability, and evolutionary history - is a basic unit in biogeography and can be considered to be a species trait (Thompson et al., 1999; Olalla-Tarraga et al., 2011). The size of a species range is, at least partially, a spatial representation of its degree of specialization (Devictor et al., 2010). Range size has been used to predict the global extinction risk (Purvis et al., 2000; Botts et al., 2013), which can provide data for one of the most important biodiversity indicators - the Red List Index. The factors determining species' range sizes likely affect their capacity to alter their ranges in response to climate change (Thomas et al., 2001; McCauley et al., 2014). Consequently, understanding the environmental factors determining the distribution of species with different range sizes can provide valuable insights for evolutionary ecology and conservation biology in the face of expected climate change.

Why some species have highly restricted geographic ranges while closely related species have widespread distributions has long fascinated ecologists and biologists (Brown et al., 1996; Gaston, 1996). A variety of hypotheses and paradigms have been proposed to explain the variation seen in geographical range sizes between species including climatic variability (Stevens, 1989), evolution (Gaston, 1996), complex interactions (Brown et al., 1996), niche breadth (Gaston et al., 1997; Gaston & Spicer, 2001), energy availability (Morin & Chuine, 2006), climate tolerance (Pither, 2003), glacial history (Jansson, 2003), colonization ability (Lowry & Lester, 2006), and a combination of habitat area and climate stability (Morueta-Holme et al., 2013). Among these hypotheses, the niche breadth hypothesis, which has recently gained more support, suggests a positive correlation between niche breadth and geographical range size (Boulangeat et al., 2012; Botts et al., 2013). Brown (1984) indicated that species which can utilize a greater array of resources and that can maintain viable populations under a wider variety of conditions should become more widespread. Based on this, the niche breadth hypothesis states that species with a broad niche can persist in a wide range of different habitat types, while species with a narrow niche will be restricted to those places where their specific niche requirements are met.

Botts et al. (2013) and Slatyer et al. (2013) defined three general categories for the niche breadth: climate tolerance, habitat tolerance and diet. In terms of climate tolerance, Stevens (1989) proposed that species able to tolerate a larger climate variation should occupy larger geographical areas than species with less tolerance. In addition, the climate extreme hypothesis (represented by the lowest temperature of the coldest month or quarter) also gained support in some studies (Pither, 2003; Kreyling et al., 2014). Meanwhile, climate- and soil-related variables are often used together as representations of habitat in species' range size studies (Kockemann et al., 2009; Pannek et al., 2013). The reasoning is that climatic and edaphic variables are the functional variables of temperature and water- and nutrient-availability that limit the growth and distribution of plants (Munns, 2002). Thus tolerance to a wide range of climatic and edaphic conditions should be associated with greater range sizes (Morin & Lechowicz, 2013). Furthermore, topography also contains information about a region's climatic history, hydrology and geodynamics and it determines the light available for plant growth. It is therefore often considered as a representation of habitat. In addition, topographical barriers are physiological barriers for species dispersal and affect distribution patterns including range sizes (Janzen, 1967; Ghalambor et al., 2006).

However, the relative importance of these basic factors of 'niche breadth' (i.e. climate, topography and soil) in shaping the distribution of plant species with different range sizes is unclear. The question is whether these basic factors are equally important in explaining the distribution of narrow- and wide-ranging species within a large extent? Or is climate alone more important for the narrow-ranging species that are expected to be more sensitive to climate change? Additionally, the term 'climate' refers to a diverse set of measurable variables. It matters which variables are important for the distribution of a species if we want to determine the impact of projected trajectories of climatic change on species' shifts in ranges.

In recent years, alpine and subalpine plant species have increasingly become a conservation concern because it is anticipated they will be affected by climate change (Theurillat & Guisan, 2001; Pérez-García et al., 2013). Alpine and subalpine plant species that cover a wide geographical range could also be expected to cover a wide elevational range (Blackburn & Ruggiero, 2001). However, a species with a narrow geographical range might still occupy a wide elevational range, for example when it occupies one specific but long hill or mountain slope. This may lead to different conclusions about which environmental factors are most important for species with a given range size. Interestingly, most macro-ecological studies have only considered geographical ranges, while the relationship between geographical and elevational range sizes has been less well studied (McCain, 2006). Very few studies have related these two types of range sizes together. Blackburn and Ruggiero (2001) showed that there was a strong correlation between geographical and elevational range size for Andean passerines, while McCain (2006) reported no relationship between geographical and elevational ranges for Costa Rican rodents. White and Bennett (2015) recently found that elevational range size is a strong independent predictor of extinction risk that is complementary to geographical range size.

In this study, we examined the factors that control the subcontinental distribution of a key alpine and subalpine genus, the Rhododendrons (Ma et al., 2014). The Rhododendrons genus forms a major component of vegetation in the Himalayan alpine zone (Li et al., 2013; Ma et al., 2014). Moreover, Rhododendrons display a great variation in range size (Kumar, 2012). Some Rhododendron species occur throughout most of the northern hemisphere, while others are highly restricted to small regions. A number of Rhododendron species have a wide elevational range, from 800-3,000 m, while other species only grow in the upper part of the montane zone (Liang & Eckstein, 2009). The Rhododendron species' large variation in geographical and elevational range sizes, and their dominant role in alpine and subalpine ecosystems, makes the Rhododendron an ideal genus to test how climatic, topographic and edaphic variables shape the distribution of narrow- and wide-ranging species.

This study addresses three inter-related questions: 1) Do alpine and subalpine plant species with narrow geographical ranges also have narrow elevational ranges? 2) Are climatic, topographic and edaphic variables equally important in determining the distribution of alpine and subalpine plant species with different range sizes? 3) What factors determine the variation in geographical and elevational ranges of alpine and subalpine plant species?

3.2 Methods

3.2.1 Study area and species data

The study area covers the whole of China (Figure 3.1). China harbours about 571 Rhododendron species, which are widely distributed across most regions (except Xinjiang and Ningxia provinces) with a wide range of climatic, topographic and edaphic conditions. Records on Rhododendron presence were collected from seven herbaria and botanical museums (Herbarium of the Institute of Botany, Herbarium of the Kunming Institute of Botany, South China Botanical Garden, Wuhan Botanical Garden, Sichuan University of Botany, Sichuan Forest School and Lushan Botanical Garden). Because a high locational accuracy is required for studying plant species distribution, all records with inadequate descriptions of the location (e.g. mentioning only a county or mountain) were excluded. Our resulting dataset with 406 species comprised 13,126 georeferenced records with a spatial uncertainty of less than 1 km.

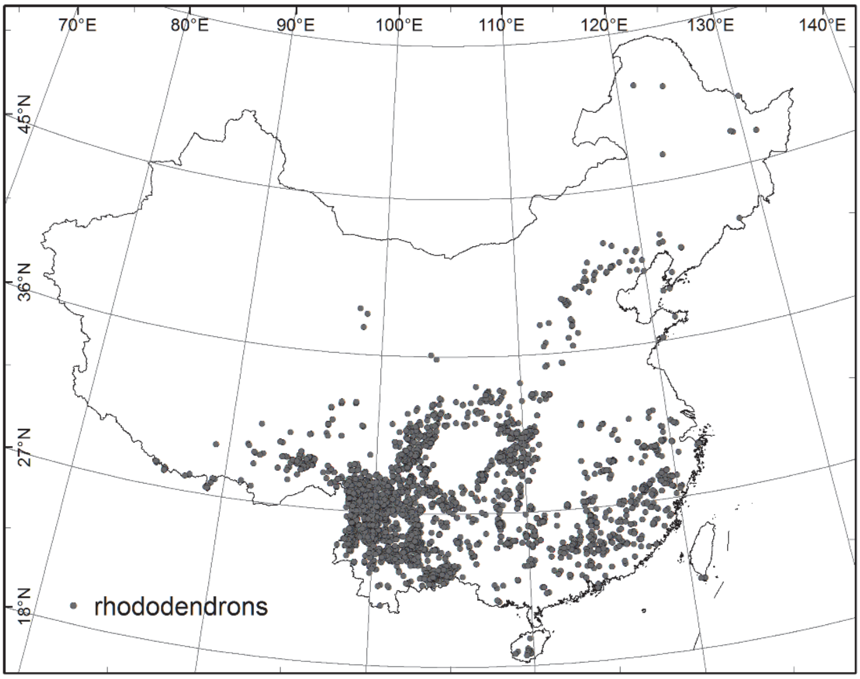


Figure 3.1 Study area and the locations of 80 Rhododendron species in China used in the species distribution models

3.2.2 Environmental variables

We collected climatic, topographic and edaphic data from a number of sources, and included a total of 27 variables (Table 3.1). For the climatic data we used the bioclim variables (Hijmans et al. 2005, available at http://www.worldclim.org) which are based on the current (1950-2000) conditions at 30 arc-seconds resolution (~1 km at the equator). The Digital Elevation Model (DEM) was derived from the SRTM (http://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1#download), with a resolution of 90 m. Slope gradient and aspect were calculated from the DEM using Horn's algorithm in ArcGIS10.2 (ESRI, Inc., Redlands, California, USA). Edaphic data was collected from the global 3D soil information system SoilGrid at 1 km spatial resolution (ftp://ftp.soilgrids.org/; Hengl et al. 2014). From the available data layers we selected soil pH, organic carbon and soil texture (i.e. sand-, silt- and clay fraction). The mean value of organic carbon was based on a depth of 0-30 cm, because the content of organic carbon decreases with the soil depth, and the top 20 cm is the layer which has the highest correlation of soil organic carbon and vegetation type (Jobbagy & Jackson, 2000). Given that Rhododendrons cover many life-forms, we selected the 30-60 cm depth for measuring the other soil characters (i.e. soil pH and soil texture, Hengl et al. 2014). We used 1 km as a standard resolution for all the environmental variables because this is the highest resolution SoilGrid provides.

Table 3.1 Environmental variables used for modelling the distribution of Rhododendrons

Category	Variable	Abbreviation	Unit
Climate	Annual mean temperature	Bio1	℃
	Mean diurnal range	Bio2	℃
	Isothermality	Bio3	-
	Temperature seasonality	Bio4	℃
	Max temperature of warmest month	Bio5	℃
	Min temperature of coldest month	Bio6	℃
	Temperature annual range	Bio7	℃
	Mean temperature of wettest quarter	Bio8	℃
	Mean temperature of driest quarter	Bio9	℃
	Mean temperature of warmest quarter	Bio10	℃
	Mean temperature of coldest quarter	Bio11	℃
	Annual precipitation	Bio12	mm
	Precipitation of wettest month	Bio13	mm
	Precipitation of driest month	Bio14	mm
	Precipitation seasonality	Bio15	-
	Precipitation of wettest quarter	Bio16	mm
	Precipitation of driest quarter	Bio17	mm
	Precipitation of warmest quarter	Bio18	mm
	Precipitation of coldest quarter	Bio19	mm
Topography	Elevation	Elev	m
	Northness	North	-
	Slope	Slope	degree
Soil	Soil organic carbon (dry combustion)	OrcC	g kg^{-1}
	pH index(H_2O solution)	pH	10^{-1}
	Sand content (gravimetric)	Sand	kg kg^{-1}
	Silt content (gravimetric)	Silt	kg kg^{-1}
	Clay content (gravimetric)	Clay	kg kg^{-1}

3.2.3 Species distribution modelling

Species distribution models (SDMs) have often been used to assess the importance of environmental variables in explaining species distributions. In this study, we used maximum entropy modelling (MaxEnt, version 3.3.3e, Phillips et al. 2006) because it generally performs well with presence-only species records (Phillips & Dudik, 2008), and it provides appropriate background samples to deal with sample biases (Prates-Clark et al., 2008; Elith et al., 2011). Because our data were collected from seven herbaria and botanical museums which hold Rhododendron records over more than 50 years, we would consider absences in certain regions reflect absences of Rhododendron, rather than absence of sampling effort.

When fitting SDMs there is ideally no strong correlation between the explanatory variables, i.e. no collinearity. If our aim is to predict the distribution of Rhododendrons, we cannot do any analysis without eliminating the multi-collinearity. However, we focus on the determining factors of Rhododendrons with different range sizes, a priori information about selecting the determining factor was not available for Rhododendrons. Therefore, excluding variables from our analysis would be mainly subjective. In addition, MaxEnt has an internal procedure to handle multi-collinearity of environmental variables, which has been verified by a number of studies (Prates-Clark et al., 2008; Elith et al., 2011). Meanwhile, we used the correlation matrix (Appendix Figure 3.A1) to provide an objective reference for our discussion. Therefore, the corresponding categorical variables for each model were all retained.

To reduce the effects of spatial autocorrelation, occurrences of Rhododendron observations at least 2 km apart from each other were retained, we used the 'spatially rarefy occurrence data tool' in SDMtoolbox (http://sdmtoolbox.org/) to complete this process. Species with at least 30 occurrences were selected for modelling (Wisz et al., 2008). While data sources and analyses often stop at political boundaries, species ranges obviously do not. In order to eliminate the potential effects caused by artificial boundaries, only the 80 species endemic to China were used in this study (Figure 3.1). For each species, 70% of the occurrence data was used for model training and 30% for validation (Williams et al., 2009; Kumar, 2012; Jiang et al., 2014). For each selected Rhododendron species, four models using different suites of input data (climatic, topographic, edaphic and all variables combined) were generated (the number of samples used for training and evaluation in the full model are given in the Appendix, Table 3.A1). The recommended default values were used for the convergence threshold (10^{-5}) and maximum iterations (500), while 10 0000 background points were accepted (Phillips et al., 2006). The regularization values that were included to reduce over fitting were set to 1, and the selection of 'auto feature' was carried out automatically by the program. Cross validation was selected to estimate model performance. Feature selection and the regularization value are two key parameter settings in MaxEnt. Tuning of the feature and regularization value may produce different results, especially for datasets with a geographic sampling bias and small sample sizes (i.e. less than 20 species localities) according to Anderson and Gonzalez (2011). This, however, was not the case in our study, given the amount of sampling effort and large sample size (at least 30 occurrences for each species). We therefore regard the default settings for feature selection and regularization in MaxEnt as appropriate here.

In order to compare the importance of four categories (climate, topography, soil and full), we employed the area under the receiver operating characteristic curve (AUC) statistic (Fielding & Bell, 1997), a threshold-independent method, and the true skill statistic (TSS) (Allouche et al. 2006), which is a threshold-dependent, goodness-of-fit method. AUC ranges between 0.5 to 1, with 1 denoting a perfect discrimination between presence and absence, and 0.5 denoting random discrimination. TSS is an index that takes sensitivity (probability that a predicted presence is a true presence) and specificity (probability that a predicted absence is a true absence) into account. To calculate TSS, model output (which ranges continuously between [0,1]) needs to be converted into presence or absence using a threshold value. The threshold was set to the value at which TSS is maximised (TSS_{max}). This version of TSS is not sensitive to prevalence (the fraction of presences in the training dataset; Liu et al. 2013). TSS is calculated from: TSS = Sensitivity + Specificity -1. TSS ranges from -1 to +1, where +1 indicates perfect agreement, -1 indicates a perfect inverse prediction (i.e. predicted absences are in fact presences, and vice versa), and values of zero indicate a performance no better than random (Allouche et al., 2006).

3.2.4 Species' range size

We projected all records to a Lambert Azimuthal Equal Area coordinate system and calculated the geographical range size of each species as the summed area of occupied grid cell with a grain size of 3,528 km^2 (59.4×59.4 km,~ 0.5°×0.5°). The grain size of 0.5° was chosen because these medium-sized grid cells allow for a trade-off between high accuracy and informative value regarding the size of the species ranges at a large extent (Wang et al., 2012a; Köster et al., 2013). Elevational range size was calculated as the difference between the maximum and minimum elevation of each species. The estimated range sizes might be subject to a certain degree of bias due to varying sampling efforts (Köster et al., 2013), however, as we have mentioned above, considering the long term and intensive collecting work of Rhododendron data, we would not regard sampling bias as a problem in this study.

We then ranked the 80 species from the most narrow-ranging to the most wide-ranging, and partitioned the species over the four quartiles: small (Q_g1 and Q_e1), medium (Q_g2 and Q_e2), large (Q_g3 and Q_e3) and very large (Q_g4 and Q_e4) quartiles (20, 20, 20 and 20 species per quartile, respectively) for both geographical (Q_g) and elevational (Q_e) range sizes (Figure 3.2).

3.2.5 Statistical analyses

We used the non-parametric Spearman's rank-order correlation to estimate the relationship between geographical and elevational range sizes, because the geographical range sizes had a very skewed distribution due to four species having a very large range size (over 3×10^6 km^2, Figure 3.2a). We performed a non-parametric Mann-Whitney U test to examine whether the difference of model performance (AUC and

TSS$_{max}$) was significant. We used variable contribution, a standard output of MaxEnt expressed as percentage, to estimate the importance of variables in explaining the distribution of the Rhododendron species. Response curves, which are also part of the output from MaxEnt, were used to interpret how individual variables affect the probability of presence of Rhododendron species belonging to the different quartiles of range sizes.

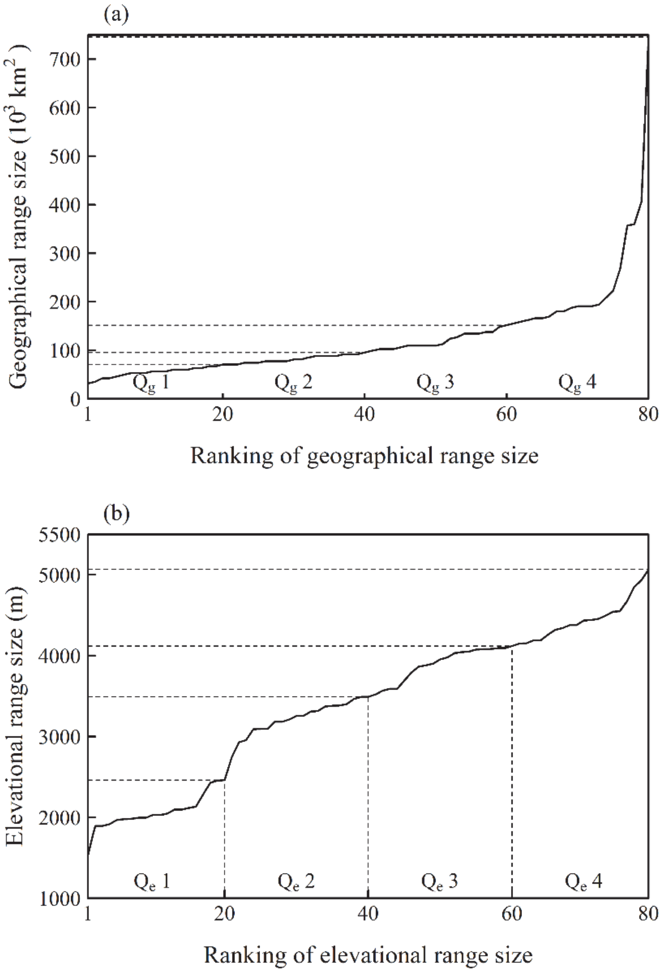


Figure 3.2 The geographical (a) and elevational (b) range sizes covered by the quartiles

3.3 Results

3.3.1 Relationship between geographical and elevational range size

The correlation between geographical and elevational range sizes of Rhododendron species was not significant (*r* = 0.17, *P* = 0.13; Figure 3.3), indicating that geographically narrow-ranging species do not necessarily also have a narrow range in elevation and vice versa. Thus elevational range size can be considered as another trait than geographical range size. In our further analyses, geographical and elevational range size groups will be analysed separately.

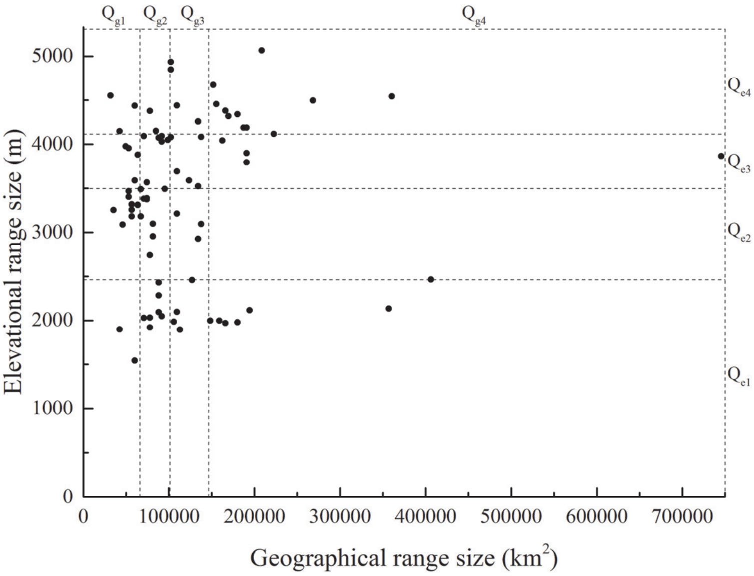


Figure 3.3 Correlation between geographical range size and elevational range size of Rhododendron species

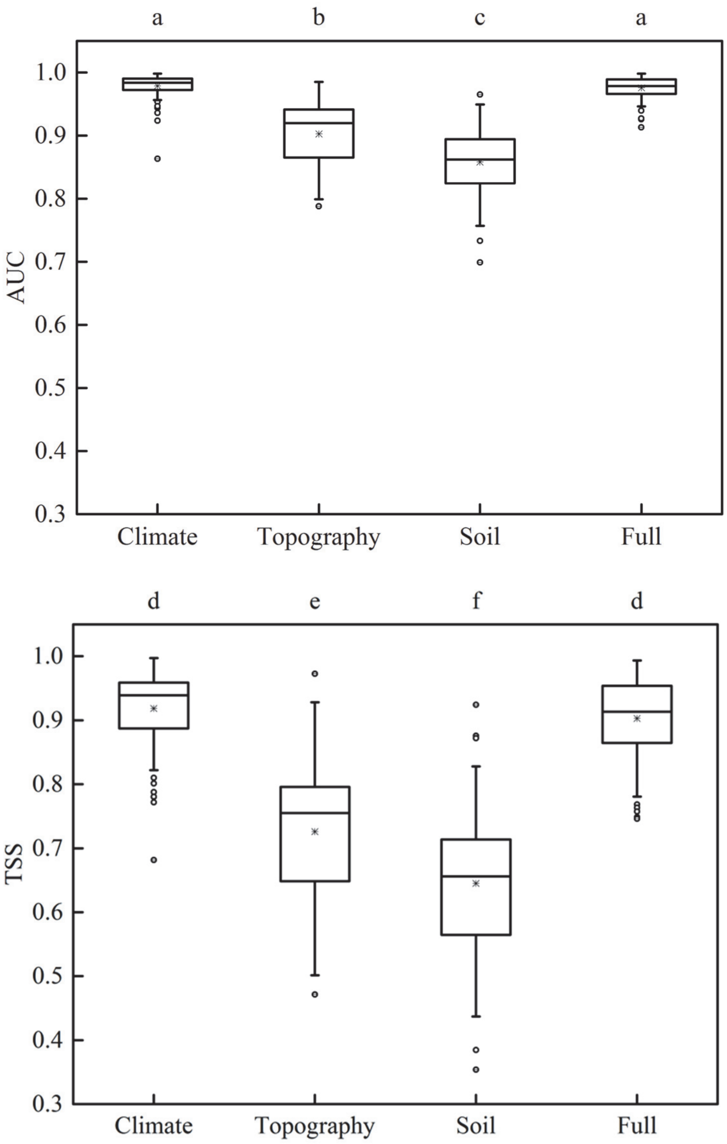


Figure 3.4 Comparison of the prediction accuracy of four categorical environmental variables for the distribution of 80 Rhododendron species in China. Different letters indicate significant differences ($P < 0.01$)

3.3.2 Model performance of the four categories of environmental variables

The fitted models based on climatic, topographic, edaphic and all (full) variables showed differences in prediction accuracies (Figure 3.4, $P < 0.01$). When comparing each model's AUC and TSS for all 80 Rhododendron species, the climatic and full models had significantly higher predictive accuracy than the topography and soil models. With a mean AUC value of 0.978 and TSS value of 0.919, the climate model had slightly higher absolute scores compared to the full model (AUC = 0.975, TSS = 0.903, model performance of 80 species see Appendix Table 3.A1), but the difference was not significant.

3.3.3 Importance of variables across geographical range sizes

We considered the top five most explaining variables for further analysis, which in total explained between 60-70% of the distribution of species (Figure 3.5). The mean contribution of variables across all species within a range size groups is reported hereafter. The average importance of isothermality (Bio3; ~33%) for geographically narrow-ranging species (Q_g1) became gradually less for geographically wide-ranging species (~11%), while the average importance of seasonality (Bio4) and temperature annual range (Bio7) increased for the geographically wide-ranging species (~19% and 9%). Elevation and precipitation in the driest month (Bio14) had a similar importance across range sizes. The importance of annual precipitation (Bio12) also changed significantly across range sizes, only contributing ~2% for Q_g1, but up to 12% for the other three quartiles (Q_g2, Q_g3 and Q_g4). Slope was only important for the geographically narrow-ranging species.

The responses of the important variables in the prediction for the four geographic range size groups as well as for each species were showed in Figure 3.6 and Figure 3.S2, respectively. According to the response curves, the geographically narrow-ranging species (Q_g1) occurred in areas with less variation in the diurnal temperature range than in the annual temperature range (i.e. higher values for isothermality (Bio3) of about 0.4-0.55) compared with the other three quartiles (with ranges in Bio3 of 0.2-

0.55). They also occurred in areas with a narrower range of temperature seasonality (Bio4 between 2.75 to 6). Precipitation in the driest month (Bio14) from 5-30 mm and a slope gradient of 15-40° would be favoured by Q_g1. In general, the geographically wide-ranging species (Q_g2 - Q_g4) can be found over broader ranges of these conditions than the geographically narrow-ranging species (Q_g1).

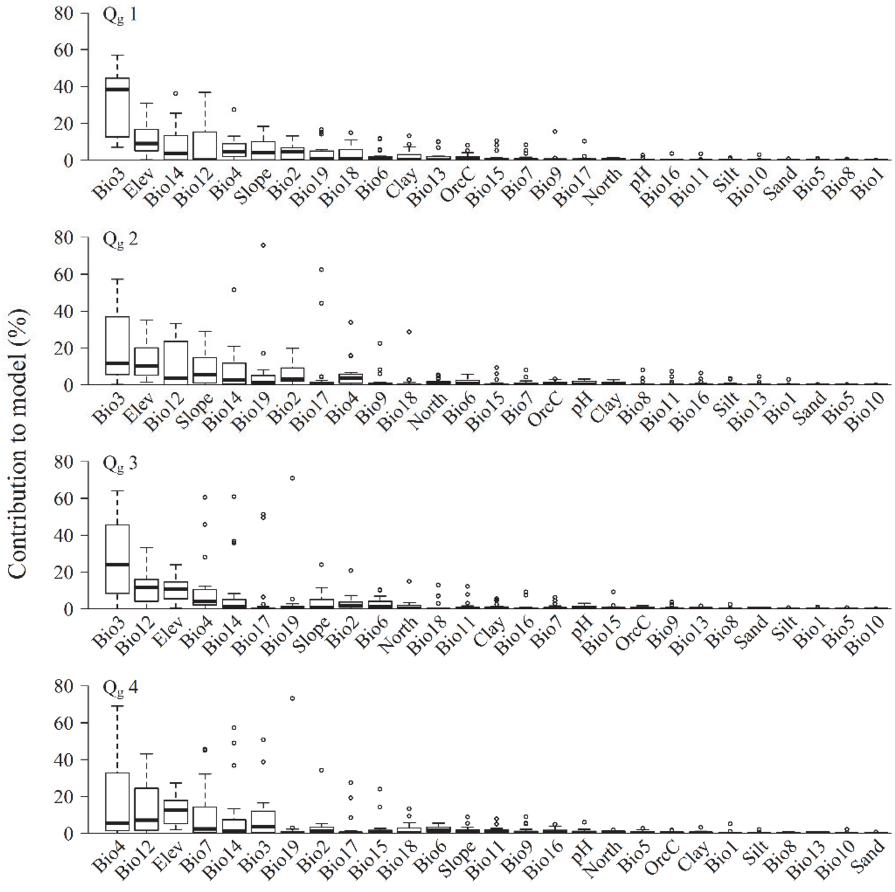


Figure 3.5 Contributions of the 27 environmental variables sorted from highest to lowest across geographical range size groups (Q_g1-Q_g4, see Figure 3.2)

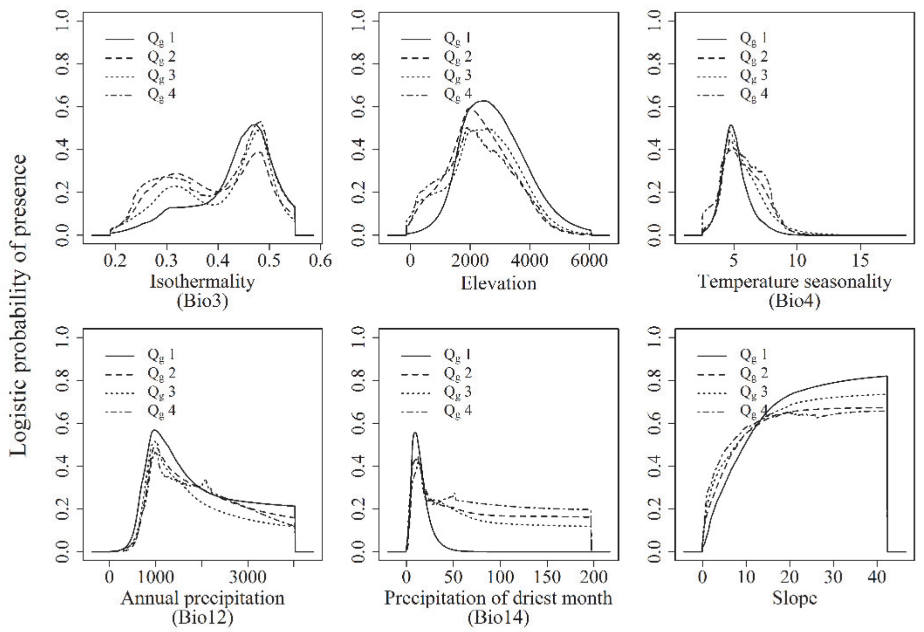


Figure 3.6 Averaged response curves of the four geographical range size groups for the six most important environmental variables based on the full model

3.3.4 Importance of variables across elevational range sizes

For the elevational range size groups (Figure 3.7), isothermality (Bio3) was significantly important (32%) for the middle-ranging species (Q_e2 and Q_e3). Ranked as the third important variable, elevation contributed around 10% for all four groups. Temperature seasonality (Bio4, ~17%) and annual temperature range (Bio7, ~8%) were more important for elevationally wide-ranging species (Q_e4), while precipitation in the driest month (Bio14, ~20%) and in the driest quarter (Bio17, ~14%), and the precipitation of the coldest quarter (Bio19, ~11%) were only important for species with a narrow elevational range (Q_e1).

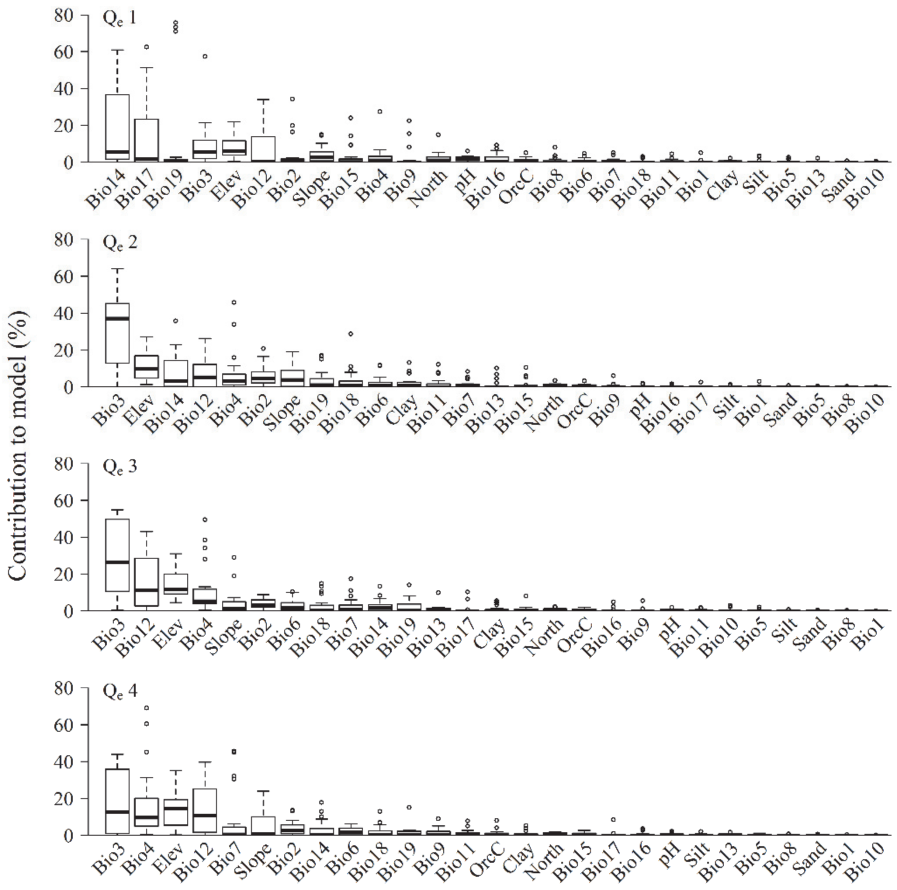


Figure 3.7 Contributions of the 27 environmental variables, sorted from highest to lowest importance, across elevational range size groups (Q_e1-Q_e4, see Figure 3.2)

The responses of the important variables in the prediction for the four elevational range size groups as well as for each species were indicated in Figure 3.8 and Figure 3.S3, respectively. The responses curves showed that the species with elevationally medium- and wide-range (Q_e2, Q_e3 and Q_e4) did not in fact tolerate a wider range of conditions than the narrow-ranging species. In general, narrow-ranging species (Q_e1) showed a shifted pattern compared to the other quartiles. For example, Isothermality (Bio3) played a primary role in all the groups (significantly important for Q_e2 and Q_e3), but the narrow-ranging species were generally found in areas with large variations in diurnal temperature relative to the annual temperature range (i.e. low values [0.2-0.35] of isothermality). Precipitation in the driest month (Bio14) was the most important factor for Q_e1. Narrow-ranging species occurred in areas where precipitation in the driest month (Bio14) was ≥ 20 mm (up to 200 mm), while the other three quartiles occurred in areas with up to 50 mm at most. Q_e1 also occurred in the temperature seasonality (Bio 4) range of 2-10°, while this range shrank to 2-8° for the medium- and wide-ranging groups.

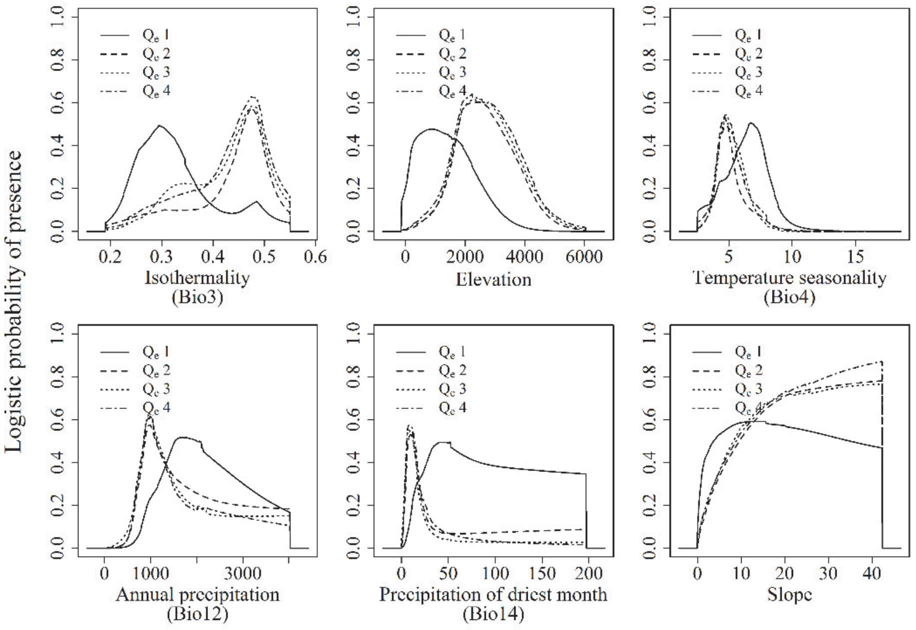


Figure 3.8 Averaged response curves of the four elevational range size groups for the six most important environmental variables based on the full model

3.4 Discussion

3.4.1 Climatic variables are more important as a measure of niche breadth at large spatial extents

Our results support earlier studies which concluded that climatic variables play an important role in shaping plant species' range when they occur over large spatial extents or areas (Kockemann et al., 2009; Thomas, 2010; Morin & Lechowicz, 2013). Given our results show a consistently large importance of isothermality (Bio3) across all groups, and a substantial importance of temperature seasonality (Bio4) for the wide-ranging species, both geographically and elevationally, we would emphasize that climatic variables, and especially seasonal variation, should be included as a measure of the niche breadth that determines species' distributional ranges over large areas. This is in line with Quintero and Wiens (2013) who concluded that seasonal variation explains most of the variation in climatic niche breadths among species.

Isothermality quantifies how much the diurnal (day-to-night) temperatures oscillate relative to the summer-to-winter (seasonal/annual) oscillations. Some biogeographical studies have noted coincidences between geographical range boundaries and temperature isotherms (Calosi et al., 2010). However, isothermality was often overlooked in studies that correlated environmental factors with species' range sizes. This is most probably because isothermality is derived from annual mean diurnal range (Bio2) and annual temperature range (Bio7). It would therefore be excluded if a collinearity analysis was performed before any further analysis. In our study area, isothermality is strongly correlated with annual mean diurnal range (Bio2; r = 0.9) and precipitation seasonality (Bio15; r = 0.86), which, on the one hand, indicates that Bio2 and Bio15 are also important, but they did not exhibit a high importance because Bio3 took their places. On the other hand, it could be because the bioclimatic information in Bio3 is more relevant in explaining the distribution of Rhododendrons. Temperature seasonality (Bio4) is a measure of temperature change during the year. Over a large area, seasonality indicates periodic departures from the climatic optima for organisms, so high seasonality favours species with adaptations to cope with unevenly distributed resources or conditions. In this sense, seasonality could be acting as an environmental filter for species distributional range (Gouveia et al., 2013). Because of the strong correlation between temperature seasonality (Bio4) and temperature annual range (Bio 7), we suspect that temperature annual range is potentially also important, particularly for the wide-ranging species. So climatic variation is considered as a vital determinant for the distribution of alpine and subalpine plant species.

Conversely, although soil properties have been employed as important factors of niche breadth related to variation of geographical range size (Morin & Lechowicz, 2013; Pannek et al., 2013), the minor importance of edaphic variables in the distribution of all range size groups of Rhododendron species seen in our study does not provide any support for this. One possible explanation may lie in the issue of scale. The importance of explanatory variables for species with different range sizes depend both on grain and extent. Different processes determine geographical ranges as the spatial extent of the investigation changes (Baltzer et al., 2007; Slatyer et al., 2013). Climatic variables are the most important in determining species' distribution on continental to global scales, whereas edaphic variables are more important at smaller scales (Pearson & Dawson, 2003; Morin & Chuine, 2006).

The topographic explanatory variables ranked as the second most important set of explanatory variables. Elevation is always among the top five most important variables across range size groups. We therefore infer that a combination of climate variables changing with elevation (Janzen, 1967), and the influence of topography itself (as a barrier to dispersion) might lead to the relative importance of elevation. The moderate to strong correlations we found between topographic and climatic variables (Appendix Figure 3.A1) can partly explain the secondary importance of elevation.

3.4.2 Climatic niche breadth determines variation in geographical range size

We found that the geographically wide-ranging species occurred across a broader range of climatic niche conditions, which suggests that species capable of enduring wide ranges of climate conditions can occupy larger geographical ranges. In other words, our results provide empirical support for the climatic variability hypothesis, which can be considered as a sub-hypothesis of the niche breadth hypothesis for explaining the variation in geographical range size of plant species. However, it is worth noting that a critical assumption in the climatic variability hypothesis is that there is indeed an appropriate gradient (latitudinal, altitudinal or otherwise) in climatic variability (Addo-Bediako et al., 2000). In most cases, geographical range size is an analogue of latitudinal gradients, and climate shows less variation at lower latitudes than higher latitudes within China. Our results therefore support the climatic variability hypothesis. Since this hypothesis was proposed by Stevens (1989) , it has been confirmed by a number of studies. More recent studies have used the term ‘climatic niche breadth’ rather than ‘climatic variability’ to illustrate the ability (range) that can be tolerated by one species (Fisher-Reid et al., 2012; Köster et al., 2013; Arellano et al., 2014). Sheth et al. (2014) showed that climatic niche breadth, which is the range of climatic condition a species occurs in, explained more variation than the niche position, which is a species’ niche relative to the central tendency of climatic conditions in a study region for the geographical range size of monkeyflower species (genus Mimulus). Sheth and Angert (2014) also explained the positive strong relationship between the capacity of a species to cope with climatic variability and its geographical range size from an evolutionary viewpoint. They suggested that a species with a broader climate tolerance may be composed of phenotypically plastic genotypes. This would allow for stronger local adaptations by divergent subpopulations to their individual environments. Such species could also harbour greater genetic variation, allowing for a greater environmental tolerance.

Meanwhile, we have shown that variation in elevational range sizes can be mainly explained by shifts in niche range, rather than by differences in the width of these ranges. Precipitation in the driest month seems to be a crucial factor. Elevationally narrow-ranging species require more rainfall in the driest month than the other range size groups, suggesting that these species are more sensitive to drought conditions than wider-ranging species. A combination of orographically induced increases in precipitation with increasing elevation, and decreasing moisture availability at higher altitudes (due to shallower soils) might help create optimal conditions only at very specific elevations (Allamano et al., 2009; Quintero & Wiens, 2013). In addition, although climatic variability was also proposed to explain the variation of elevational range size (Stevens, 1992), it only applies when the climatic variability increases with elevational range. We thus speculate that there is no linear correlation between climatic niche breadth and elevation range in our study of Rhododendron species in China. However, steep elevation-induced environmental gradients may limit the habitat available for a species and also act as dispersal barriers between similar environment, effectively restricting the range size (Morueta-Holme et al., 2013). In fact, variation of elevational range size has been paid little attention in the past years. This is partly due to the conclusion that variation of elevational range is only an extension of variation of geographical range (Stevens, 1992). In addition, the relative few available studies focused on mountain systems and elevational gradients (see White & Bennett, 2015). More taxa thus need to be tested to confirm if there is a more general pattern to be identified.

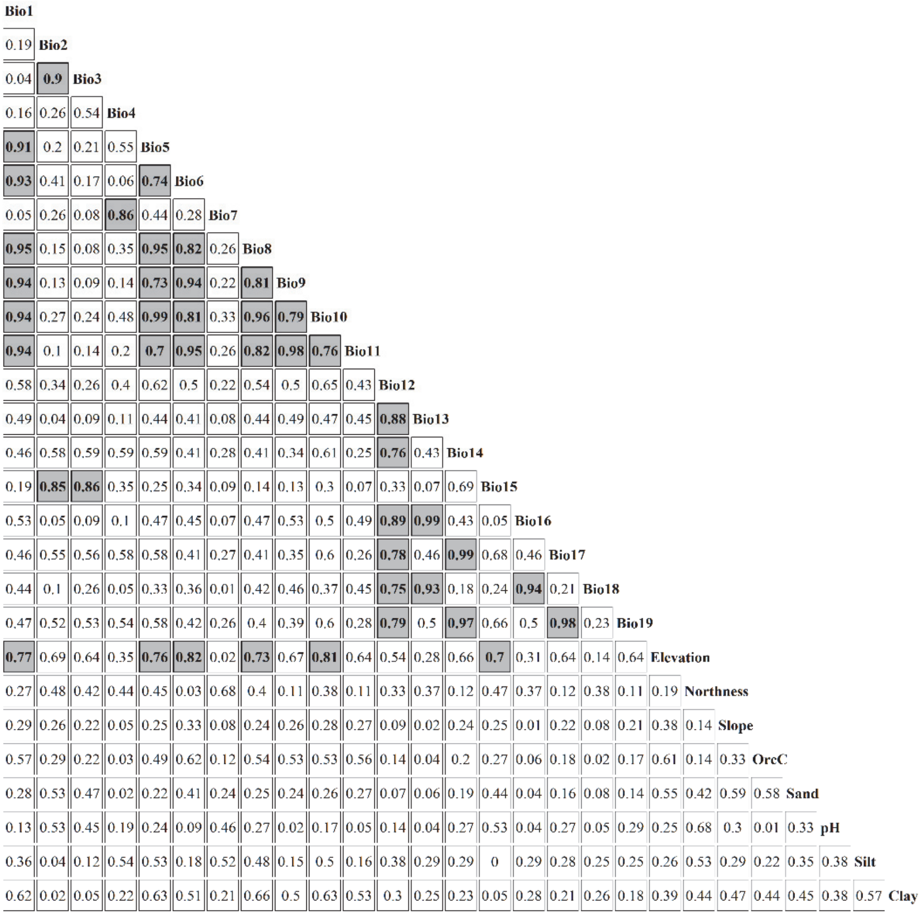
3.4.3 Differences between species with narrow geographical and elevational range sizes

The geographically narrow-ranging species occur where there are small variations in diurnal, seasonal and annual temperatures, and where small amounts of precipitation in the driest month can be expected. The elevationally narrow-ranging species occur where there are large variations in diurnal, seasonal and annual temperatures, and where there is still ample precipitation in the driest month. Possibly it is the elevationally narrow-ranging species that grow on the middle part of a mountain, where precipitation is ample and temperature variability is relatively high. The geographically narrow-ranging species could be mainly restricted to specific valleys where the temperatures are more stable. The very weak correlation between both types of range sizes and the distinctly different niche conditions, where narrow-ranging species of both groups occur, suggests that elevational range size can be seen as a complementary trait to geographical range size, containing different information on the environmental requirements of plants. Therefore, we propose that elevational range size should be considered in assessing extinct risk of alpine and subalpine plant species in face of rapid of environmental change.

3.4.4 Implications of climate change

The high importance of isothermality (Bio3), temperature seasonality (Bio4), and precipitation in the driest month (Bio14) in the fitted models in this study suggests that changes of these three variables in the future would have the most profound effects on the distribution in alpine and subalpine plant species. This would especially be the case for species with narrow tolerance ranges. When we compared the current ranges and projections of two models, HadGEM2-ES and MIROC-ESM (available at: http://www.worldclim.org/cmip5_30s), isothermality was expected to stay constant but temperature seasonality and precipitation in the driest month were expected to decrease over the whole of China until 2070. This will affect both the geographically narrow- ranging species that have small tolerance ranges for these variables, as well as the elevationally narrow-ranging species that require higher amounts of precipitation in the driest months. Geographically and elevationally wide-ranging species may be affected to only a limited extent by these changes.

Appendix



	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19	Elevation	Northness	Slope	OrcC	Sand	pH	Silt
Bio1																										
Bio2	0.19																									
Bio3	0.04	**0.9**																								
Bio4	0.16	0.26	0.54																							
Bio5	**0.91**	0.2	0.21	0.55																						
Bio6	**0.93**	0.41	0.17	0.06	**0.74**																					
Bio7	0.05	0.26	0.08	**0.86**	0.44	0.28																				
Bio8	**0.95**	0.15	0.08	0.35	**0.95**	**0.82**	0.26																			
Bio9	**0.94**	0.13	0.09	0.14	**0.73**	**0.94**	0.22	**0.81**																		
Bio10	**0.94**	0.27	0.24	0.48	**0.99**	**0.81**	0.33	**0.96**	**0.79**																	
Bio11	**0.94**	0.1	0.14	0.2	**0.7**	**0.95**	0.26	**0.82**	**0.98**	**0.76**																
Bio12	0.58	0.34	0.26	0.4	0.62	0.5	0.22	0.54	0.5	0.65	0.43															
Bio13	0.49	0.04	0.09	0.11	0.44	0.41	0.08	0.44	0.49	0.47	0.45	**0.88**														
Bio14	0.46	0.58	0.59	0.59	0.59	0.41	0.28	0.41	0.34	0.61	0.25	**0.76**	0.43													
Bio15	0.19	**0.85**	**0.86**	0.35	0.25	0.34	0.09	0.14	0.13	0.3	0.07	0.33	0.07	0.69												
Bio16	0.53	0.05	0.09	0.1	0.47	0.45	0.07	0.47	0.53	0.5	0.49	**0.89**	**0.99**	0.43	0.05											
Bio17	0.46	0.55	0.56	0.58	0.58	0.41	0.27	0.41	0.35	0.6	0.26	**0.78**	0.46	**0.99**	0.68	0.46										
Bio18	0.44	0.1	0.26	0.05	0.33	0.36	0.01	0.42	0.46	0.37	0.45	**0.75**	**0.93**	0.18	0.24	**0.94**	0.21									
Bio19	0.47	0.52	0.53	0.54	0.58	0.42	0.26	0.4	0.39	0.6	0.28	**0.79**	0.5	**0.97**	0.66	0.5	**0.98**	0.23								
Elevation	**0.77**	0.69	0.64	0.35	**0.76**	**0.82**	0.02	**0.73**	0.67	**0.81**	0.64	0.54	0.28	0.66	**0.7**	0.31	0.64	0.14	0.64							
Northness	0.27	0.48	0.42	0.44	0.45	0.03	0.68	0.4	0.11	0.38	0.11	0.33	0.37	0.12	0.47	0.37	0.12	0.38	0.11	0.19						
Slope	0.29	0.26	0.22	0.05	0.25	0.33	0.08	0.24	0.26	0.28	0.27	0.09	0.02	0.24	0.25	0.01	0.22	0.08	0.21	0.38	0.14					
OrcC	0.57	0.29	0.22	0.03	0.49	0.62	0.12	0.54	0.53	0.53	0.56	0.14	0.04	0.2	0.27	0.06	0.18	0.02	0.17	0.61	0.14	0.33				
Sand	0.28	0.53	0.47	0.02	0.22	0.41	0.24	0.25	0.24	0.26	0.27	0.07	0.06	0.19	0.44	0.04	0.16	0.08	0.14	0.55	0.42	0.59	0.58			
pH	0.13	0.53	0.45	0.19	0.24	0.09	0.46	0.27	0.02	0.17	0.05	0.14	0.04	0.27	0.53	0.04	0.27	0.05	0.29	0.25	0.68	0.3	0.01	0.33		
Silt	0.36	0.04	0.12	0.54	0.53	0.18	0.52	0.48	0.15	0.5	0.16	0.38	0.29	0.29	0	0.29	0.28	0.25	0.25	0.26	0.53	0.29	0.22	0.35	0.38	
Clay	0.62	0.02	0.05	0.22	0.63	0.51	0.21	0.66	0.5	0.63	0.53	0.3	0.25	0.23	0.05	0.28	0.21	0.26	0.18	0.39	0.44	0.47	0.44	0.45	0.38	0.57

Figure 3.A1 Correlation coefficients between variables. All the correlations were significant ($P < 0.05$). Correlations higher than 0.7 are given in bold with a grey background

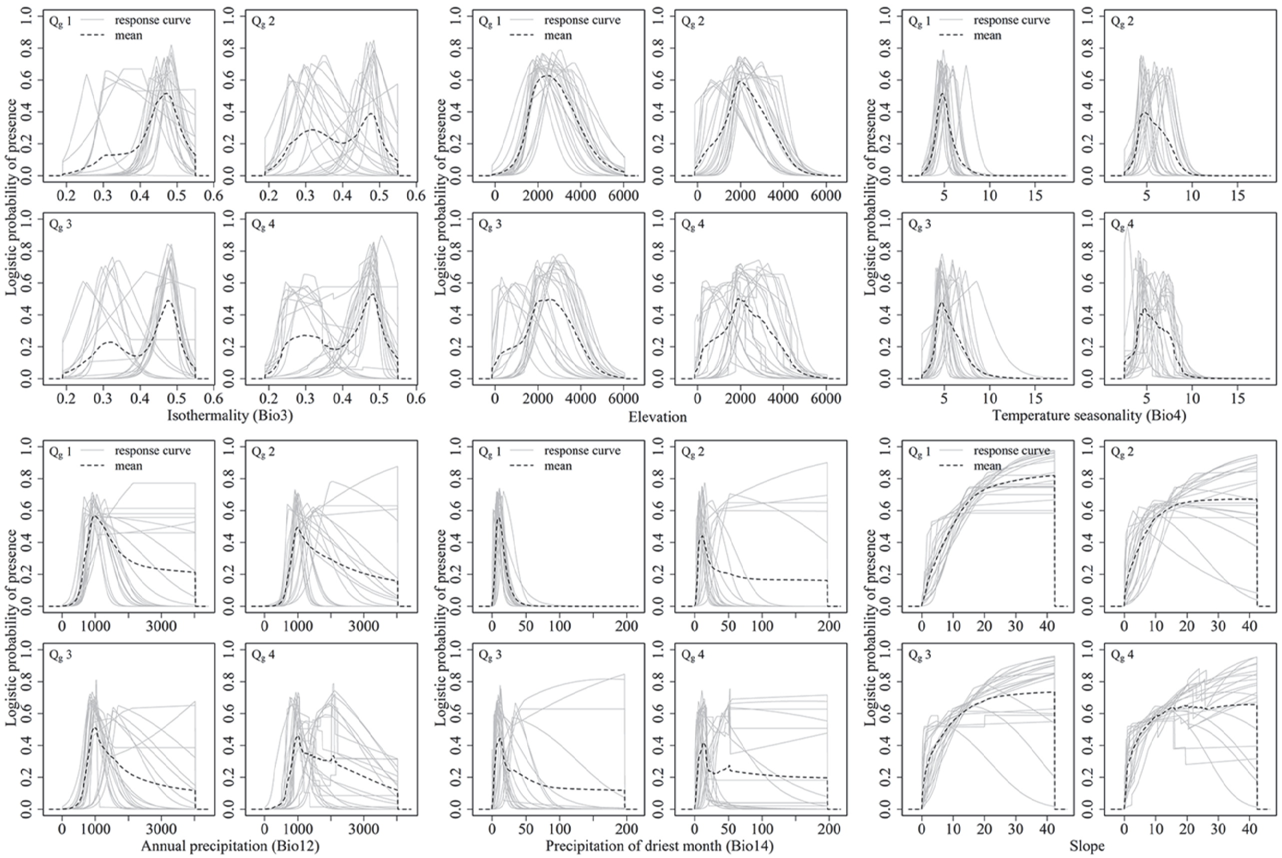


Figure 3.S2 Response curves of each species in the four geographical range size groups

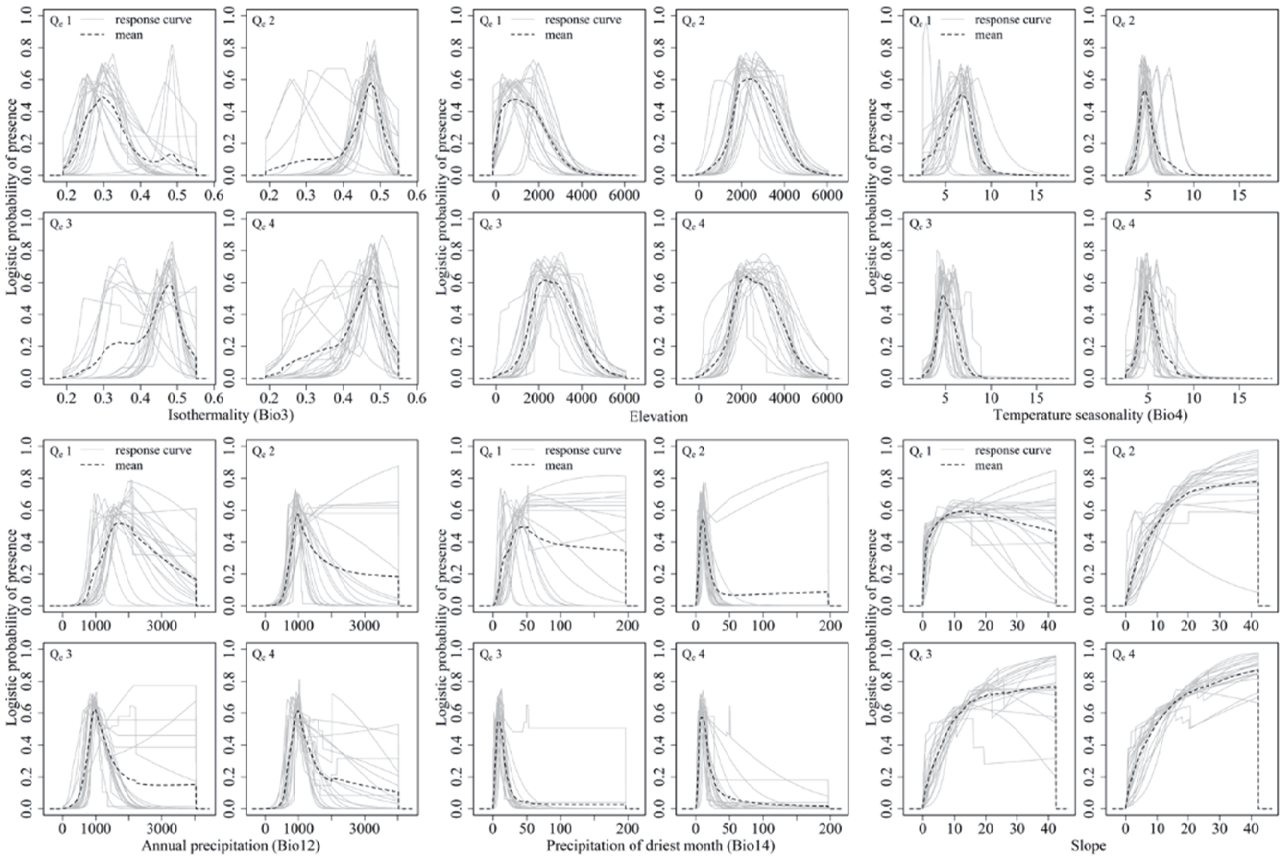


Figure 3.S3 Response curves of each species in the four elevational range size groups

Table 3.A1 Number of samples used for model training/evaluation and AUC/TSS of the full model

Species	Training samples	Test samples	AUC	TSS
R. aganniphum	96	40	0.973	0.914
R. agastum	21	9	0.986	0.968
R. alutaceum	33	14	0.987	0.916
R. ambiguum	27	11	0.989	0.977
R. argyrophyllum	40	17	0.976	0.865
R. augustinii	101	43	0.96	0.841
R. auriculatum	26	11	0.963	0.865
R. bachii	63	27	0.96	0.851
R. brevinerve	28	12	0.981	0.884
R. bureavii	27	11	0.979	0.956
R. calophytum	55	23	0.989	0.954
R. calostrotum	22	9	0.99	0.946
R. cavaleriei	36	15	0.961	0.849
R. championae	59	24	0.963	0.866
R. citriniflorum	28	12	0.988	0.903
R. concinnum	70	30	0.968	0.904
R. coriaceum	21	9	0.997	0.991
R. davidsonianum	35	14	0.962	0.749
R. decorum	212	90	0.97	0.921
R. delavayi	114	48	0.976	0.906
R. discolor	47	20	0.958	0.833
R. eclecteum	35	15	0.995	0.991
R. faberi	29	12	0.991	0.962
R. farrerae	26	10	0.972	0.929
R. floccigerum	33	14	0.952	0.832
R. fortunei	69	29	0.958	0.768
R. fulvum	52	22	0.989	0.96
R. haematodes	42	17	0.995	0.985
R. heliolepis	89	37	0.97	0.935
R. henryi	28	12	0.976	0.935
R. hippophaeoides	42	18	0.978	0.891
R. hypoglaucum	22	9	0.978	0.877

(Continued) Table 3.A1 Number of samples used for model training/evaluation and AUC/TSS of the full model

Species	Training samples	Test samples	AUC	TSS
R. irroratum	92	39	0.981	0.921
R. liliiflorum	26	10	0.972	0.889
R. lukiangense	39	16	0.986	0.954
R. lutescens	55	23	0.979	0.926
R. maculiferum	29	12	0.939	0.81
R. mariae	45	18	0.967	0.877
R. mariesii	147	63	0.926	0.763
R. microphyton	60	25	0.986	0.957
R. molle	31	13	0.927	0.757
R. neriiflorum	31	13	0.979	0.904
R. nivale	62	26	0.958	0.808
R. oreodoxa	48	20	0.959	0.79
R. ovatum	142	60	0.946	0.818
R. pachytrichum	28	11	0.989	0.941
R. phaeochrysum	92	39	0.975	0.891
R. polylepis	33	14	0.992	0.965
R. primuliflorum	53	22	0.973	0.893
R. protistum	21	9	0.998	0.993
R. racemosum	159	67	0.98	0.953
R. rex	75	31	0.983	0.949
R. rivulare	43	18	0.967	0.807
R. roxieanum	46	19	0.975	0.865
R. rubiginosum	103	43	0.98	0.913
R. rupicola	48	20	0.971	0.86
R. saluenense	46	19	0.98	0.911
R. sanguineum	47	20	0.984	0.944
R. scabrifolium	61	26	0.992	0.985
R. selense	45	19	0.99	0.948
R. seniavinii	30	12	0.962	0.878
R. siderophyllum	73	31	0.953	0.821
R. simiarum	63	27	0.965	0.836
R. simsii	316	135	0.913	0.746

(Continued) Table 3.A1 Number of samples used for model training/evaluation and AUC/TSS of the full model

Species	Training samples	Test samples	AUC	TSS
R. sinonuttallii	25	10	0.998	0.991
R. sperabiloides	26	10	0.991	0.948
R. spiciferum	62	26	0.988	0.957
R. spinuliferum	98	42	0.987	0.934
R. stamineum	109	46	0.951	0.781
R. strigillosum	27	11	0.991	0.969
R. sutchuenense	29	12	0.97	0.893
R. tanastylum	36	15	0.983	0.914
R. tatsiense	56	24	0.991	0.952
R. telmateium	25	10	0.994	0.984
R. traillianum	35	15	0.995	0.988
R. trichostomum	41	17	0.97	0.913
R. triflorum	26	11	0.996	0.985
R. uvariifolium	63	27	0.99	0.979
R. vernicosum	70	29	0.974	0.909
R. wardii	58	24	0.988	0.944

Chapter 4

Rhododendron diversity patterns and priority conservation areas in China

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This chapter is based on: Yu, F.Y., Skidmore, A.K., Wang, T.J., Huang, J.H., Ma, K.P., and Groen, T.A. 2017. Rhododendron diversity patterns and priority conservation areas in China. *Diversity and Distributions* (in press).

Abstract

Rhododendrons form a major component of the montane ecosystem in the Himalayan subalpine and alpine zone. However, Rhododendrons is one of the most neglected groups of plants in terms of scientific inquiry. Understanding the spatial distribution pattern and prioritising conservation areas at national level are required to effectively monitor and conserve Rhododendrons. We predicted the distribution of 212 Rhododendron species applying a spatially explicit species assemblage modelling (SESAM) framework on a 10×10 km grid across China. We evaluated Rhododendron diversity based on species richness, β-diversity, and weighted endemism (also known as range size rarity), and then identified hotspots formed by the top 1%, 5%, 25%, and 50% of record-containing grid cells for each diversity metric separately and for the combination of the three diversity metrics. We determined the priority conservation areas for Rhododendrons by overlaying the hotspots with the map of the 2139 nature reserves existing in China, and calculated the percentage of hotspots that is protected. The same analysis was also applied to threatened Rhododendron species. Rhododendron species richness, β-diversity and weighted endemism decrease within China from the southwest to the northeast, mainly along mountain ranges. In total, 12 general hotspots for Rhododendron species are detected, covering 1.4% of China's land area. Five separately discerned hotspots (i.e. southern Chongqing, south-eastern Tibet, north-western Yunnan, south-western Sichuan, and northern Guangdong) comprising threatened Rhododendron species largely overlap (86.3%) with the general hotspots, and form priority areas for conservation. However, the remaining hotspots, especially southern Zhejiang and north-eastern Guizhou, should not be overlooked. To the best of our knowledge this is the first comprehensive study of Rhododendron diversity patterns across the whole of China in terms of species richness, β-diversity, and weighted endemism, thereby offering a sound basis for the conservation of Rhododendrons in China. We demonstrate that as much attention should be paid to the small hotspots in south-western and south-eastern China, as to the largest hotspot (i.e. Mt Hengduan), to achieve conservation of

Rhododendrons. We suggest that these three diversity metrics plus an appropriate level of congruence and the list of threatened Rhododendron species are jointly considered to define hotspots and select priority conservation areas.

4.1 Introduction

The natural occurrence of the genus Rhododendrons, containing about 1,025 species of trees, herbs, shrubs, and even epiphytes, is concentrated in south-eastern Asia (Gibbs et al., 2011). In addition Rhododendrons are globally cultivated as ornamental plants (Chamberlain et al. 1996, Ma et al. 2014). As the largest genus in the family of Ericaceae, Rhododendrons form a major component of the montane ecosystem in the Himalayan subalpine and alpine zone, which has been identified as one of the most fragile ecosystems in the world (Kumar, 2012). Rhododendrons also play a vital role in slope stabilization and watershed protection in the Himalayas, where many of Asia's major rivers originate. Nevertheless, Rhododendrons form one of the most neglected groups of plants in terms of scientific inquiry (Kumar, 2012). China has approximately 571 Rhododendron species, accounting for nearly 55% of the world's total (Ma et al., 2014). Rhododendrons occur in most of China's provinces (except Xinjiang and Ningxia), and are found across 60% of China's land area. Over 74% of the Rhododendrons occurring in China are endemic species (Wu, 2005; Ma et al., 2014). Rhododendrons exhibit a great diversity and are often prized for their horticultural value, but our knowledge of their spatial distribution remains limited (Zhang et al., 2004). It is important to note climate change, rapid population growth, and the ever-increasing demands for natural resources have collectively placed considerable pressure on Rhododendrons in their natural habitat (Kumar, 2012; Ma et al., 2014). Therefore, understanding the spatial distribution pattern and prioritising conservation areas at national level are required to effectively monitor and conserve Rhododendrons.

Biodiversity hotspot and gap analyses are standard approaches to select priority areas for species conservation. Hotspots are defined as either the top sites in terms of species diversity or as the sites where most threatened or most endemic species occur (Myers et al., 2000). Protected areas (PAs) which is the main tool for preventing biodiversity loss are generally designed based on the locations of hotpots (Chen et al., 2017; Sánchez de Dios et al., 2017).

Previous studies adopted different metrics to quantify species diversity and hotspots, the most commonly used metric being species richness. In addition, weighted endemism, which measures the range size rarity of species (Linder, 2001), is of interest to macro-ecologists and conservationists, and is emerging as a popular approach in conservation biology (Herkt et al., 2016; Huang et al., 2016). Weighted endemism divides the region of interest into cells of equal area and counts the species present per cell, weighting each species by the inverse of its distribution range. This weighting corresponds to the range size of each species (i.e. species with small ranges are assigned high weights, whilst species with larger ranges are assigned progressively lower weights). Thus a higher weighted endemism value generally indicates more narrow-ranging species occurring in a cell (Laffan & Crisp, 2003; Rosauer et al., 2009). Furthermore, as a key component and proxy for biological diversity, species spatial turnover (β-diversity), which measures the extent of change in community composition, can provide complementary information about the distribution of rare, endemic species as well as species richness for assessing optimal reserve locations (Marsh et al., 2010). To date, however, β-diversity has often been overlooked in conservation planning. Few studies have included β-diversity for the identification of hotspots and priority areas (Condit et al., 2002; Wiersma & Urban, 2005).

With the ongoing digitization of natural history museum collections and herbarium specimens, more data are becoming available, providing the opportunity to analyse species occurrence data in support of conservation efforts (Graham et al., 2004). Conservationists increasingly rely on spatial predictive models of biodiversity to support decision making (Franklin, 2010). Yet, records of observed species occurrence typically provide information for only a subset of sites occupied by a species. Data are often scattered and do not supply complete spatial coverage (Mateo et al., 2013). Modelling species distribution and diversity at community level has therefore become a useful tool to depict complete spatial coverage and to select priority areas for conservation (Ferrier & Guisan, 2006). Currently, two approaches are used: macroecological modelling (MEM) and stacking species distribution modelling (SSDM), both of which are built on distinct theoretical paradigms and have been used to model species diversity. MEM, which is the traditional approach of 'assemble first, predict later', tends to predict species richness more accurately than SSDM, but loses species composition information (Dubuis et al., 2011). SSDM, known as 'predict first, assemble later', tends to over-predict species richness, but does retain information on species composition. Previous studies compared MEM and SSDM and suggested that the two approaches have complementary strengths and that they could be used in combination to predict species richness and composition more accurately (Dubuis et al., 2011; Distler et al., 2015). By applying successive filters to the initial species source pool, and combining different modelling approaches and rules, Guisan and Rahbek (2011) proposed a framework: SESAM (spatially explicit species assemblage modelling). This framework integrates SSDM and MEM and has been proved to produce more realistic predictions of species richness and composition than when only using SSDM or MEM separately for plant species and insect communities (D'Amen et al., 2015b; D'Amen et al., 2015a).

In this study, we aim to use the SESAM framework in combination with gap analyses to (1) predict spatial patterns of species richness, β-diversity, and weighted endemism for the genus Rhododendron in China, (2) detect Rhododendron diversity hotspots in China, and (3) identify both gaps and priority areas for the conservation of Rhododendrons in China.

4.2 Methods

4.2.1 Species data

China forms the study area. Records on Rhododendron presence were collected from seven Chinese herbaria and botanical museums (for more details, see Yu et al., 2015). Since high locational accuracy is required for studying plant species distribution, all records presenting only a general description of the location (e.g. mentioning only a county or a mountain) were excluded. Our resulting dataset, covering 406 species, comprises 13,126 geo-referenced records, with each record having a spatial uncertainty of less than 1 km. We chose a grid cell of 10×10 km to model Rhododendron diversity as we attempt to provide as much detail as possible about the spatial patterns of Rhododendron diversity for conservation planning in order to efficiently allocate scarce resources. A grid cell of 10×10 km matches the input data used in this study (see the following section for details). Only species with more than 10 occurrences in a 10×10 km grid cell were retained for further analysis. This approach narrowed the dataset down to 212 species with 9,360 occurrence records. The geographic coordinates of each record were projected onto an Albers equal-area conic conformal coordinate system to avoid the latitudinal biases of geographic coordinate systems (for the distribution map, see Figure 4.1). We are aware that the sample distribution may influence the output of the distribution modelling (Phillips et al., 2009; Merow et al., 2014). But after an initial test involving the manipulation of the background data, and recognising the long term and intensive data collection efforts by the various herbaria, we consider sampling bias to be unlikely.

4.2.2 Environmental variables

We selected a comprehensive set of environmental variables that were considered to be the main factors influencing the distribution of plant species (Körner, 1999; Dirnbock et al., 2003). To deal with collinearity, we only considered variables with a variance inflation factor (VIF) less than 8. The climatic variables used in this study were: isothermality (the ratio of the mean diurnal temperature range to the annual temperature range, indicating whether daily or seasonal temperature fluctuations are more dominant), temperature seasonality, annual precipitation, and precipitation of driest month, all obtained from the WorldClim database (1950-2000) at a resolution of 5 arc minutes (Hijmans et al., 2005). As measures of habitat heterogeneity, we used elevation range and solar radiation, which were derived from a digital elevation model (USGS GTOPO 30 https://lta.cr.usgs.gov/GTOPO30) with a resolution of 30 arc seconds. In addition, normalized difference vegetation index (NDVI) and potential evapotranspiration (PET), which have both proved useful in predicting plant species distribution and richness (Williams et al., 2009; Cramer & Verboom, 2017), were also utilized. The NDVI data (8 km resolution) was derived from the third generation Global Inventory Modelling and Mapping Studies (GIMMS 3g) product (http://glam1.gsfc.nasa.gov/), and averaged annually over the years 1982 to 2003. The PET data (at 30 arc seconds) were derived from the Consortium for Spatial Information (http://www.cgiar-csi.org/data/global-aridity-and-pet-database). The environmental layers were re-projected into the same Albers equal-area conic conformal coordinate system as the species data using R 3.1.3 (R Core Team, 2015) and aggregated to 10 km grid cells.

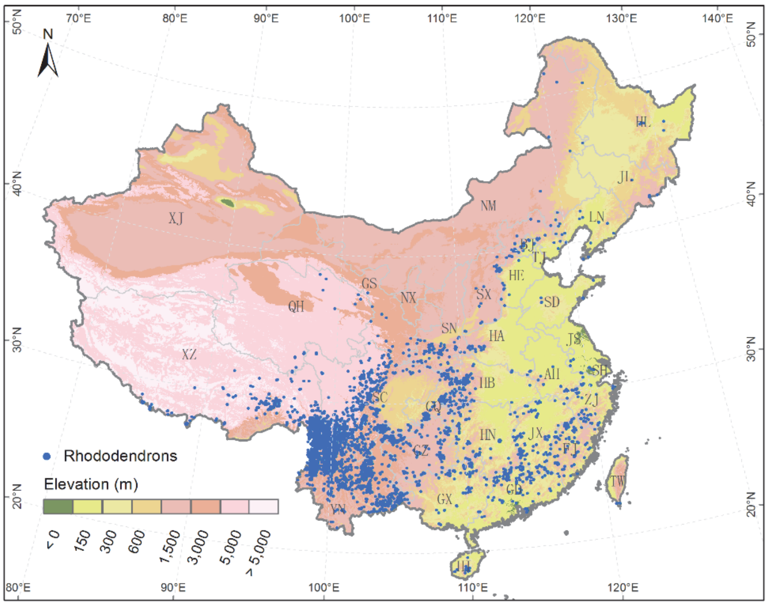


Figure 4.1 Spatial distribution of georeferenced Rhododendron occurrences in China. Abbreviation of province names: BJ Beijing, TJ Tianjin, HE Hebei, SX Shanxi, NM Inner Mongolia, LN Liaoning, JL Jilin, HL Heilongjiang, SH Shanghai, JS Jiangsu, ZJ Zhejiang, AH Anhui, FJ Fujian, JX Jiangxi, SD Shandong, HA Henan, HB Hubei, HN Hunan, GD Guangdong, GX Guangxi, HI Hainan, CQ Chongqing, SC Sichuan, GZ Guizhou, YN Yunnan, XZ Tibet, SN Shaanxi, GS Gansu, QH Qinghai, NX Ningxia, XJ Xinjiang, TW Taiwan.

4.2.3 Spatially explicit species assemblage modelling (SESAM)

Following the method proposed by Guisan and Rahbek (2011), we used four steps and two evaluation indices in our implementation of SESAM.

Step 1 - Species pool: the species pool was defined based on the most frequently occurring Rhododendron species (212 species) in our study area (criteria see above).

Step 2 - Habitat suitability modelling (SSDM): this step used a species distribution model (SDM) to model the suitability of the habitat for the 212 Rhododendron species. The SSDM was built in three stages: (1) each species was modelled individually, using boosted regression trees (BRT) with the package Biomod2 in R (for detailed information about BRT, see Appendix Table 4.A1 in Supporting Information), while each model was fitted using 70% of the observed data, and evaluated by means of the area under the curve (AUC, Fielding and Bell, 1997), true skill statistic (TSS, Allouche et al. 2006) and the Kappa of the remaining 30% of the data. Pseudo-absence data were generated by selecting a 10-fold of random locations compared to the presence data, and every model was repeated three times. (2) each SDM prediction was converted from a continuous suitability map to a presence/absence binary map, based on the criterion of 'maximum sensitivity plus specificity', a threshold that has been shown to produce reliable predictions (Liu et al., 2013); (3) these binary maps were summed to build the richness model SSDMbs.

Step 3 – Macro-ecological constraints: this step limits the number of species that can theoretically co-occur in a given unit. The Macro-ecological model was implemented in two stages: (1) observed species richness of Rhododendrons was calculated as the total number of species in each geographical unit (grid cell, 10×10 km); (2) predicted species richness of Rhododendrons was then modelled with a BRT using the same environmental variables as used in the SSDM.

Step 4 - Integration of ecological assembly rules: this step determines which species will be able to coexist in each unit, constrained by the maximum value of species richness modelled in step 3. Which species were included in a grid cell was determined by the 'probability ranking rule', which assumes that species with a higher probability of occurrence (i.e. habitat suitability) are more competitive. This rule has been shown to significantly improve the prediction of community richness and composition compared to the alternative 'trait range rule', which includes vegetative height, specific leaf area and seed mass (D'Amen et al., 2015b). Probabilities obtained from the SDM calculations (step 2) were used in the implementation of the probability ranking rule. Because the ratio of presence and pseudo-absence was kept constant across species, the calculated relative probabilities can be compared between species.

4.2.4 Geographical pattern of species richness, β-diversity and weighted endemism

Rhododendron species richness was determined by the total number of species in each geographical unit. Many indices have been used to calculate β-diversity (Tuomisto, 2010). We used Simpson’s beta (β_{sim}, equation 4.1) index, which corrects for differences in species richness between sites (Joger et al., 2014; Zhang et al., 2016). The pattern of β-diversity was estimated using a moving-window method (Lennon et al., 2011). Based on previous β-diversity studies in China (Wang et al., 2012a), we set the window size at $r = 50$ km. To avoid a possible bias in β-diversity estimates near the border, grid cells covered by less than half of the moving window were excluded. In order to assess the β-diversity pattern at grid scale, we calculated β-diversity for each cell as the mean of the dissimilarity values between this focal cell and each of its adjacent cells.

$$\beta_{\mathrm{sim}_{ij}} = 1 - \frac{\mathrm{A}}{\mathrm{A}+\min(\mathrm{B},\mathrm{C})} \tag{4.1}$$

where A is the number of species found in both cells *i*, and *j*; B is the number of unique species in cell *i*; and C is the number of unique species in cell *j*. The range of β_{sim} runs from 0 to 1, with 1 denoting no species in common between two grid cells (complete dissimilarity), and 0 denoting that two grid cells contain identical species (no dissimilarity). Weighted endemism was calculated by first weighting the presence cells of each species by the inverse of its predicted range size (frequency of occurrences in 10×10 km grids), and then calculating the sum of these scores cell by cell (Williams et al., 1996; Herkt et al., 2016, equation 4.2).

$$\text{Weighted endemism} = \sum_{\{t \in T\}} \frac{1}{R_t} \tag{4.2}$$

where t is a species in {T}, {T} is a set of species found in the study area, and R_t is the range size of species t. For consistency, the patterns of species richness and weighted endemism were also generated with a moving window (r = 50 km). All the spatial analyses were conducted using Biodiverse 1.1 (Laffan et al., 2010).

4.2.5 Model evaluation

Species richness, β-diversity, and weighted endemism predicted from SESAM were compared with the observed values using the Spearman rank correlation. To evaluate the species composition output of SESAM, a confusion matrix was used in which all species were classified into either true positive (TP), true negative (TN), false positive (FP), or false negative (FN) for every grid cell, with the total number of species (SP) as defined in step 1. Next, the assemble prediction success (see equation 4.3) and Sørensen index (see equation 4.4) were calculated for each grid cell, based on this matrix.

$$\text{Prediction success} = \frac{\text{TP}+\text{TN}}{\text{SP}} \tag{4.3}$$

$$\text{Sørensen index} = \frac{2\text{TP}}{2\text{TP}+\text{FN}+\text{FP}} \tag{4.4}$$

4.2.6 Identification of Rhododendron diversity hotspots

Various criteria have been used to quantify biodiversity hotspots in previous studies, for example, top 5% of record-containing grid cells (Prendergast et al., 1993), 0.5% of all plant species world-wide (Myers et al., 2000), top 2.5% of grid cells regarding species richness (Orme et al., 2005), and 5% of total land area with highest biodiversity (Huang et al., 2016). In this study, given that we were evaluating a single genus with three diversity metrics and a grid cell of 10×10 km, the above criteria may not be suitable as the concept was developed for multiple genera and coarser grid cells (Zhao et al., 2016; Pardo et al., 2017). Therefore, we identified hotspots by considering the top 1%, 5%, 25%, and 50% of record-containing 10 km cells regarding species richness, β-diversity, and weighted endemism separately, as well as jointly (i.e. spatial congruence, quantified by counting the cells that belong to hotspots of species richness, β-diversity and weighted endemism at the same time).

4.2.7 Analysis of the conservation gaps

The conservation gap areas were identified by overlapping the three metrics with the distribution of Chinese nature reserves (Figure 4.2). To quantify Rhododendron’s conservation status, we calculated the proportion of hotspots protected by nature reserves relative to the total area of hotspots, based on different levels (the top 1%, 5%, 25%, and 50%) of diversity for defining the hotspots. Of the 212 Rhododendron species, 43 species are 'threatened' species as classified under the IUCN Red List Categories of Critically Endangered, Endangered, and Vulnerable (IUCN, 2001; Gibbs et al., 2011). Given the high conservation value of threatened species, we repeated the calculations for the threatened Rhododendron species. This procedure was implemented in ArcGIS 10.2 (ESRI Inc., Redwoods, USA) and R 3.1.3 (R Core Team, 2015).

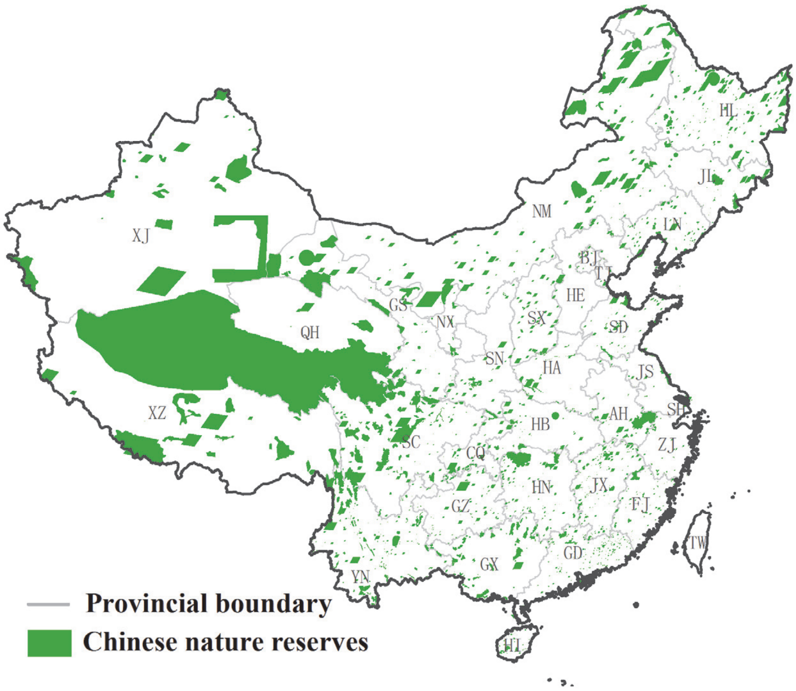
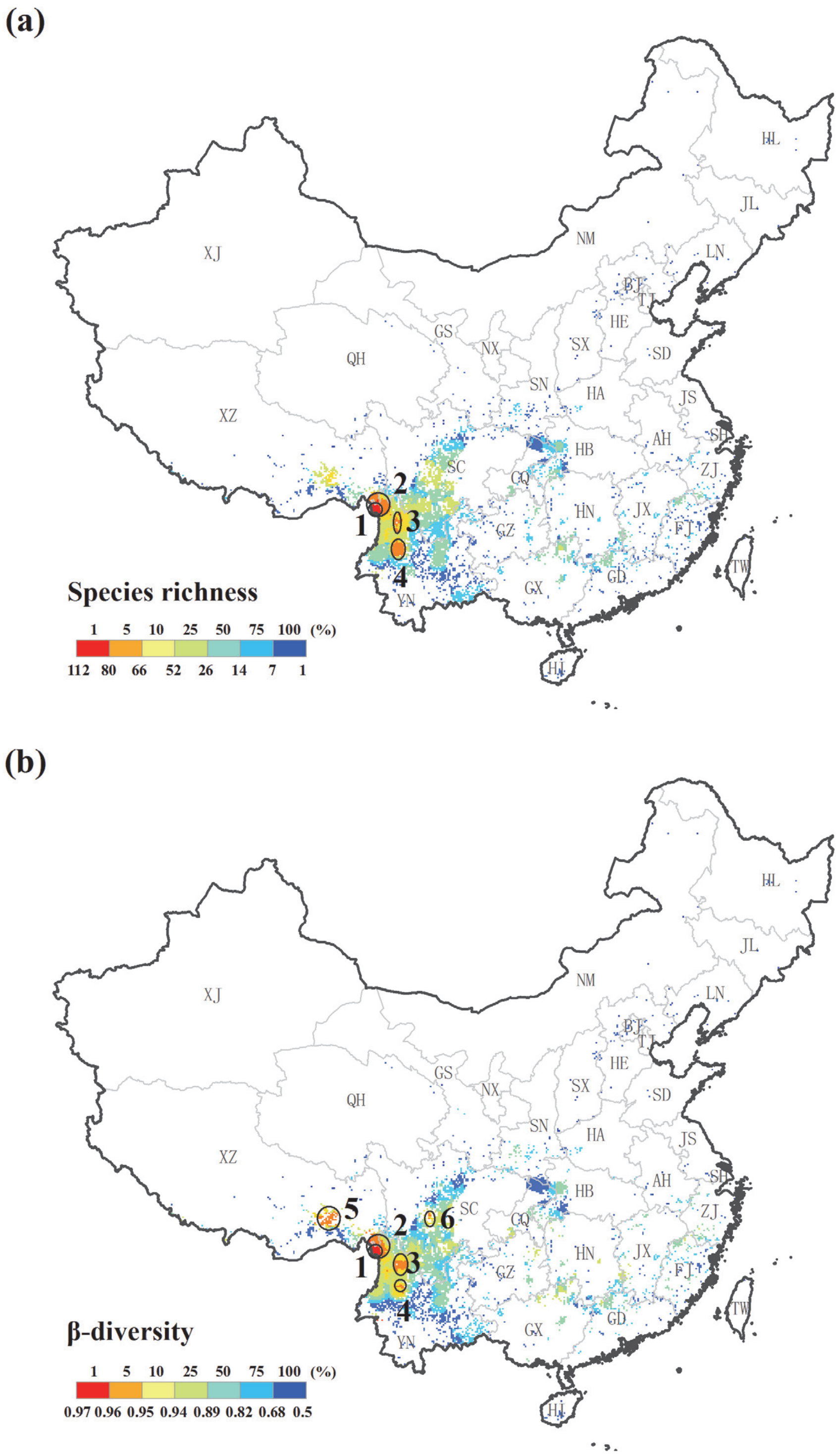


Figure 4.2 Geographic distribution of Chinese nature reserves. Abbreviation of province names see Figure 4.1

4.3 Results

4.3.1 Distribution patterns of Rhododendron diversity

The individual SDMs that were integrated in the SESAM have high AUC (0.98 ± 0.01), TSS (0.94 ± 0.03), and Kappa (0.76 ± 0.05) scores. The correlation between the three predicted diversity metrics, (i.e. species richness, β-diversity, and weighted endemism) and the observed ones is 0.96, 0.85, and 0.71, respectively ($p < 0.05$, Appendix Figure 4.A1). The two composite prediction indices vary from 0.6 to 0.9 for the prediction success, from 0.1 to 0.9 for the Sørensen index, while rising across all grid cells (Appendix Figure 4.S2).


(a)
XJ
QH
XZ
GS
NX
NM
HL
JL
LN
BJ
TJ
HE
SX
SD
SN
HA
JS
AH
SH
HB
ZJ
SC
CQ
HN
JX
FJ
GZ
TW
GD
GX
YN
HI
1
2
3
4
Species richness
1 5 10 25 50 75 100 (%)
112 80 66 52 26 14 7 1
(b)
XJ
QH
XZ
GS
NX
NM
HL
JL
LN
BJ
TJ
HE
SX
SD
SN
HA
JS
AH
SH
HB
ZJ
SC
CQ
HN
JX
FJ
GZ
TW
GD
GX
YN
HI
1
2
3
4
5
6
β-diversity
1 5 10 25 50 75 100 (%)
0.97 0.96 0.95 0.94 0.89 0.82 0.68 0.5

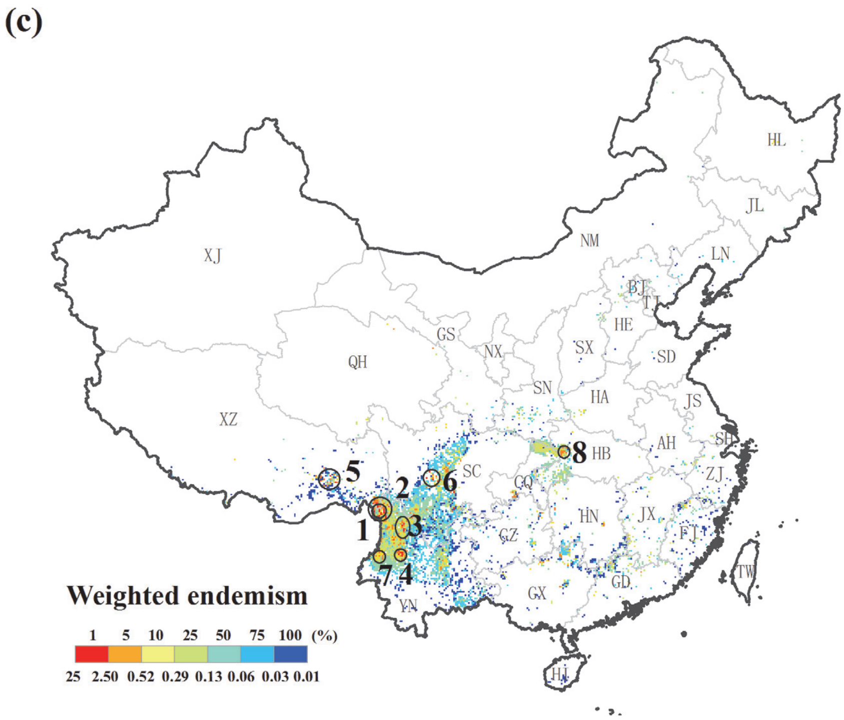
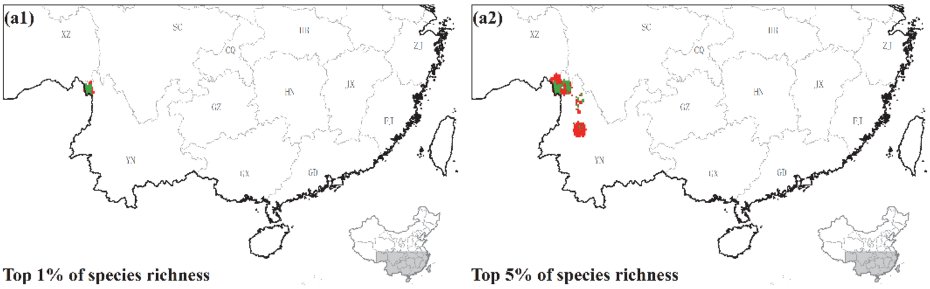


Figure 4.3 Predicted species richness (a), β-diversity (b), and weighted endemism (c) patterns of total Rhododendron species in China. 1. Gongshan (YN) 2. Deqin (YN) 3. Lijiang (YN) 4. Dali (YN) 5. Motuo (XZ) 6. Luding (SC) 7. Tengchong (YN) 8. Badong (HB)

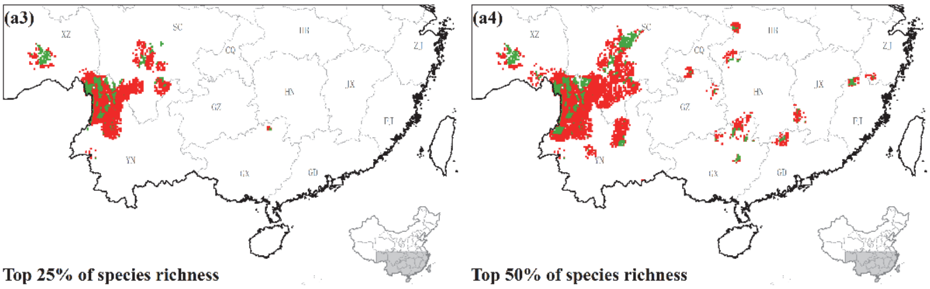
Overall, Rhododendron species richness, β-diversity, and weighted endemism (Figure 4.3a, 4.3b, and 4.3c) display a similar trend across China, decreasing from the southwest (Mt Hengduan) to the northeast (Mt Daxinganling), mainly along the mountain ranges. The highest species richness (> 80), β-diversity (> 0.96) and weighted endemism (> 2.5) are all located in southwestern China (i.e. north-western Yunnan), while the large area in north-eastern China exhibits the lowest diversity (species richness < 7, β-diversity < 0.68, and weighted endemism < 0.03). In the northwest, especially in Xinjiang and Ningxia province, Rhododendron is not expected to occur at all.

4.3.2 Distribution patterns of Rhododendron hotspots



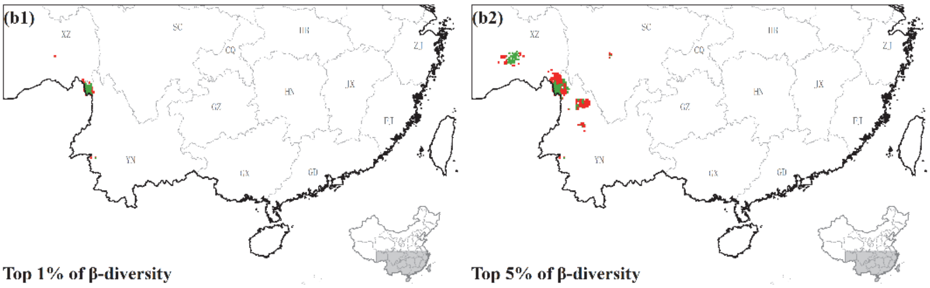
Top 1% of species richness

Top 5% of species richness



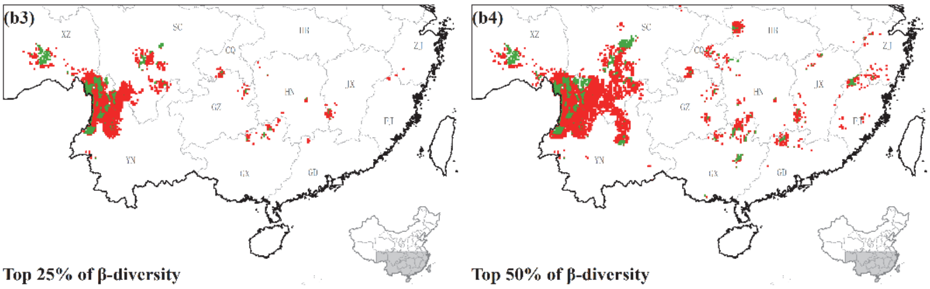
Top 25% of species richness

Top 50% of species richness



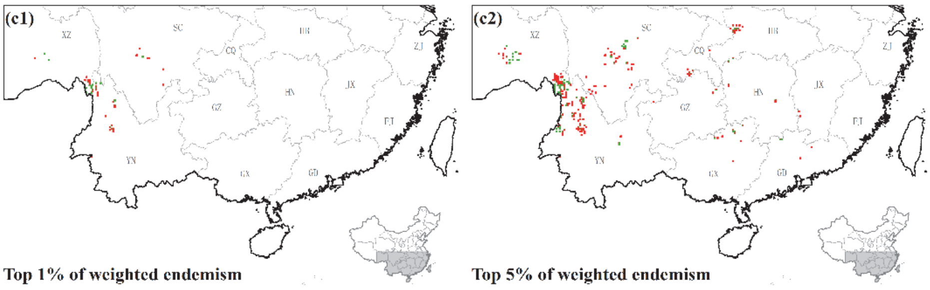
Top 1% of β-diversity

Top 5% of β-diversity



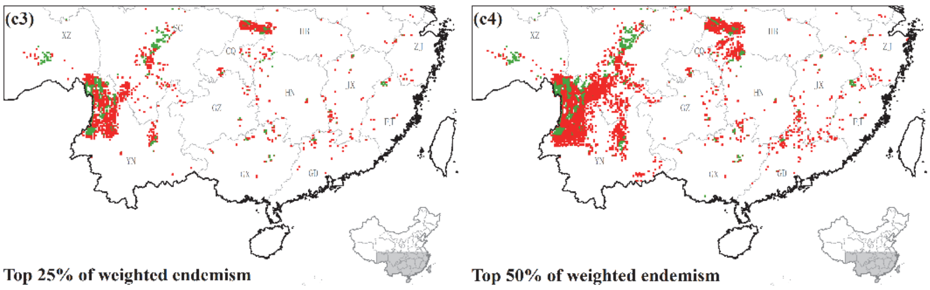
Top 25% of β-diversity

Top 50% of β-diversity



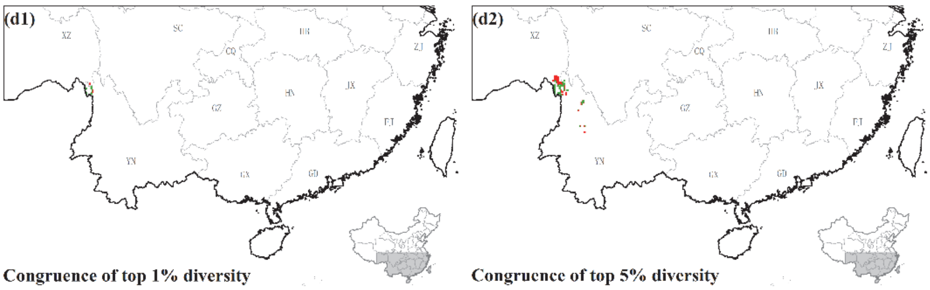
Top 1% of weighted endemism

Top 5% of weighted endemism



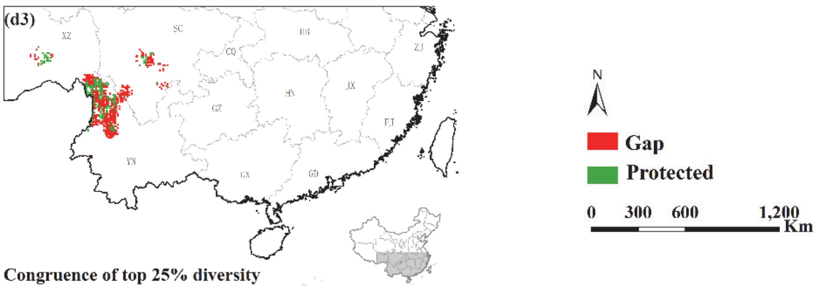
Top 25% of weighted endemism

Top 50% of weighted endemism



Congruence of top 1% diversity

Congruence of top 5% diversity



Congruence of top 25% diversity

Figure 4.4 Protected and gap areas of Rhododendrons at the top 1%, 5%, 25%, and 50% of Rhododendron occurring grid cells. a: species richness, b: β-diversity, c: weighted endemism, d: spatial congruence of a, b, and c

When defining the top 1% of grid cells as hotspots, the hotspots identified by the three diversity metrics, separate (circle 1 in Figure 4.3a, 4.3b, and 4.3c, also see Figure 4.4a1, 4.4b1, and 4.4c1) as well as combined (Figure 4.4d1), are all concentrated in Gongshan County (north-western Yunnan). When the hotspot defining level is expanded to the top 5% of grid cells, the hotspots of species richness include three more patches (i.e. Deqin, Lijiang, and Dali) in north-western Yunnan (circle 2, 3, and 4 in Figure 4.3a, and see also 4.4a2), while another two more locations (i.e. Motuo and Luding, circle 5 and 6 in Figure 4.3b, and see also 4.4b2) are detected using the β-diversity metric. Hotspots of weighted endemism are distributed sporadically in north-western Yunnan, south-eastern Tibet, south-western Sichuan, and also a small patch in western Hubei (Figure 4.3c, and see also 4.4c2). But the congruent hotspots are only found in north-western Yunnan (Figure 4.4d2). When defining the top 25% grid cells as hotspots, south-eastern Tibet and south-western Sichuan emerge as species rich (Figure 4.4a3), while more spots, including southern Chongqing, south-western Jiangxi and northern Guizhou, are detected by β-diversity (Figure 4.4b3). North-western Chongqing (Mt Daba) is a relatively large hotspot detected by weighted endemism (Figure 4.4c3), but the congruent hotspots are mainly at Mt Hengduan and in south-western Sichuan (Figure 4.4d3). When defining the top 50% grid cells as hotspots, more hotspots emerge in south-eastern China (Figure 4.4a4, 4.4b4, and 4.4c4). The congruent hotspots of the three metrics then cover about 133,200 km^2, which accounts for 1.4% of the total land area of China. Meanwhile, the congruent hotspots account for 56.4% of the area defined by the three metrics (Figure 4.5a), and the difference in overlap between these three metrics is largest at this level (Figure 4.5b), which indicates that the most unique hotspots based on either species richness, β-diversity, or weighted endemism can be found at the 50% level. Therefore, we consider the spatial congruence (common area) of the richest 50% grid cells of three metrics as the ideal threshold for defining Rhododendrons hotspots. In total, 12 hotspots are identified (Figure 4.6), which are: (1) southern Chongqing (Mt Jinfo), (2) south-eastern Tibet, (3) Mt Hengduan (Yunnan) and north-eastern Yunnan, (4) south-western Sichuan (Mt

Shaluli, Mt Daxue and Mt Qionglai), (5) northern Guangdong (Mt Danxia), (6) southern Zhejiang, (7) north-eastern Guizhou (Mt Fanjing), (8) western Hubei (Mt Daba), (9) south-eastern Jiangxi, (10) south-western Hubei and northern Hunan, (11) northern Guangxi (Mt Maoer and Mt Yuanbao), and (12) northern Fujian.

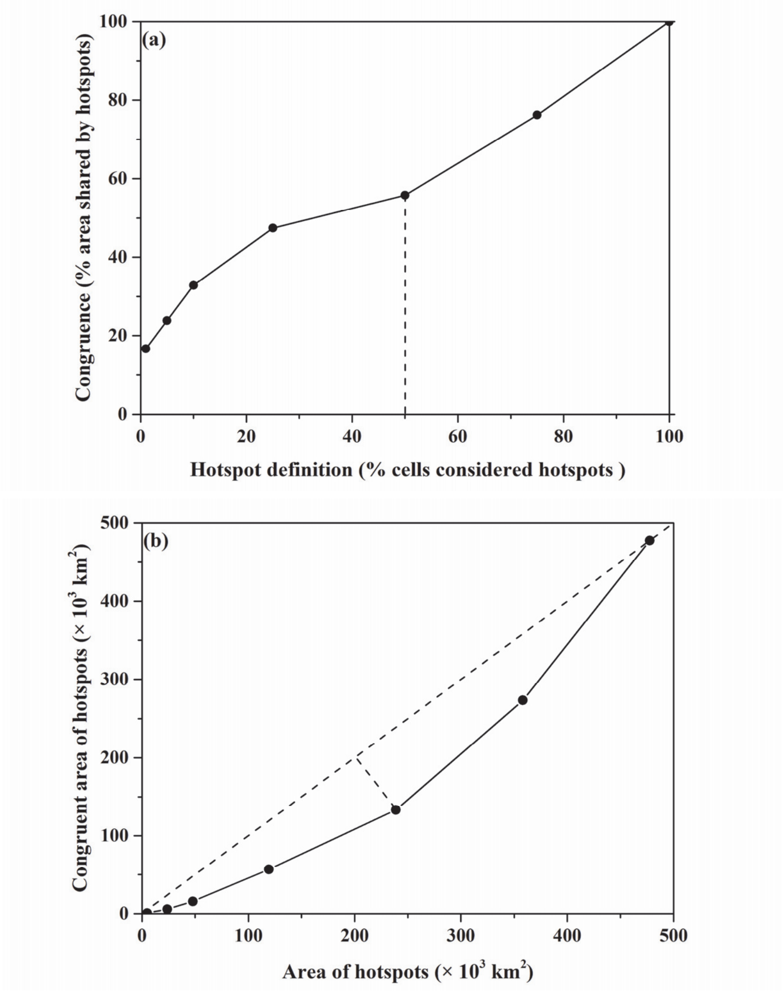


Figure 4.5 Correlation between the congruence of species richness, β-diversity, and weighted endemism and the hotspots definition. (a) Ratio of congruent area of three metrics to area defined as hotspots at top 1, 5, 10, 25, 50, 75, and 100% cells level. (b) Congruent area of three metrics against area defined as hotspots at top 1, 5, 10, 25, 50, 75, and 100% cells level

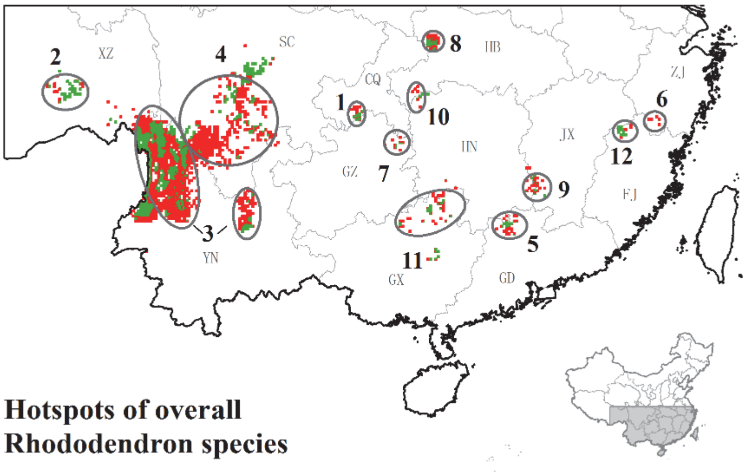
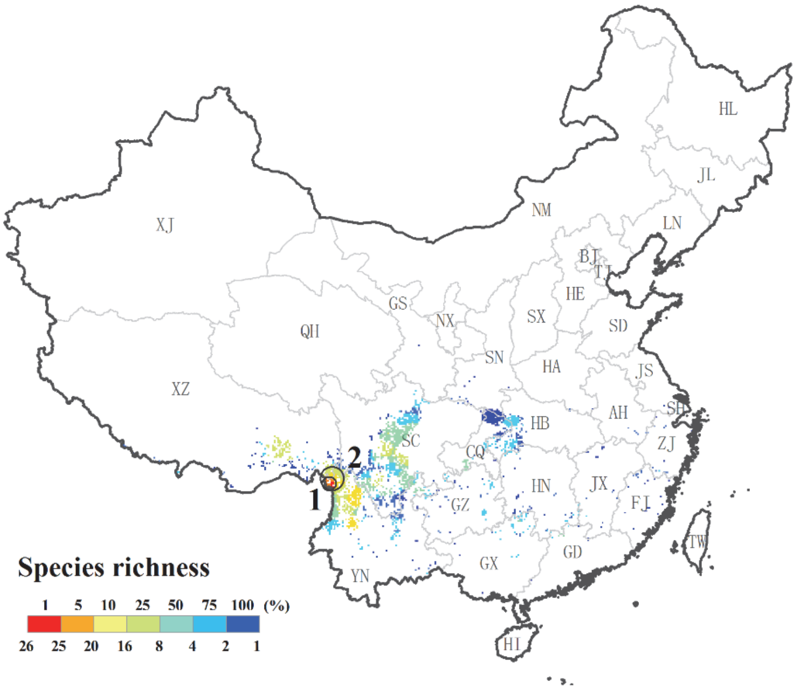


Figure 4.6 Hotspots and gap areas of overall Rhododendron species. Hotspots are defined as the congruence of the richest 50% of grid cells of species richness, β-diversity, and weighted endemism of overall Rhododendrons. (1) southern CQ (Mt Jinfo), (2) south-eastern XZ, (3) Mt Hengduan (YN) and north-eastern YN, (4) southern SC (Mt Shaluli, Mt Daxue and Mt Qionglai), (5) northern GD (Mt Danxia), (6) southern ZJ, (7) north-eastern GZ (Mt Fanjing), (8) western HB (Mt Daba), (9) south-eastern JX, (10) south-western HB and northern HN, (11) northern GX (Mt Maoer and Mt Yuanbao), and (12) northern FJ

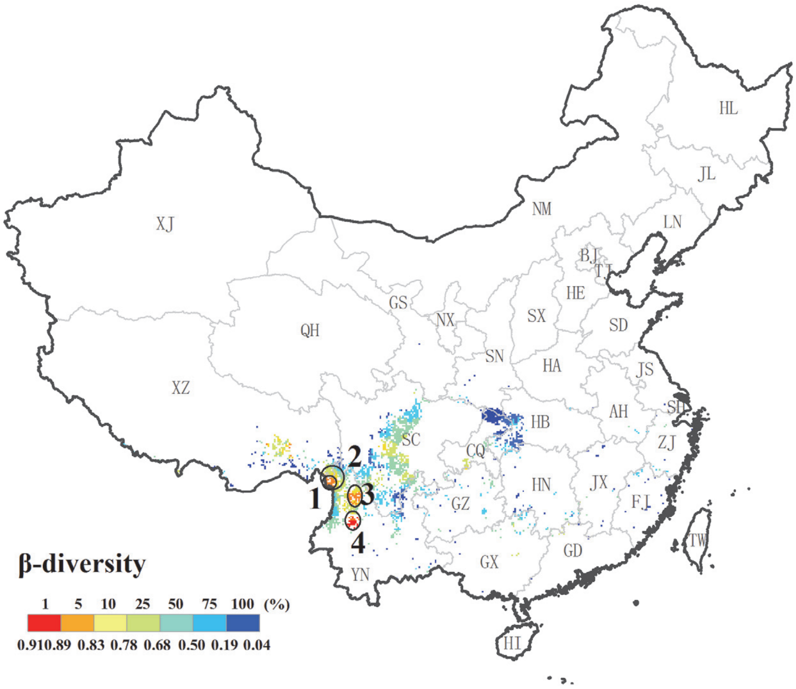
4.3.3 Diversity patterns and hotspots of threatened Rhododendrons

Patterns of species richness, β-diversity, and weighted endemism for threatened Rhododendron species (Figure 4.7) are consistent with the diversity patterns of overall Rhododendron species. Following the hotspot definition of overall Rhododendron species, the spatial congruence of the top 50% of grid cells of the three diversity metrics, we found that the hotspots of threatened Rhododendron species are largely overlapping (86.3%) with hotspots of overall Rhododendron species. The five hotspots for threatened Rhododendron species are (Figure 4.8): southern Chongqing (Mt Jinfo), south-eastern Tibet, north-western Yunnan, south-western Sichuan, and northern Guangdong.

(a)


HL
JL
LN
NM
XJ
BJ
TJ
HE
SX
SD
GS
NX
QH
SN
HA
JS
XZ
AH
SH
HB
SC
CQ
ZJ
2
1
HN
JX
FJ
GZ
TW
GD
GX
YN
HI
Species richness
1 5 10 25 50 75 100 (%)
26 25 20 16 8 4 2 1

(b)


HL
JL
LN
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SD
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QH
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XZ
AH
SH
HB
SC
CQ
ZJ
2
1
3
4
HN
JX
FJ
GZ
TW
GD
GX
YN
HI
β-diversity
1 5 10 25 50 75 100 (%)
0.91 0.89 0.83 0.78 0.68 0.50 0.19 0.04

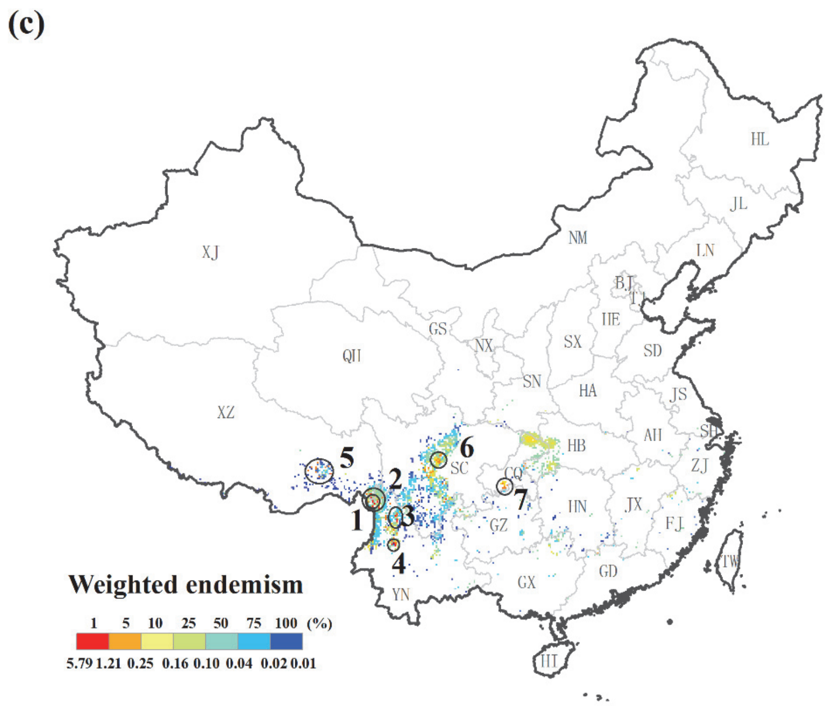


Figure 4.7 Predicted species richness (a), β-diversity (b), and weighted endemism (c) patterns of threatened Rhododendron species in China. 1. Gongshan (YN) 2. Deqin (YN) 3. Lijiang (YN) 4. Dali (YN) 5. Motuo (XZ) 6. Baoxing (SC) 7. Mt Jinfo (CQ)

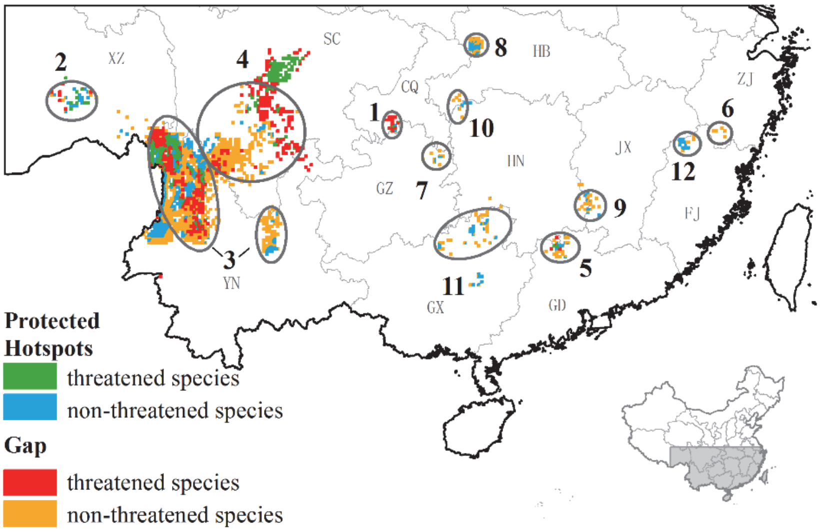


Figure 4.8 Hotspots and gap areas of threatened and non-threatened Rhododendron species

4.3.4 Priority areas for Rhododendron conservation

The hotspots of Rhododendrons are only partly covered by the 2139 nature reserves in China (Figure 4.4 and Figure 4.6). The hotspots and the nature reserves have 38,106 km^2 in common, which accounts for 2.3% of the total area of China's nature reserves. The proportion of protected hotspots by nature reserves (Figure 4.9) shows that about 96.7% of the congruent hotspot areas at the top 1% level are protected, though this ratio decreases to 52.9% when the congruent hotspot threshold is extended to the 5% level. In general, the protection ratio decreases with a decrease in the threshold defining the hotspots. For the top 25% of congruent hotspots, the average protection ratio is only approximately 28.3%. Given that these hotspots are mainly located in 12 provinces, we present the proportions of the hotspots that are protected for threatened and overall Rhododendron species in the 12 provinces (Table 4.1). It should be noted that southern Chongqing is identified as a hotspot for both threatened and overall Rhododendron species. However, in this area only 23.1% of threatened Rhododendrons are protected. In Tibet, which has also been identified as hotspot area for both threatened and overall

Rhododendron species, 27.4% of threatened and 36.3% of overall Rhododendrons are protected. In the largest hotspot (i.e. north-western Yunnan), which harbours more than half of the threatened Rhododendron species in China, the protection ratios for threatened and overall Rhododendron species are 39.6% and 31.8%, respectively. In the second largest hotspot (i.e. south-western Sichuan) 40.4% and 20.2% of, respectively, the threatened and overall Rhododendrons are protected. The two small hotspot areas with least numbers of Rhododendron species, namely southern Zhejiang (hotspot 6 in Figure 4.8, about 500 km^2) and north-eastern Guizhou (hotspot 7 in Figure 4.8, about 849 km^2), are barely protected at all.

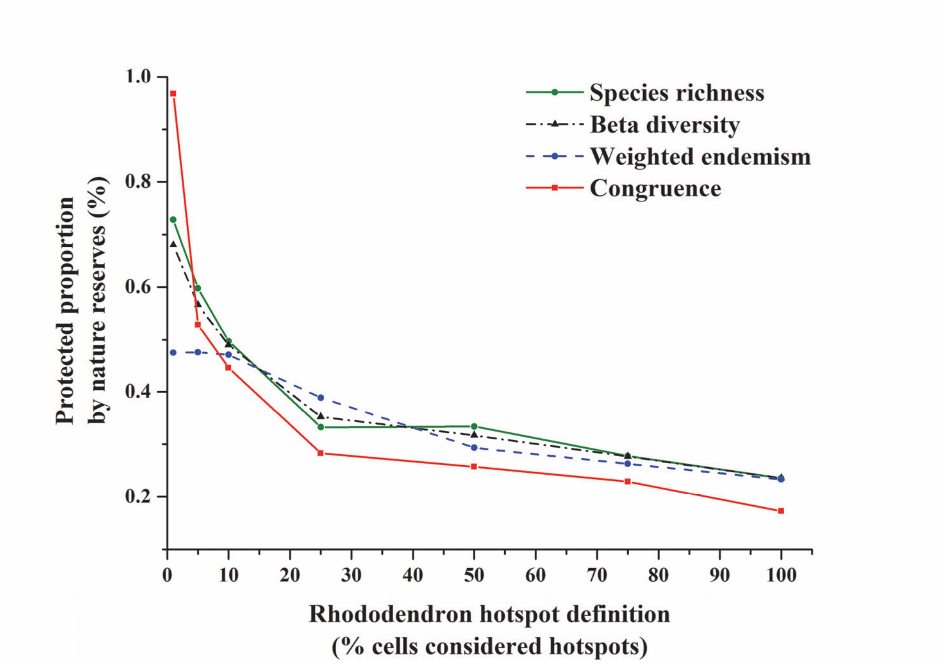


Figure 4.9 Cumulative curves of the proportion of hotspots of overall Rhododendron species protected by nature reserves using different definitions of hotspots

Table 4.1 Conservation status of Rhododendron hotspots in China

Priority level	Number of hotspots	Province located	Protected area of hotspot (km^2)	Total area of hotspot (km^2)	Protection ratio Po* (%)	Protection ratio Pt* (%)
I	1	Chongqing	442	1473	30.0	23.1
I	2	Tibet	2974	8203	36.3	27.4
I	3	Yunnan	22710	71356	31.8	39.6
I	4	Sichuan	7137	35362	20.2	40.4
I	5	Guangdong	428	2043	20.9	52.0
II	6	Zhejiang	1	500	0.2	-
II	7	Guizhou	147	849	17.3	-
II	8	Hubei	832	3080	27.0	-
II	9	Jiangxi	523	1838	28.4	-
II	10	Hunan	676	2261	29.9	-
II	11	Guangxi	1448	4179	34.6	-
II	12	Fujian	688	1174	58.6	-

* Po is protection ratio of hotspots for overall Rhododendron species, Pt is protection ratio of hotspots for threatened Rhododendron species

4.4 Discussion

4.4.1 Patterns, potential hotspots, and the conservation status of Rhododendrons in China

Rhododendrons form a keystone element of montane ecosystems in the alpine and subalpine zones of south-eastern Asia. Rhododendrons growing at higher altitudes are sensitive to disturbance by natural factors, such as climate change, landslides and forest fires. Rhododendrons that grow at lower altitudes are exposed to threats from human activity, such as the rising demand for agricultural land, road construction, and the growing tourism industry (Ma et al., 2014). To the best of our knowledge this is the first comprehensive study of Rhododendron diversity patterns across all of China in terms of richness, composition and rarity, thereby providing a foundation for decision-making regarding the conservation of Rhododendrons in China. The high diversity of Rhododendron species in the mountains (versus the low diversity in the plains, basins and deserts) is consistent with the Chinese woody plant diversity pattern

(Wang et al., 2011) and endemic seed plant species diversity patterns (Huang et al., 2015). The species richness pattern of higher plants also tends to follow the trend of larger species numbers in the south and lower numbers in the north of China (Zhao et al., 2016). The 12 Rhododendron hotspots identified in China in this study are mainly located in southern China. Seven of these are considered to be centres of endemism of Chinese plant taxa (Lopez-Pujol et al., 2011), and eight are considered to be hotspots of Chinese threatened plant species (Zhang & Ma, 2008). All 12 hotspots have been identified as hotspots of Chinese endemic seed plants (Huang et al., 2016). Thus, to some extent, the Rhododendron hotspots represent plant diversity centres in China. However, the 12 hotspots identified in our study are only partly situated in nature reserves. The proportion of the Rhododendron hotspots protected by nature reserves in our study is low for both the small hotspots (southern Chongqing and southern Zhejiang, middle to low elevation regions) and the large hotspots (north-western Yunnan and south-western Sichuan, both high elevation regions). North-western Yunnan has been recognized as the origin and distribution centre of Rhododendron species (Li et al. 2013). Consequently, we consider conservation of this genus to be a high priority. The hotspots of threatened Rhododendron species, especially southern Chongqing, should be considered very high priority areas (priority level I in Table 4.1) for conservation, while the remaining hotspots, especially southern Zhejiang and north-eastern Guizhou, should also be considered for conservation reasonably soon (priority level II in Table 4.1). We conclude that equal attention should be paid to the hotspots in south-eastern China, which are located in densely populated areas and are seriously affected by land-use change (Yang et al., 2014), as to the well-known hotspots at Mt Hengduan and southern Chongqing.

4.4.2 Influence of diversity metrics and spatial scales on hotspots

In recognition of the increasing importance of protected areas in biodiversity conservation, the Convention on Biological Diversity (CBD) lays great emphasis on in-situ conservations of variable populations and call for the establishment and higher effective of protected areas

(Montesino Pouzols et al., 2014). Hotspots are the common reference for protected areas construction (Chen et al., 2017). However, hotspot locations may differ depending on how the hotspot is defined. The selected diversity metrics, the level of spatial congruence of diversity metrics, and spatial scale (i.e. the grid cell used in the analysis) are all critical factors that may lead to diverging results (Ceballos & Ehrlich, 2006; Marsh et al., 2010; Zhao et al., 2016). Various biodiversity metrics, including species richness, weighted endemism, phylogenetic diversity, and biogeographically weighted evolutionary distinctiveness, have been used to portray species diversity, define hotspots and select priority areas for conservation (Huang et al., 2016; Pardo et al., 2017). Species richness is the most widely-used metric, while weighted endemism has also gained much attention recently (Herkt et al., 2016; Huang et al., 2016). However, β-diversity (the dissimilarity of species composition between two sites) has not been commonly used to identify biodiversity hotspots. As one of the fundamental components of species diversity, β-diversity has attracted less attention than species richness (also called α-diversity on a local scale or γ-diversity on a larger scale). McKnight et al. (2007) demonstrated that β-diversity provides critical information for conservation planning when striving to represent biodiversity within practical constraints such as an area or coast. Marsh et al. (2010) used both species richness and β-diversity to model bird and butterfly diversity on the Comoro Islands, and concluded that species richness and β-diversity together provide comprehensive understanding when assessing optimal reserve locations. Socolar et al. (2016) concluded that understanding β-diversity is essential for protecting regional diversity and directly assists conservation planning. Our results confirm that species richness, β-diversity and weighted endemism describe different attributes of species diversity. Weighted endemism can be of value identifying 'rarity hotspots' of species. Conservationists are interested in areas of endemism, because of the importance to conserve endemic species, which have a narrow distribution to a particular area (Crisp et al., 2001). And β-diversity facilitates the optimal spatial arrangement of conservation areas, capturing variation in species assemblages, as well as underlying environmental heterogeneity necessary for long term persistence (McKnight et al., 2007). Therefore, we advocate that besides species richness, β-diversity and weighted endemism are employed for identifying hotspots, to provide a more comprehensive assessment of species diversity, consequently leading to more informed conservation prioritization. Hotspots of species richness, threatened species and endemism do, however, not always correspond (Orme et al., 2005), although our study did not encounter this problem. We did notice that there are few quantitative studies on the spatial distribution of threatened species and thus advocate emphasizing the quantitative assessment of threatened species in a diversity and hotspots study.

The importance of the chosen level of congruence in detecting hotspots, has been clearly demonstrated in Figure 4. Based on the top 1-5% of grid cells of species richness, β-diversity, and weighted endemism, only one hotspot emerged, namely Mt Hengduan, which is considered a global biodiversity hotspot (Myers et al., 2000). At this level the remaining 11 potential hotspots would have gone unnoticed in the extremely diverse Himalayan region. Most hotspots are only unveiled when the 'hotspots defining level' is expanded. The common area of the top 50% grid cells of species richness, β-diversity, and weighted endemism was used as threshold to identify the Rhododendron hotspots, because, based on these three metrics, this level identified most hotspots. In addition, our hotspots are defined based on 'record-containing grid cells'. This leads to the issue of grid cell size, which is important for hotspots identification in ecological studies (Zhao et al., 2016; Pardo et al., 2017). In continental and global biodiversity studies, a grid cell of 100×100 km or 50×50 km is usually used for data analysis (Orme et al., 2005; Wang et al., 2011; Huang et al., 2015), but these larger grid cell sizes are not suitable for local areas with extremely rich biodiversity or for large areas with relatively low biodiversity (Zhao et al., 2016). Pardo et al. (2017) found that the amount of diversity was exaggerated due to the coarse spatial scale of species-occurrence data. Given that we are trying to identify hotspots of a single genus, rather than broad biological groups (e.g. vascular species, higher plants, or woody species), and that we are trying to provide as much detail as possible on the spatial patterns of Rhododendrons, a grid cell size of 10×10 km was selected. At finer scales, hotspots defined by different metrics have appeared more inconsistent (Prendergast et al., 1993). Therefore, we suggest that the hotspots and priority areas selection should take diversity metrics, the level of congruence, and the basic grid cell size for data analysis into account, as well as comprehensively consider the specific circumstances of the region and the taxon involved.

4.5 Conclusions

Our study presents Rhododendron diversity patterns and identifies a number of potentially important but overlooked hotspots based on an analysis of species richness, β-diversity and weighted endemism of Rhododendrons in China. Although certain Rhododendrons are protected by the existing natural reserves in China, a large number of areas is still unprotected and many Rhododendron species are still threatened. The information provided in this study may assist in setting priorities regarding the conservation of this important genus in China. As species richness, β-diversity and weighted endemism display complementary traits of diversity, these three metrics, combined with an appropriate level of congruence for defining hotspots, and a suitable spatial scale, should be taken into consideration when selecting priority conservation areas.

Appendix

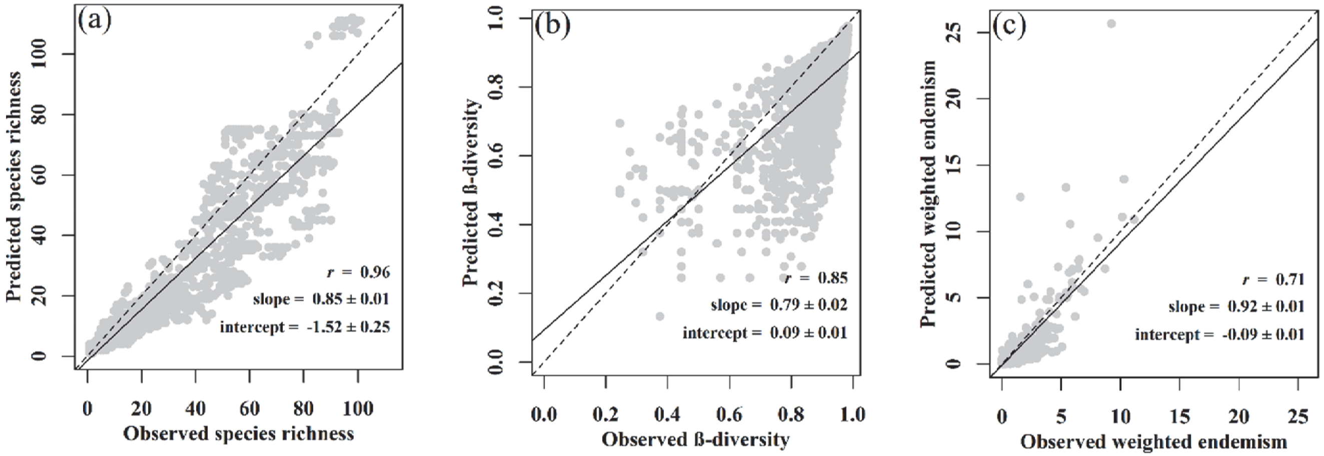
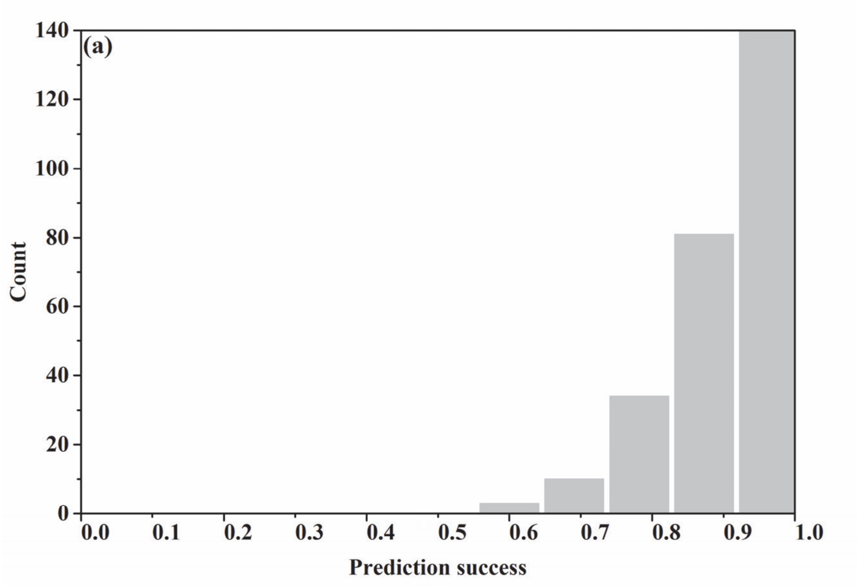


Figure 4.A1 Spearman correlation between predicted and observed species richness (a), β-diversity (b), and weighted endemism (c)



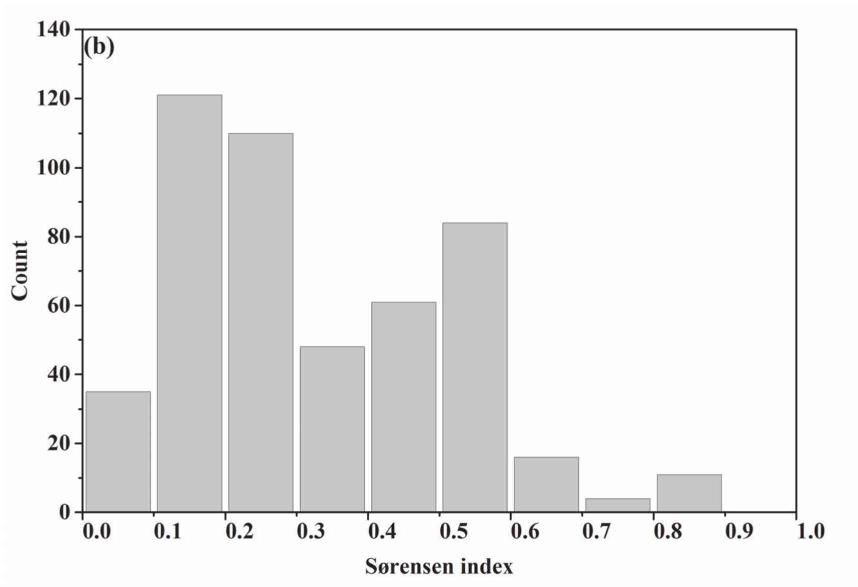


Figure 4.S2 Histograms of prediction success (a) and Sørensen index (b) of the SESAM framework

Table 4.A1 Key modelling parameters of boosted regression tree for species distribution model (SDM)and macro-ecological model (MEM)

Parameters	SSDM	MEM
Learning rate	0.001	0.1
Tree-complexity	7	7
Family	Bernoulli	Poisson
Number of trees	5000	50
Bag fraction	0.5	0.5

Chapter 5

Narrow-ranging and threatened Rhododendron species facing a high risk of extinction in the wild

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This chapter is based on: Yu, F.Y., Wang, T.J., Groen, T.A., Skidmore, A.K., Yang, X.F., and Ma, K.P. Narrow-ranging and threatened Rhododendron species facing a high risk of extinction in the wild.

Abstract

Biodiversity loss and variation in species responses to climate and land use change have been found across broad taxonomic groups. However, whether species from the same taxonomic group with distinct geographical ranges will respond differently is poorly understood. The aim of this study is to predict the potential impacts of future climate and land use change on the distribution of narrow- and wide-ranging Rhododendron species, and estimate their relative contribution in China. We applied the presence-only ecological niche model MaxEnt to predict the distribution of 10 narrow-ranging and 10 wide-ranging Rhododendron species for the year 2070, using three general circulation models and three scenarios of climate and land use change. We measured the predicted distribution change of each species using change ratio, distance and direction of core range shifts, and niche overlap using Schoener's D. We found that the distribution areas of six narrow-ranging species would decrease, of which one species would go extinct. The remaining four narrow-ranging species would experience range expansion. Distribution of all the wide-ranging Rhododendron species would decrease. All Rhododendrons will shift to the northwest. We conclude that Rhododendron species generally will be negatively affected by the climatic and land use change expected in 2070 from the three scenarios evaluated in this study, but some narrow-ranging species may be positively influenced. Narrow-ranging Rhododendron species are more vulnerable compared to wide-ranging Rhododendron species. This study demonstrated that the effects of climate and land use change on alpine and subalpine plant species is species-specific, thereby strengthening our understanding of the impacts of climate and land use change on plant distribution.

5.1 Introduction

Rapid climate change has resulted in distributional changes for a wide range of taxa (Parmesan, 2006; Chen et al., 2011). In general, species are predicted to shift poleward in latitude and upward in elevation as global temperatures increase (Parmesan & Yohe, 2003; Lenoir et al., 2008). If current greenhouse emission trajectories continue many species, especially narrowly distributed species with small populations, may go extinct over the next century (Pearson et al., 2014) although extinction estimates differ widely depending on the taxa, spatial scale, and methods used (Frishkoff et al., 2016). The Convention on Biological Diversity (CBD) Aichi Target 12 calls for preventing the extinction of threatened species (CBD, 2010). Predicting the distribution of narrow-ranging species therefore provides scientific-based suggestions for protecting threatened species and biodiversity.

Apart from climate change impacts, human-caused habitat loss and fragmentation (mainly through land use change) has long been considered a primary cause for biodiversity loss and ecosystem degradation worldwide (Foley et al., 2005; Oliver & Morecroft, 2014). The land use change includes deforestation, road construction, agricultural encroachment, dam building, irrigation, mining, expansion of urban environments, and other activities. The cumulative or synergistic interactions between climate change and human land use are believed to have an even greater impact on biodiversity over the coming century (Sala et al., 2000; Brook et al., 2008). Therefore, predicting species' responses to climate and land use change is becoming increasingly important for biodiversity conservation. A key question when managing sustainable landscapes is whether a species is likely to be able to persist in a landscape that underwent a certain degree of habitat loss in combination with changing climatic conditions, or whether it will be able to migrate to new regions as they become climatically suitable (Travis, 2003). A number of studies have emphasized the importance of integrating climate and land use change when studying change in species distributions into the future (Sala et al., 2000; Sirami et al., 2016). Nevertheless, the effect of climate and land use change is frequently studied in isolation, with the combined effects of climate and land use change on biodiversity and the distribution of particular species remaining poorly understood (Sirami et al., 2016; Titeux et al., 2016).

In recent years, geographical range size has been used as a proxy measure for predicting extinction risk, as well as to prioritize species for conservation actions in the face of rapid global environmental change (Thuiller et al., 2005; Pompe et al., 2008; Gallagher, 2016). The range of resources that a species use (i.e. niche breadth) determines its geographical range (Slatyer et al., 2013). There is substantial recent evidence, from a variety of taxa, supporting the theory that narrow-ranging species are declining more quickly, or are more vulnerable to climate change and habitat loss than their broader niche relatives (Purvis et al., 2000; Walker & Preston, 2006; Yu et al., 2017). Species with a small geographical range size, as is the case with many endemic species, could be more sensitive or vulnerable to climate change due to lack of plasticity and insufficient genetic variation to respond to novel selection pressure (Sheth & Angert, 2014). While broadly distributed species with large population sizes and that usually have a wide climatological niches may be buffered against extinction due an evolved tolerance to a broad range of climatic conditions (Pearson et al., 2014; Yu et al., 2017). In addition, the narrowly distributed species are highly threatened by land use change because they are less resilient (Köster et al., 2013), and the relative less effect in widely spread species may be due to their ability to exploit a wide range of ecological niches (Harcourt et al., 2002; Cleary & Mooers, 2006). Biodiversity loss and variation in species responses to environmental change has been found across broad taxonomic groups (Hickling et al., 2006; Pompe et al., 2008), but what about within taxonomic groups? Is there any intraspecific variation in response to environmental change? Will narrow-ranging and wide-ranging species of the same taxonomic group respond differently to change in climate and land use? And if they do respond differently, what is the difference?

The genus Rhododendron, comprising 1,025 species, forms a major component of alpine and subalpine ecosystems in the Himalayas. The Himalayan region has been recognized as one of the most fragile zones in the world, and is experiencing large change due to climate and land use change (Xu et al., 2009b; Kumar, 2012). The Rhododendron genus is the only group of plants that covers a continuum from the subalpine up to the alpine zones, maintaining biological sustenance in the Himalayas. Rhododendrons play a vital role in slope stabilization and watershed protection in the Himalayas, where many of Asia's major rivers originate (Gibbs et al., 2011). However, Rhododendrons are among the most neglected groups of plants in terms of scientific inquiry (Kumar, 2012). It is worth to note that Rhododendron species have quite distinct distribution ranges, some species occurring throughout the entire Himalayas, whilst others are highly restricted to small region, such as rocks and boulders of the mountain top (Gibbs et al., 2011). In view of the status as a 'big genus' and it's various distributional ranges, Rhododendron species are considered to be excellent candidates for exploring the difference of narrow- and wide-ranging species in response to climate and land use change. Predicting the distribution of narrow- and wide-ranging Rhododendron species under climate and land use change would, on the one hand, help us to understand the evolution and diversification of flora in the light of global change, while on the other hand, could provide insights for conservation planning about the strategies required to maintain the sustainable alpine and subalpine ecosystem in the future. In this study, we aim to (1) predict distribution of narrow- and wide-ranging Rhododendron species under climate and land use change, and (2) estimate the relative contributions of climate and land use on the spatial distribution of narrow-ranging and wide-ranging Rhododendron species.

5.2 Methods

5.2.1 Study area and species data

China harbours 571 Rhododendron species, which are widely distributed across most regions (except Xinjiang and Ningxia provinces) (Ma et al., 2014). We collected Rhododendron presence records from seven Chinese herbaria and botanical museums (for more details, see Yu et al., 2015). Since high locational accuracy is required for studying plant species distribution, we excluded all records presenting only a general description of the location (e.g. mentioning only a county or a mountain). Our resulting dataset, covering 406 species, comprises 13,126 geo-referenced records, with each record having a spatial uncertainty of less than 1 km. In this study, we selected a total of 2,628 location records for 20 species (see selection criteria below) which were pooled into narrow- and wide- ranging species (Table 5.1). Locations of the 20 species can be seen in Figure 5.1. The selection was based on the combination of the following criteria: (1) endemism: species are endemic to China, (2) sampling design: samples for included species should be taken from more than 10 localities with each sample at least 2 km apart in order to lessen the spatial autocorrelation effect, and (3) range size: we projected all species records using a Asia North Albers Equal-Area Conic projection, and calculated the geographical range size of each species as frequency of occurrences of each species in a 1×1 km grid over the whole of China. We then ranked the species based on their geographical range sizes, and selected the 10 most narrow ranging and 10 most wide ranging species.

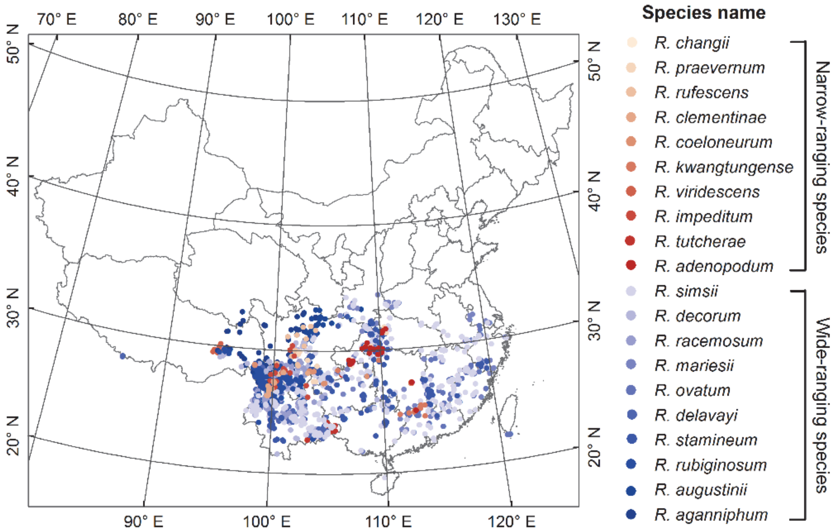


Figure 5.1 Locations of the 20 narrow- and wide-ranging Rhododendron species selected in this study

Table 5.1 List of Rhododendron species considered in this study

Code	Species name	Geographic range (km^2)	Elevation range (m)
N1	*R. changii*	11	2000-3000
N2	*R. praevernum*	15	1350-2350
N3	*R. rufescens*	17	3800-4500
N4	*R. clementinae*	18	3200-4100
N5	*R. coeloneurum*	18	1200-2300
N6	*R. kwangtungense*	18	800-1600
N7	*R. viridescens*	18	3000-3400
N8	*R. impeditum*	21	2500-4600
N9	*R. tutcherae*	22	1200-2000
N10	*R. adenopodum*	36	1100-2200
W1	*R. simsii*	526	500-2700
W2	*R. decorum*	328	1000-4200
W3	*R. racemosum*	263	1500-3500
W4	*R. mariesii*	248	600-1500
W5	*R. ovatum*	242	< 1000
W6	*R. delavayi*	180	1400-1800
W7	*R. stamineum*	179	500-1600
W8	*R. rubiginosum*	171	2800-4200
W9	*R. augustinii*	151	1300-3000
W10	*R. aganniphum*	146	2700-4700

N: narrow-ranging species, W: wide-ranging species

5.2.2 Climate and land use data

Based on the physiology and environmental requirements of Rhododendrons, we selected a set of climatic variables useful for predicting Rhododendrons distribution (Yu et al., 2017). To deal with collinearity, we performed a Pearson correlation analysis, and obtained six climatic variables ($r < 0.7$) from the WorldClim database (Hijmans et al., 2005) at a 30 seconds resolution to model the current distribution of each species. These variables included: isothermality (Bio3), temperature seasonality (Bio4), minimum temperature of coldest month (Bio6), annual precipitation (Bio12), precipitation of wettest month (Bio13), and precipitation of driest month (Bio14). We used the same bioclimatic variables from three general circulation models (GCMs) comprising the Beijing Climate Centre Climate System Model (BCC-CSM1-1), Community Climate System Model (CCSM4), and Hadley Global Environment Model 2 - Earth System (HadGEM2-ES) in order to project species distributions (2070, average for 2061-2080). For each GCM, we used three emission scenarios (representative concentration pathways: RCP 2.6, RCP 4.5, and RCP 8.5) to represent the most optimistic and most pessimistic concentrations of glasshouse gases (GHG) over the next few decades (John Weyant, 2009). RCP 2.6 is the lowest GHG concentration pathway in which radiative forcing (global energy imbalances) levels reach 3.1 W/m^2 by mid-century and drops 2.6 W/m^2 by 2100. RCP 4.5 is a stabilization scenario in which the total radiative forcing reaches to 4.5 W/m^2 by 2100 and stabilizes due to the employment of a range of technologies and strategies for reducing GHG emissions. Likewise, RCP 8.5 also represents stabilization by 2100, this time at 8.5 W/m^2 by 2100 (van Vuuren et al., 2011).

We obtained current and future land use data with 30 m resolution from Finer Resolution Observation and Monitoring-Global Land Cover (FROM-GLC (Li et al., 2016), available at http://data.ess.tsinghua.edu.cn/data/Simulation/) which provides the most current (2010) and the finest-scale global future land use and land cover dynamics using four RCP scenarios (RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5). For consistency with climatic data, we used the time period of 2010 and 2070 (average 2061-2069, three RCP scenarios (i.e. RCP 2.6, RCP 4.5, and RCP 8.5)) as representative of the current and future land use scenarios. All land use data were resampled to a 30 second resolution using a 'majority' interpolation.

5.2.3 Species distribution model

Of the species distribution models, machine-learning algorithms (such as MaxEnt, Boosted Regression Trees, and Random Forests) frequently outperform regression based approaches (Beaumont et al., 2016). In this study, we used MaxEnt 3.3 (Phillips et al., 2006) because it has shown higher predictive accuracy compared with other methods across a wide range of sample sizes (Wisz et al., 2008), and performs well to estimate potential range shifts of species (Hijmans & Graham, 2006). Using the recommended default parameters (i.e. regularization multiplier = 1, maximum number of backgrounds points = 10,000, maximum iterations = 500, and convergence threshold = 10^{-5}), we ran a 10-fold cross validation for the current distribution. Based on the assumption that current envelopes reflect species' environmental preferences, which will be retained under climate and land use change scenarios, we applied the models fitted to current conditions to future conditions to derive potential future distributions. We calculated the Boyce index (Boyce et al., 2002; Hirzel et al., 2006) of the current potential predictions for evaluate predictive accuracy. Contrary to common evaluation measures, for example, AUC and TSS which may present problems for presence-only data, the Boyce index only requires presence data, and measures how much model predictions differ from a random distribution of the observed presences across the prediction gradients (Petitpierre et al., 2012). The Boyce index is fairly insensitive to species prevalence, it varies between -1 and 1. Positive values indicate a model which presents predictions that are consistent with the distribution of presences in the evaluation dataset, values closed to zero mean that the model is not different from a random model, and negative values indicate predicting poor quality areas where presences are more frequent (Hirzel et al., 2006).

We created binary distribution maps of suitable and unsuitable ranges from the continuous probability predictions of each species by using the threshold of 'maximum sensitivity and specificity' (Liu et al., 2013). We averaged the final binary result of each species for each RCP from 10 times prediction across 3 GCMs.

We evaluated the effect of climatic and land use variables on the Rhododendron distribution using the 'percent contribution' (relative contributions of the covariates to model results), a standard output of MaxEnt. We calculated the averaged contribution of climatic and land use variables for the narrow- and wide-ranging groups, respectively.

5.2.4 Geospatial analyses

To measure the predicted distribution change for each species, we projected the binary SDMs onto Asia North Albers Equal-Area Conic projection in ArcGIS 10.2 (Redwoods, USA), and used three metrics to examine the magnitude and direction of shifts in potential distributions for all species across the narrow- and wide-ranging groups. Firstly, we calculated the change ratio following the equation C = (A – B) / B, where C is the change ratio, while A and B are the future and current potential distribution area (km^2) of each species using a python-based GIS toolkit SDMtoolbox (Brown & Anderson, 2014). Secondly, we calculated distance and direction of core range shifts by comparing the centroids of current and future binary SDMs and the vectors between them using the SDMtoolbox (Brown & Anderson, 2014). Lastly, we calculated Schoener's D (Schoener, 1970; Broennimann et al., 2012) as the overlap between current and future distribution of Rhododendron species using 'ENMeval' package (Muscarella et al., 2014) in R 3.1 (R Core Team, 2015). The value of Schoener's D ranges from 0 (no overlap) to 1 (identical predictions). ENMeval calculated Schoener's D by comparing two normalized predicted probability distributions produced by MaxEnt with

$$D(P_x, P_y) = 1 - \frac{1}{2}\sum_{n=i} | P_{x,i} - P_{y.i}| \tag{5.1}$$

where $P_{x,i}$ and $P_{y.i}$ represents the probability assigned by distribution model to grid cell i for current (x) and future (y) distribution of one species, respectively. We used the non-parametric Mann-Whitney U-test to test if statistically significant differences were found in model performance and the three metrics.

5.3 Results

5.3.1 Projected distributions of Rhododendrons

We obtained high-performing species distribution models for all 20 Rhododendron species with the Boyce index ranging from 0.73 to 0.99. Averaging across the six narrow-ranging species, which we predicted to experience range contractions, the distribution areas of the six species decreased with average ratios of -56.4%, -61.5%, and -77.5% from the current condition through to 2070 under the RCP 2.6, RCP 4.5, and RCP 8.5 projection scenarios (Figure 5.2a). It worth noting that we predicted that one species (N1: *R. changii*) would go extinct, with a change ratio of -96.0%, -99.9%, and -100% under RCP 2.6, RCP 4.5 and RCP 8.5 respectively (Figure 5.3a-N1). Interestingly, we predicted the remaining four narrow-ranging species would experience a range expansion in 2070 (Figure 5.2a), with an average of change ratio at 79.7%, 52.6%, and 40.3% under RCP 2.6, RCP 4.5, and RCP 8.5. *R. viridescens* (N7) had the largest predicted distribution expansion with change ratios of 290.8%, 130.3% and 148.3% under the three scenarios (Figure 5.3a-N7). Meanwhile, we predicted the distribution ranges of the wide-ranging group would decrease for all these species, with average change ratios of -19.8%, -21.3% and -35.6% under RCP 2.6, RCP 4.5 and RCP 8.5 (Figure 5.2b). The distribution areas of *R. stamineum* (W7) would shrink -35.4%, -34.4%, and -70.3% in 2070 respectively, representing the largest drop in distribution range among the wide-ranging species (Figure 5.3b-W7). The distribution range of *R. simsii* (W1) that had the largest geographical range size, would decline by -8.5%, -13.8% and -28.4% (Figure 5.3b-W1).

The overlap between the current and future distributions for the narrow-ranging group (0.49, 0.42, and 0.29 under RCP 2.6, RCP 4.5, and RCP 8.5 respectively, Figure 5.4a) were significantly ($p < 0.05$) lower than for the wide-ranging group, which was 0.76, 0.71, and 0.55 under RCP 2.6, RCP 4.5, and RCP 8.5 (Figure 5.4b). The overlap between current and future species distribution decreased from the low to high RCP scenarios.

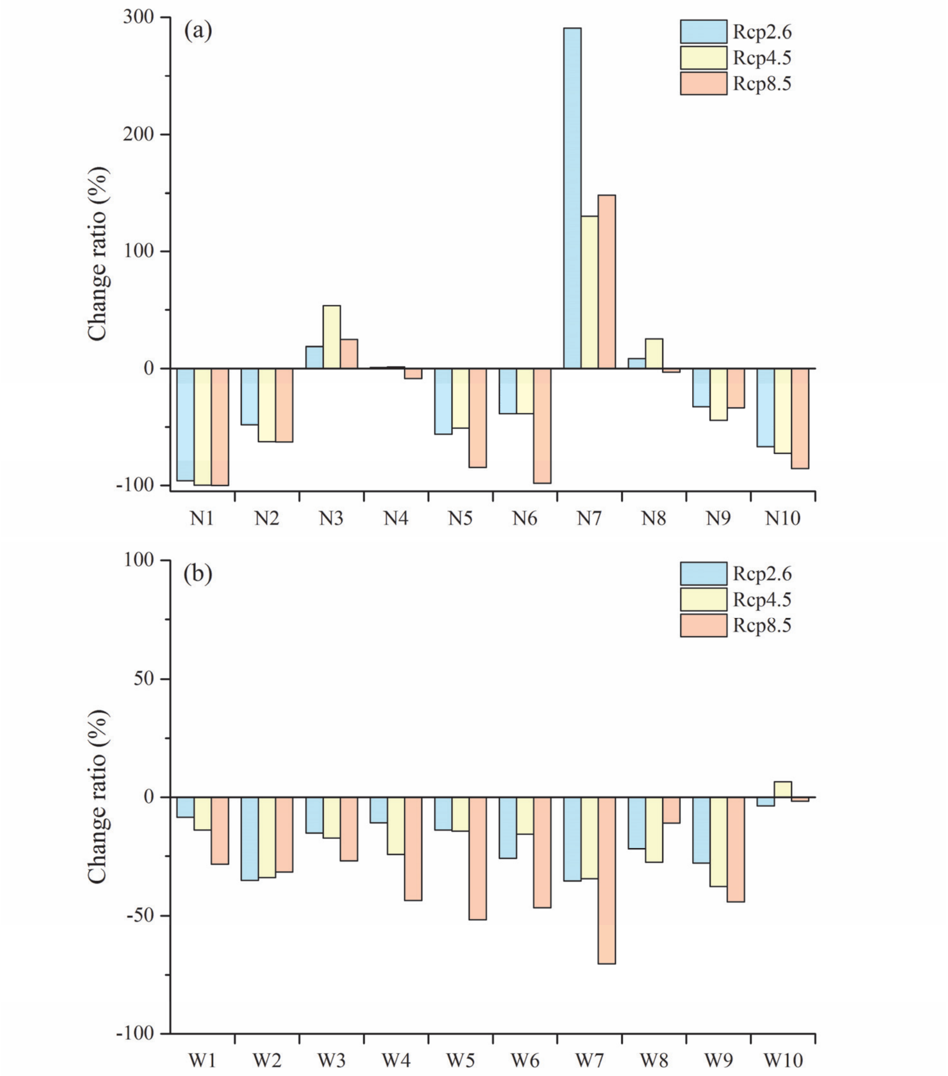
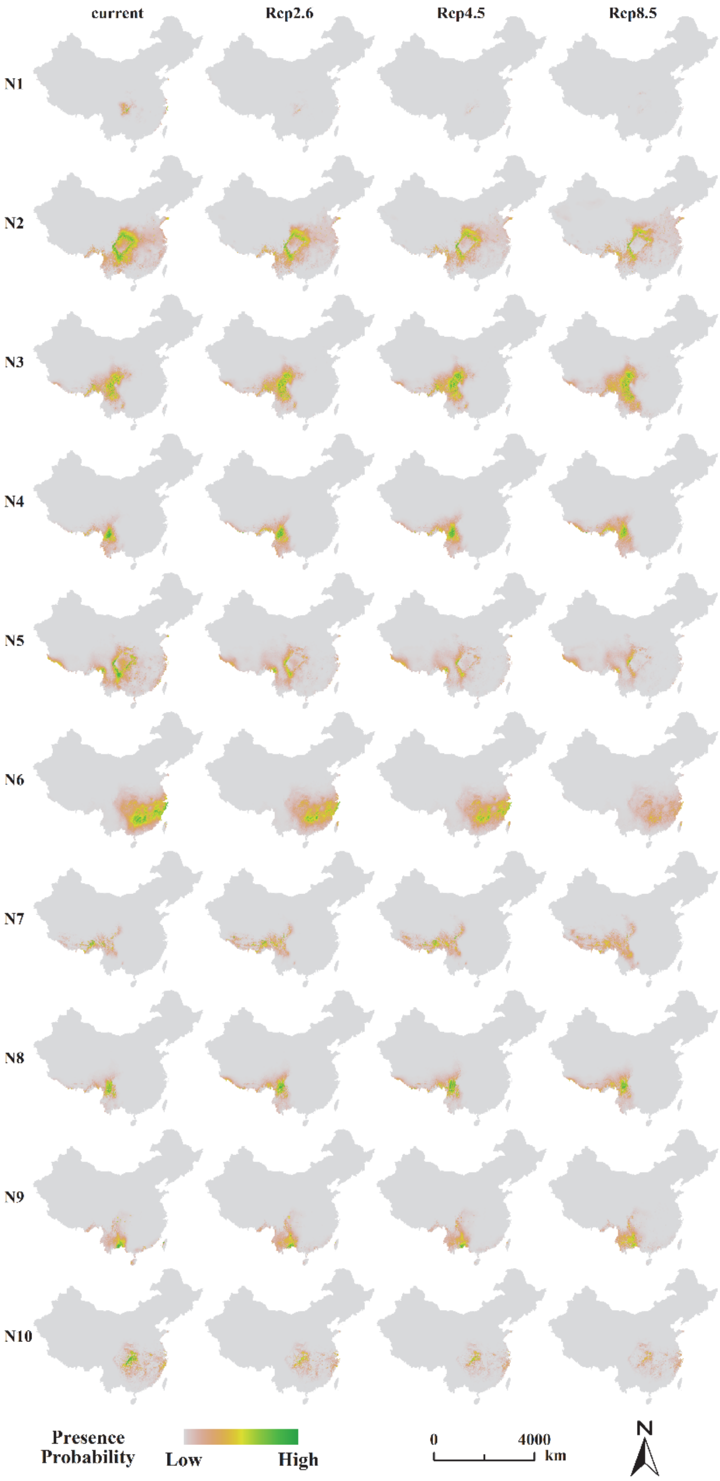


Figure 5.2 Change ratios of distribution areas for the narrow-ranging (a) and wide-ranging (b) Rhododendron species under RCP 2.6, RCP 4.5, and RCP 8.5 in 2070. Species codes N1 to N10, and W1 to W10 are explained in Table 5.1


current
Rcp2.6
Rcp4.5
Rcp8.5
N1
N2
N3
N4
N5
N6
N7
N8
N9
N10
Presence Probability
Low
High
0
4000
km
N

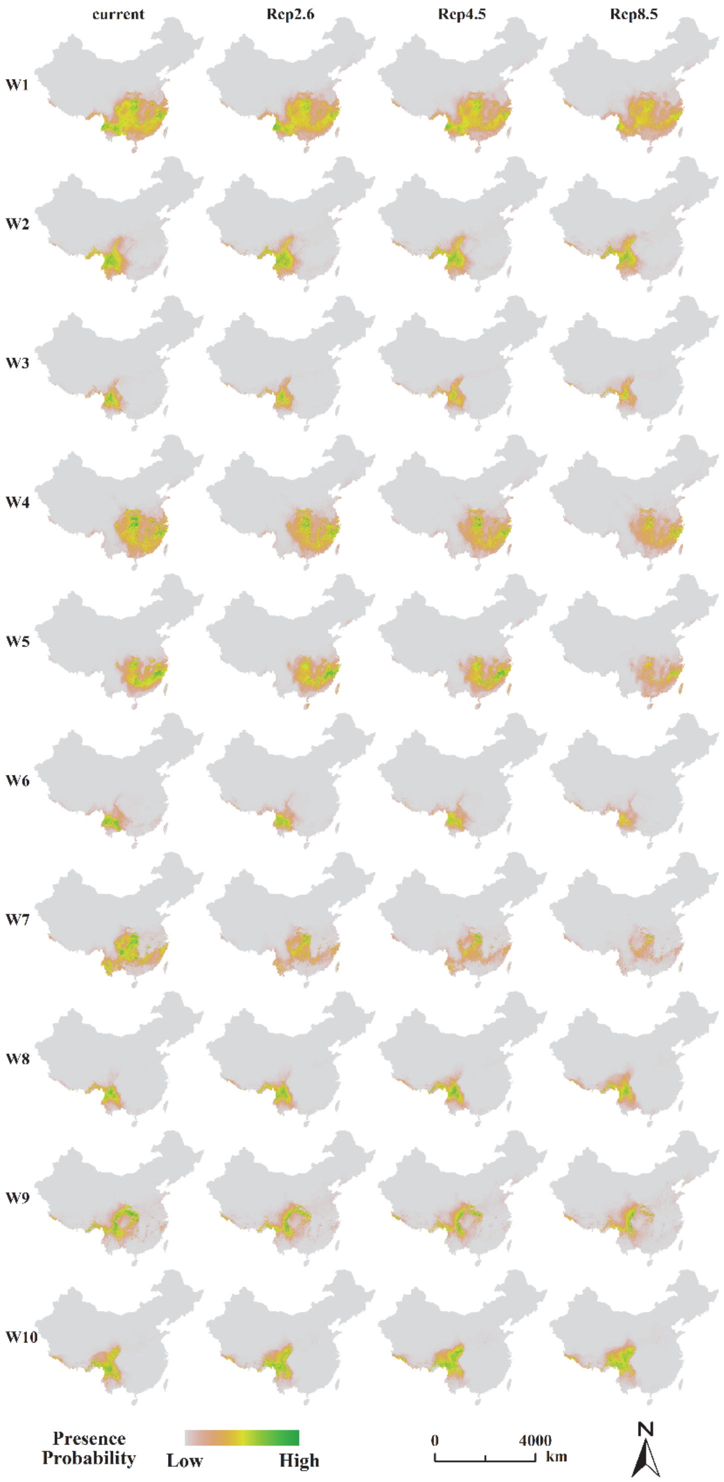


Figure 5.3 Distribution maps of the narrow-ranging and wide-ranging groups under current and future (RCP 2.6, RCP 4.5, and RCP 8.5 in 2070) climate and land use conditions. Species codes N1 to N10, and W1 to W10 are explained in Table 5.1

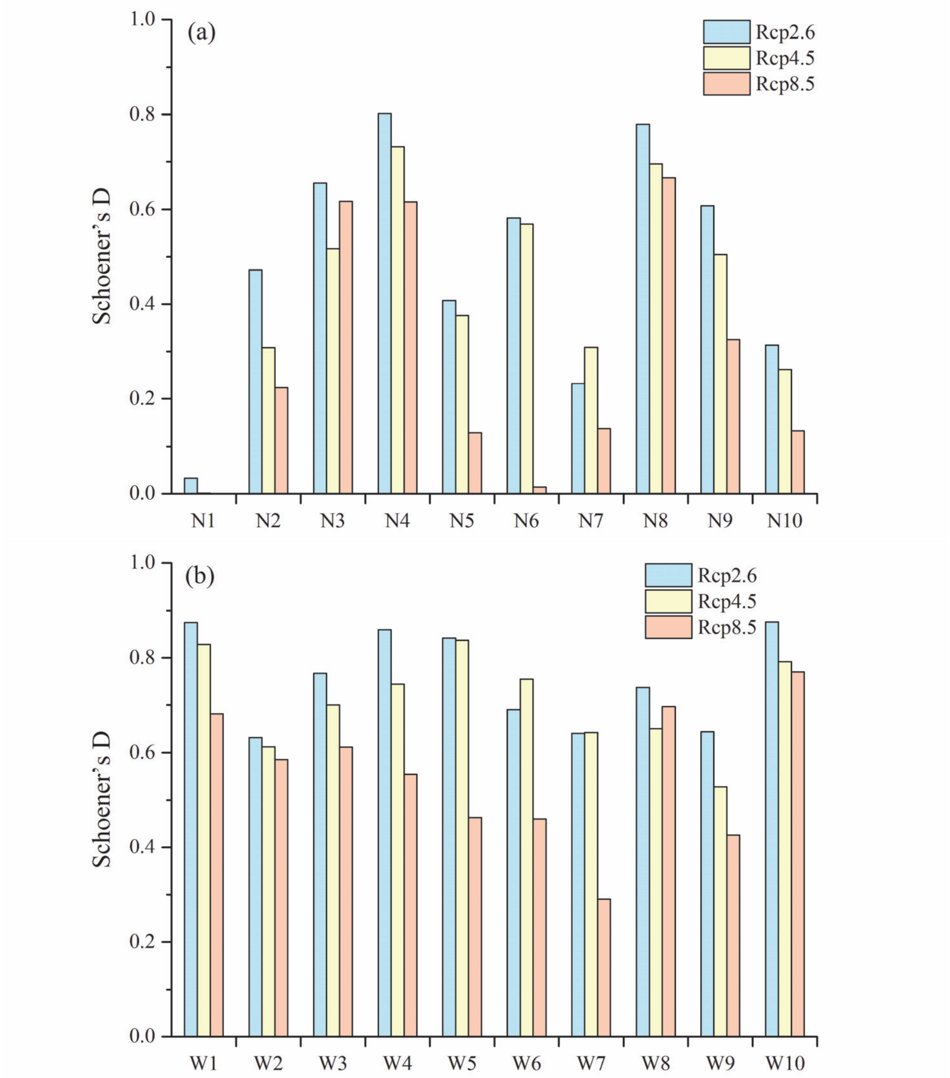


Figure 5.4 Distribution overlap (measured by Schoener's D) between current and future distribution of (a) narrow-ranging and (b) wide-ranging Rhododendron species

The core range shifts showed that 16 out of 20 species, regardless of their range sizes, would shift in a north-western direction, rather than north (the shifting direction of species under RCP 2.6 - Figure 5.5). We predicted the narrow-ranging species would shift on average 99.4 km, 219.5 km and 283.6 km, while the wide-ranging group would shift on average 73.4 km, 110.3 km, and 156.3 km under RCP 2.6, RCP 4.5 and RCP 8.5 respectively.

There was no significant difference in distances between the two groups. The shift distance increased from the low to high RCP scenarios.

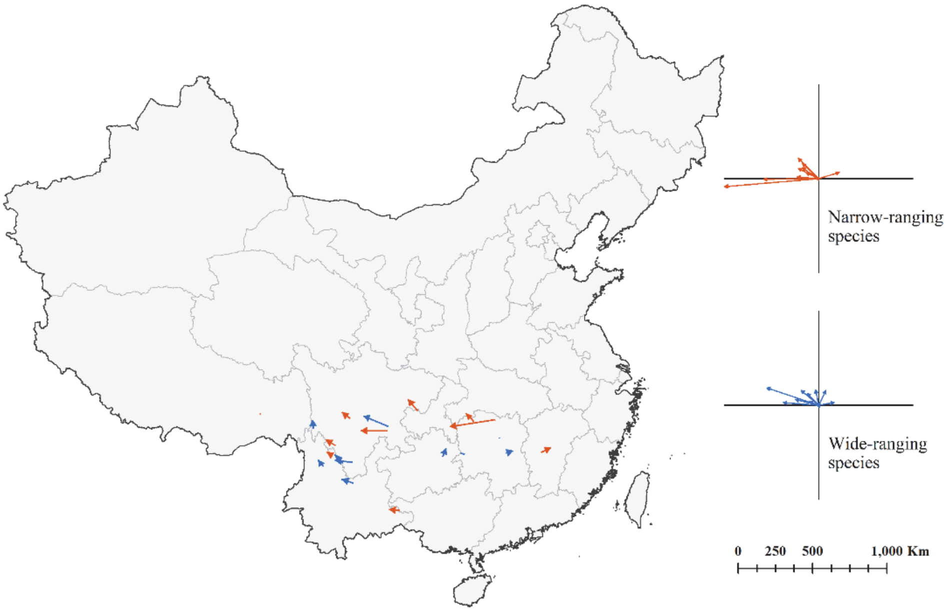


Figure 5.5 Map of core range shifts depicts the predicted change on suitable areas (based on the centres of their distributions) of narrow-ranging (red arrow) and wide-ranging (blue arrow) Rhododendron species. Each line depicts the distance and direction of change at the centroid of distribution of species from current (2010, start of arrow) to 2070 (end of arrow) under RCP 2.6. The wind roses summarize the distance and direction of shift for two groups

5.3.2 Relative contributions of climate and land use change to the future distribution of Rhododendrons

Both climatic and land use factors play a role in determining the distribution of Rhododendron species across the three scenarios, with relative impacts that are species-specific (Figure 5.6). In general, climatic variables contributed greatly, with isothermality (Bio3) and precipitation of driest month (Bio14) providing 26.0% and 24.7% of the contribution to distribution of narrow-ranging species. Temperature seasonality (Bio4) and annual precipitation (Bio12) were the most important variables for wide-ranging species, with an average contribution of 41.1% and 25.3%. The minimum temperature of coldest month (Bio6) ranked the third important factor for both narrow-ranging and wide-ranging species, the contribution being 14.7% and 12.8% respectively. In contrast, land use had a more significant contribution to models for narrow-ranging species, with an average of contribution of 8.3%, but varying between 2.9% to 27.1%. For wide-ranging species, the contribution of land use varied from 0.2% to 4.9%.

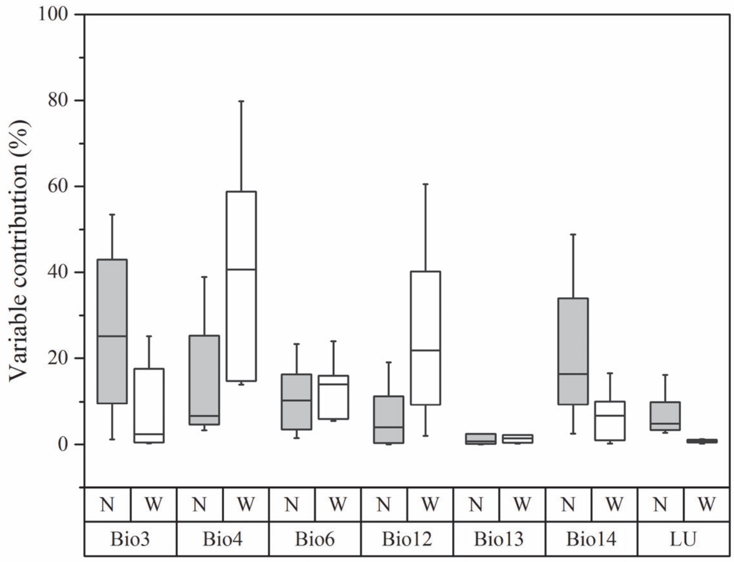


Figure 5.6 Importance of climate and land use for the narrow-ranging (N) and wide-ranging (W) Rhododendron species

5.4 Discussion

5.4.1 Future distribution of Rhododendrons under climate and land use change

Our results show that Rhododendron species generally will be negatively affected by the anticipated climatic and land use change for 2070, but some narrow-ranging species may be positively influenced. The variation of distribution change for narrow-ranging Rhododendron species is more significant than it is for the wide-ranging Rhododendron species. This results are consistent with previous studies which showed that some plant species may expand their distribution, while others experience range loss or even go extinct under global change (Pompe et al., 2008). In a broader sense, a species' geographical range can be used as a proxy for its ecological well-being. Species with small ranges are regarded as more vulnerable to extinction (Davies et al., 2009), because species with a limited distribution typically possess narrower ecological tolerances, and even slight environmental change may affect those species (Murray et al., 2011). Species with wider distribution ranges are expected to be more resilient to climate and land use change (Williams et al., 2006; Carrillo-Angeles et al., 2016). However, impacts of climate and land use change may have a disproportionate effect on some closely related species or clades (Zhang et al., 2017). It is possible that narrow-ranging species, which occupy warm climatological niches, will persist or even benefit from the climate change (Barry et al., 1995; Frishkoff et al., 2016), while other narrow ranging species may go extinct. In this study, we grouped narrow- and wide-ranging species based on their geographical ranges. In a previous study we found that species with narrow geographical ranges may have large elevational ranges (Yu et al., 2017). The results of the current study confirmed that species which are both geographically and elevationally narrow ranging (e.g. *R. changii* in this study) will be most vulnerable under climate and land use change. Species that have a narrow geographical range, but a relatively wide elevational range (e.g. *R. viridescens* in this study), may have a wider tolerance to climate variability, which implies a possibility of future expansion (Valladares et al., 2014), We suggest that the elevational range and geographical range should be considered together when evaluating the distribution change of narrow-ranging species. Lenoir and Svenning (2015) also advocated using multi-facetted approaches, at least two geographical dimensions (latitude and elevation) simultaneously, to assess distribution shifts or abundance change either at the leading edge, the trailing edge or the optimum positions.

Poleward shifts and shifts to higher elevations are the most frequent types of range shifts that have been reported in response to contemporary climate change. However, the number of reports documenting other types of range shifts, such as in east-west directions across longitudes or, even more unexpectedly, towards tropical latitudes and lower elevations is rapidly increasing (Lenoir & Svenning, 2015).

5.4.2 Role of climate and land use change in regulating the distribution of Rhododendrons

Our results indicate that climate change has a more significant effect than land use change on the distribution of Rhododendron species. There are three possible reasons, the first one is a scale issue. Previous studies proposed that land use change may outweigh the effect of climate change on species and ecosystem at finer scales (habitat to landscape, < 20 years), while climate change has been proven to be more important at broader spatial and temporal scale (regional to continental, > 50 years) (Sirami et al., 2016). In our case, the influence of climate change may override the effect of land use change, and play a more prominent role in distribution of Rhododendrons at the continental extent and the 60-year prediction horizon. A second reason could be that Rhododendrons generally grow at middle to high elevation regions, where climatic change are more dominant. Meanwhile, the relatively more intense effects of land use on narrow-ranging Rhododendron species confirm that narrow-ranging species tended to be affected by land use (Walker & Preston, 2006; Newbold et al., 2013), especially those that grow at low altitudes. The pronounced effect of land use change on plant distribution at the low altitude has been demonstrated in other studies (Feeley & Silman, 2010). Thirdly, it could be that there are strong correlations between land use change and climate change. It is difficult to test for collinearity issues between categorical and continuous variables, and hence that test was not performed here, but it seems reasonable to assume that climate change will affect how land use changes.

5.4.3 Implications for Rhododendrons conservation in China

Rhododendrons play a vital role in providing the structure of plant communities which support a wealth of biodiversity in the Himalayas. The generally shrinking distribution of most Rhododendron species would lead to potentially negative consequences for biodiversity and ecosystem functioning in the Himalayas. To the best of our knowledge, there is currently only one study about the future distribution of Rhododendrons, in which Kumar (2012) concluded that the distribution of Rhododendron species will shrink considerably under envisaged climate change scenarios in the Sikkim region of the Himalayas. However, this conclusion was based on the prediction of tree species of Rhododendrons with a total of 63 occurrences, and land use change was not included. Ma et al. (2014) reported that the rising demand for farming land, construction of roadways, hydro-electric power stations, and more recently developments associated with the tourism industry, have all collectively placed considerable pressure on Rhododendron species in China. The projected extinction for *R. changii* in our study can be regarded as a representative narrow-ranging species – where land use has a great influence on its distribution (variable importance was 9.9%). This is consistent with the description of The Red List of Rhododendrons - '*R. changii* is restricted to a single locality (Jinfoshan, Chongqing) which is a popular tourist site, and the forest habitat is under significant pressure and disturbance' (Gibbs et al., 2011). We also noticed that *R. changii* has a very narrow elevational range which is from 2000 to 3000 m, which implies that species on mountain ranges with narrow geographical and elevational ranges will experience higher risks of extinction in the future. In addition, we emphasize that *R. changii* is only one of the many Rhododendron species which have a small population, and most of these rare species did not even qualify as candidate model species because of the limited number of available records. Those species are actually more likely to be affected by either climate or land use change. Of the 246 endemic species, there are 27 species whose occurrence records contained less than 10 entries. Most of these species are critically endangered. Ma et al. (2014) conducted a field investigation for the conservation status on 10 critically endangered or endangered Rhododendron species in China. They concluded that species that grow at low altitudes and in disturbed habitats, should be given priority for ex- and in-situ conservation. We emphasize that indeed there is an urgent need for more comprehensive field surveys of Rhododendron species. Besides the critically endangered species ranked by The Red List of Rhododendrons (Gibbs et al., 2011), attention also should be given to endemic species that have narrow elevational ranges.

Chapter 6

Synthesis: Achieving the Convention on Biological Diversity’s goals for plant conservation

6.1 Introduction

It is widely recognised that biodiversity is being lost rapidly on a global scale, with humans having a significant impact on natural systems (Rockstrom et al., 2009; Steffen et al., 2015). The Convention on Biological Diversity (CBD), initially committed to achieve a significant reduction in the rate of biodiversity loss, as witnessed in 2002, by 2010. Evidence suggests that the 2010 biodiversity target has not been met (Butchart et al., 2010). Biodiversity indicators are defined as statistical measures of biodiversity that help scientists, managers, and politicians understand the condition of biodiversity, and factors that affect it (IUCN, 2015). Biodiversity indicators are identified on the premises that they carry key information for assessing progress towards the targets set by the CBD (Pettorelli et al., 2016a). The CBD parties agreed on a new set of 20 targets for the period 2011-2020, which are known as the 'Aichi Biodiversity Targets' (CBD, 2010). These targets are echoed in the United Nations' newly approved Sustainable Development Goals (SDGs), in particular, SDG's 15 that concern the conservation of terrestrial ecosystems (Hill et al., 2016).

Since the launching of the 'Aichi Biodiversity Targets', 160 biodiversity indicators have been determined that provide information for these targets (Tittensor et al., 2014). However, tracking biodiversity change is not as not simple as, for instance, measuring rainfall or temperature. A change in biodiversity can be related to extinction, shifts in range, change in abundance, or loss of genetic diversity (Walters, 2013). Different indicators may give differing results because they sample different places or taxa, or because they calculate change relative to different baselines (Hill et al., 2016). In view of the complexity and challenges, Pereira et al. (2013) proposed six classes of tentative Essential Biodiversity Variables (EBVs) on the basis of commonalities in order to help observation communities to monitor biodiversity change in a harmonious way. Skidmore et al. (2015) further proposed ten satellite remote sensing based EBVs (RS-EBVs), ranging from leaf nitrogen and chlorophyll content to seasonal change in floods and fires, to aid monitoring progress towards the 'Aichi Biodiversity Targets'. EBVs are characterized by: (1) being sensitive to change over time, (2) focus on 'state' of biodiversity, and (3) falling between low-level observation and high-level indicators of biodiversity change (Pettorelli et al., 2016b). Using EBVs could help prioritize data mobilization and modelling efforts to facilitate data integration over large spatial scales and across a broad taxonomic spectrum (Geijzendorffer et al., 2016).

One of the EBVs - species occurrence, identified by both Pereira et al. (2013) and Skidmore et al. (2015) - is the most widely collected piece of biodiversity information (Walters, 2013). Species occurrence, derived from field observations, from data found in museum collections and herbaria, and from remotely sensed data, can be used to build distribution maps, calculate diversity information (Jetz et al., 2012), and predict species range shifts (Guisan et al., 2013). Species occurrence records therefore provide data for biodiversity indictors. For instance, the Red List Index (RLI), a well-established indictor to describe the 'state' of biodiversity, measures changes in number of threatened species. It requires data from IUCN Red List categories which use species occurrence for calculating population size, range size, and abundance of species (Bubb, 2009). In addition, Protected Areas coverage (PAs), a commonly used indicator to depict the 'response' of biodiversity (Chape et al., 2005; Le Saout et al., 2013), provides multiple benefits for biodiversity conservation and sustainable development. The establishment of protected areas is mainly based on the location of hotpots of species richness, endemism or number of threated species (Mulongoy, 2004), which are also originally derived from species occurrence. The RLI and PAs are mainly related to Archi Target 11 (i.e. creating protected areas) and Target 12 (i.e. preventing the extinction of threatened species). These two targets represent the more traditional targets, but are of crucial importance in biodiversity conservation (Marques et al., 2014). The CBD puts great emphasis on in-situ conservation of variable populations and calls for the establishment and higher effectiveness of protected areas (Montesino Pouzols et al., 2014).

To protect biodiversity, biogeographical theory and principle have played fundamental roles in estimating extinction rates and establishing protected areas (Cox et al., 2016). For example, the Theory of Island Biogeography (TIB) suggests that habitat loss has a strong and consistently negative effect on biodiversity, whereas simply breaking up a habitat (fragmentation without appreciable habitat loss) has much less impact, which may even be positive or negative (MacArthur, 1967). Based on the TIB, Diamond (1975) proposed that the number of species in a protected area can maintain will be a function of its geographical area and its degree of isolation. In addition, range size criteria are an important part of the IUCN's evaluation system for its Red List of Endangered species (Cox et al., 2016). Influential schemes such as the biodiversity indicator partnership (BIP, www.bipindicators.net), conservation international's biodiversity hotspots (Myers et al., 2000), and WWF's ecoregions (Olson et al., 2001) are firmly grounded in biogeographical analysis (Cox et al., 2016).

Based on species occurrences of Rhododendrons, and biogeographical theory and analysis, this thesis investigated patterns, determinants, hotspots, and future change in distribution and diversity of Rhododendrons in China. Chapter 2 and Chapter 3 examined Rhododendron species/diversity - environment relationships. The results showed that topographic complexity is positively correlated with Rhododendron species richness, while climatic niche breadth, especially the range of seasonal variability, can explain variation in geographical range size of Rhododendrons. Chapter 4 predicted Rhododendron diversity patterns, and identified hotspots and priority areas for Rhododendron species. In total, 12 general hotspots, and five separately discerned hotspots were detected for general and threatened Rhododendron species, respectively. Chapter 5 predicted the distribution of geographical narrow- and wide-ranging Rhododendron species under climate and land use change, which demonstrated that narrow-ranging and threatened Rhododendron species are facing a high risk of extinction in the near future. Generally, the results in this thesis not only strengthen the scientific basis for designing protected areas and protecting threatened species, as aimed for in Archi target 11 and 12 of the CBD, but also provide specific suggestions about where and which Rhododendrons should be protected s in China.

6.2 Diversity and distributions - What are the roles of species distribution models?

The past decade has seen a surge in the development of species distribution models (SDMs) for supporting spatial conservation decision making (Margules & Pressey, 2000; Franklin, 2013; Guisan et al., 2013). Species and biodiversity are not distributed uniformly across the globe, and knowledge of the geographical distribution of most species is incomplete (Wallacean shortfall). Records of observed species occurrence typically provide information on only a subset of sites occupied by a species (Mateo et al., 2013). SDMs, linking species occurrence with environmental predictors, are widely used to explain and predict species distributions (Merow et al., 2014). In recent years, SDMs have been used to model biodiversity at community level (Ferrier & Guisan, 2006) by stacking (overlapping) individual species distributions, known as stacking species distribution modelling (SSDM).

In our study, SDMs were used as basic tools for explaining species ranges, predicting diversity patterns, and predicting species range shifts. Specifically, in Chapter 3, we ran the maximum entropy model (MaxEnt), a species distribution model with 27 environmental variables for exploring the environmental factors determining the distribution of Rhododendron species with different geographical and elevation range sizes. In Chapter 4, we used a spatially explicit species assemblage modelling approach (SESAM) that integrates SSDM and macro-ecological modelling (MEM) to predict spatial patterns of species richness, β-diversity, and weighted endemism, and to detect Rhododendron diversity hotspots. In Chapter 5, we applied MaxEnt to predict the shift in distribution range for Rhododendrons by the year 2070 according to three different scenarios in climate and land use change. The SDMs showed high model performance, when evaluated by AUC, TSS, and the Boyce index in our studies. Combined with geospatial analyses, SDMs provided a relatively complete picture of diversity patterns, hotspots, and future distributions of Rhododendrons in China.

Nevertheless, we did not neglect to emphasize the complexity of the application of SDMs for conservation. SDMs are not free of error and uncertainty. Factors that affect the accuracy of results from SDM modelling efforts include sample size, sampling bias, selection of predictor variables, spatial extent and resolution, as well as spatial autocorrelation. However, approaches such as selecting endemic species with more than 10 or 30 occurrences, choosing appropriate environment predictors with low collinearity and background samples, and a priori justification of model settings, as we have implemented in our studies, can reduce uncertainty to some extent.

On the whole, despite the limitations, our results confirmed the usefulness and flexibility of SDMs in species (Chapter 3 and Chapter 5) and biodiversity (Chapter 4) conservation.

6.3 Identifying conservation priority areas – Do diversity metrics and scale matter?

Establishing protected areas is one of the main tools for halting the continuing global biodiversity crisis (Rodrigues et al., 2004; Le Saout et al., 2013), while gap analysis is used to find an answer to the question of how much land area needs to be protected to meet the CBD targets. Aichi Target 11 sets out a series of quantitative goals to protect 17% of terrestrial and inland water area, and 10% of marine and coastal ecosystems in areas of particular importance for biodiversity. These protected areas should be ecologically representative, effectively managed and connected. However, without guidance on what important, representative, and effective area-based conservation measures are, efforts to achieve Target 11 may fail (Watson et al., 2016). The conservation science community therefore needs to provide guidance, definitions, methodologies, and metrics.

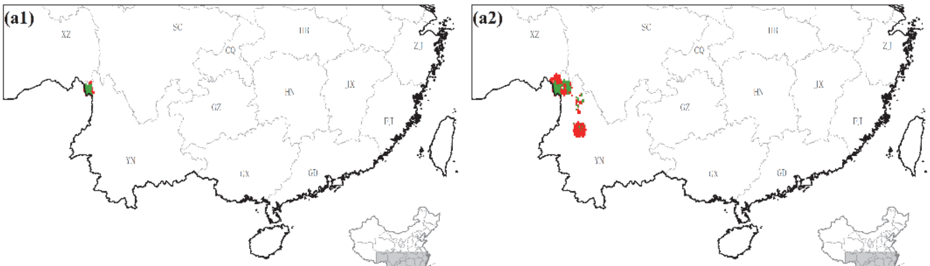
A scientific approach to how to identify biodiversity hotspots may provide essential guidance for designing and establishing a protected area framework (Jepson et al., 2011). Biodiversity hotspots, representing high species richness or high numbers of endemic or threatened species, form key areas that need to be embedded and emphasized in a protected area framework (Mulongoy, 2004). Using three metrics of diversity (i.e. species richness, β-diversity, and weighted endemism), Chapter 4 identified 12 hotpots in total, and proposed five priority areas where threatened Rhododendron species are in need of urgent protection. Seven of the 12 hotspots are considered to be endemism centres of Chinese plant taxa (Lopez-Pujol et al., 2011), and eight are considered to be hotspots of Chinese threatened plant species (Zhang & Ma, 2008). The results of gap analysis showed that only 25.7% of the Rhododendron hotspots are covered by the 2,139 nature reserves (i.e. currently protected areas) in China.

It is worth noting that hotspot locations may differ depending on how the hotspot is defined. Various biodiversity metrics, including species richness, weighted endemism, phylogenetic diversity, and biogeographically weighted evolutionary distinctiveness, have been used to portray species diversity, define hotspots and select priority areas for conservation (Huang et al., 2016; Pardo et al., 2017). In our study a demonstration of different hotspot locations using various metrics at different levels of spatial congruence can be seen in Figure 6.1. Our results demonstrated that species richness, β-diversity, and weighted endemism are complementary metrics of diversity, which can represent biodiversity and facilitate the optimal spatial arrangement of conservation areas. We advocate that these three metrics are employed together for identifying hotspots, to provide a more comprehensive assessment of species diversity, consequently leading to more informed conservation prioritization. Other metrics may provide more information for the utility of hotspots as a conservation tool; this will depend on whether these metrics are richness- and endemism-independent (Pardo et al., 2017).

Scale issues have clear relevance for the development of strategic conservation frameworks (e.g. protected areas) (Cox et al., 2016). Protected area selection criteria are based on species distribution and diversity data, which are sensitive to the scale of analysis employed (Richardson, 2005). Both spatial extent and spatial grain matter.

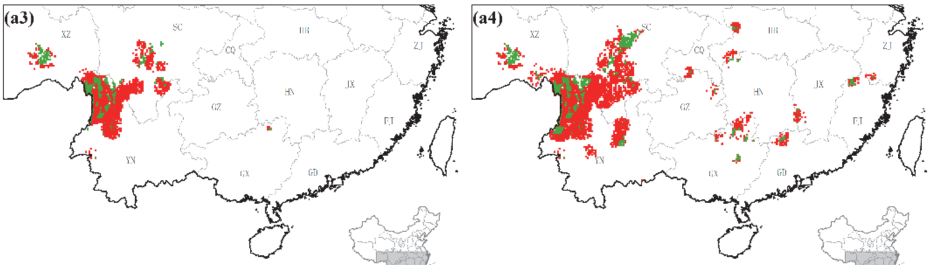
Regarding spatial extent, the CBD identifies nations as the main actors in the implementation of the Aichi Targets. Studies have found that much more effective solutions can be reached by planning conservation at national/continental/global level than at local level (Moilanen et al., 2013; Kullberg & Moilanen, 2014). All studies for this thesis were therefore carried out across all of China. Regarding spatial grain (resolution) should be mentioned that within the extent of a country, a finer spatial grain could well support decision-making relevant to Aichi Target 11 more effectively. However, not many countries have conducted a broad-extent analysis with fine resolution (Kullberg & Moilanen, 2014). Chapter 4 detected hotspots using a grain cell of 10 km × 10 km, which was the finest resolution possible given the input species and environmental data. Also, when using a finer spatial grain the identification of hotspots based on different metrics tends to show more inconsistencies (Prendergast et al., 1993). Therefore, a basic grid cell size for data analysis should be taken into account when designing protected areas. The grid cell size should be fine enough to present detailed diversity information, but large enough to capture the congruence of various metrics.

In summary, finding a balance in the selected diversity metrics, the level of spatial congruence of diversity metrics, and the spatial scale (both extent and grain) is critical in protected area design (Ceballos & Ehrlich, 2006; Marsh et al., 2010; Zhao et al., 2016). We suggest that all these factors are considered jointly when identifying hotspots and establishing protected areas.



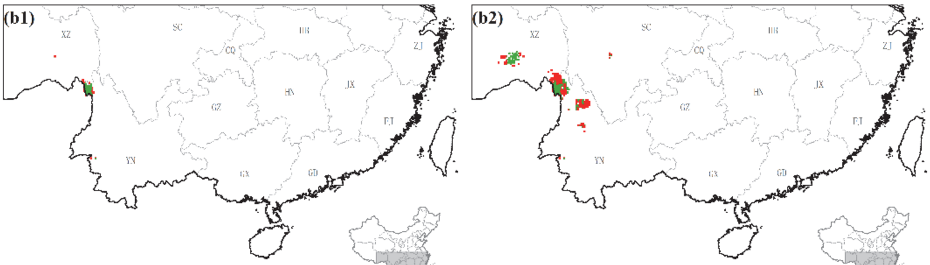
Top 1% of species richness

Top 5% of species richness



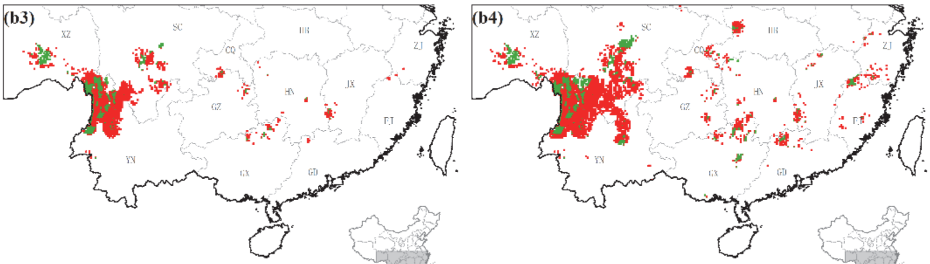
Top 25% of species richness

Top 50% of species richness



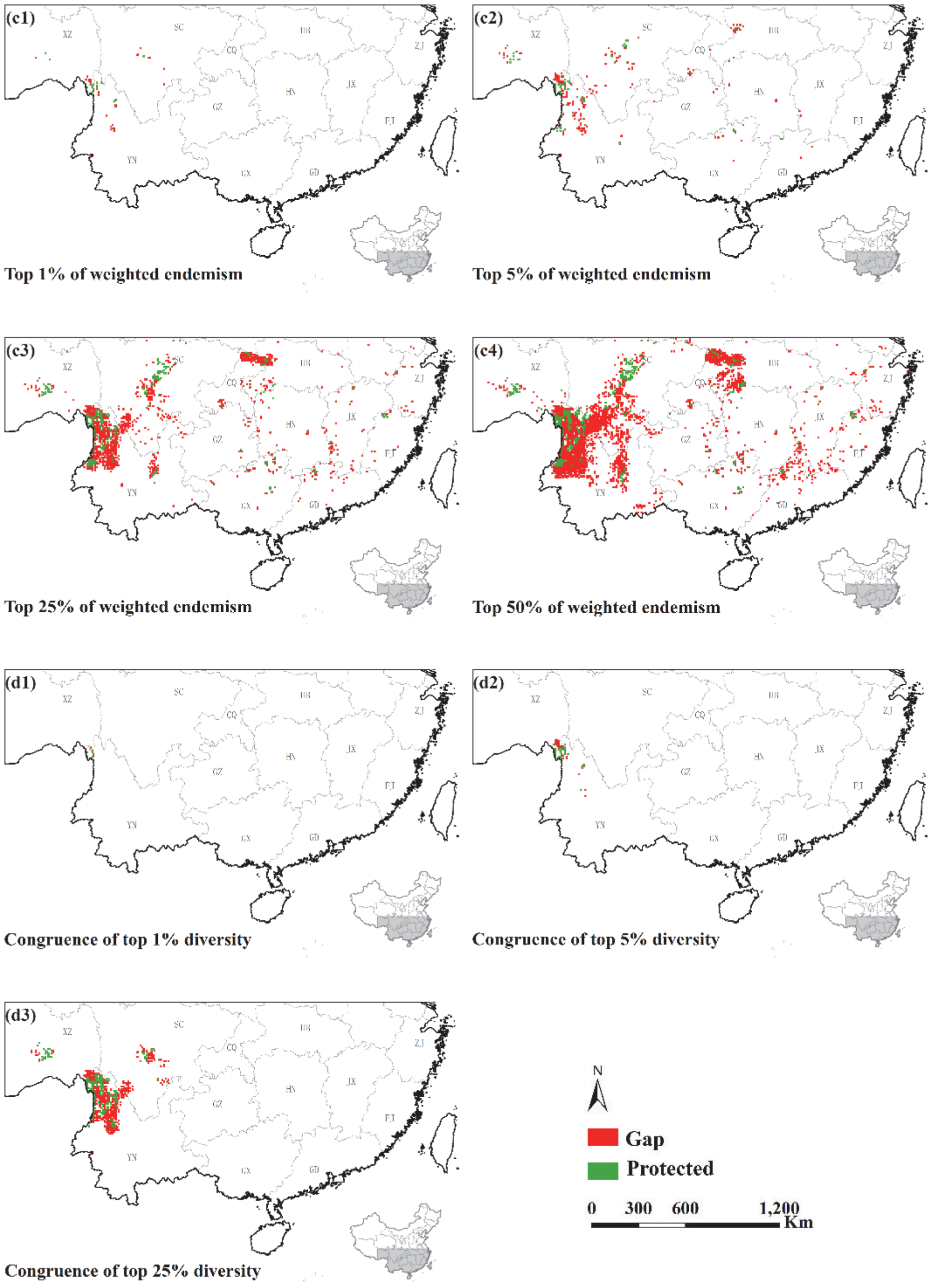
Top 1% of β-diversity

Top 5% of β-diversity



Top 25% of β-diversity

Top 50% of β-diversity



Top 1% of weighted endemism

Top 5% of weighted endemism

Top 25% of weighted endemism

Top 50% of weighted endemism

Congruence of top 1% diversity

Congruence of top 5% diversity

Congruence of top 25% diversity

Figure 6.1 Protected and gap areas of Rhododendrons at the top 1%, 5%, 25%, and 50% of Rhododendron occurring grid cells. a: species richness, b: β-diversity, c: weighted endemism, d: spatial congruence of a, b, and c

6.4 Conserving biodiversity in a changing world - What are the impacts of anthropogenic climate and land use change on narrow- and wide-ranging species?

Global climate and land use change pose a threat to biodiversity (Thomas et al., 2004; Newbold et al., 2016). Systematically planned protected areas aim to ensure representative samples of ecosystems are protected and threatened species' habitats are retained (Polak et al., 2016). The Aichi Target 12 refers specifically to preventing the extinction of threatened species. Target 11 and Target 12 are clearly connected, and both are central to biodiversity conservation (Marques et al., 2014).

Threatened species are those under the IUCN Red List Categories of Critically Endangered, Endangered, and Vulnerable (IUCN, 2001). In recent years, geographical range size has been used as a proxy measure for predicting extinction risk, as well as to prioritize species in need of conservation action in the face of rapid global environmental change (Thuiller et al., 2005; Pompe et al., 2008; Gallagher, 2016). Species with a small geographical range size, as is the case with many endemic species, could be more sensitive to both climate and land use change than species with a large geographical range size (Thuiller et al., 2005; Köster et al., 2013). Chapter 3 revealed that climatic niche breadth, especially the range of seasonal variability, could explain species' geographical range sizes. Chapter 4 identified five hotspots of threated Rhododendron species, but the protected ratio (i.e. percentage of hotspot areas protected by nature reserves) ranged only between 23.1% and 52.0%, which indicates that large areas are still unprotected and many Rhododendron species are still threatened (Figure 6.2). Chapter 5 confirmed that geographically narrow-ranging Rhododendron species were more vulnerable to climate and land use change than geographically wide-ranging Rhododendron species were (Figure 6.3). In addition, most geographically narrow- and wide-ranging species will probably be negatively affected by climate and land use change. However, some geographically narrow-ranging species may actually even be positively influenced, and expansion in the distribution of a species affected by environmental change has been noted at times

(Thomas et al., 2011; Warren et al., 2013), indicating that the impact of climate and land use change on species can be species-specific. In Chapter 3, we demonstrated that geographical and elevational range size of Rhododendrons were not significantly correlated and that elevational range size can be a complementary trait to geographical range size for alpine and subalpine plant species. Therefore, we propose that elevational range size be considered in assessing extinction risk of alpine and subalpine plant species in the face of rapid climate and land use change.

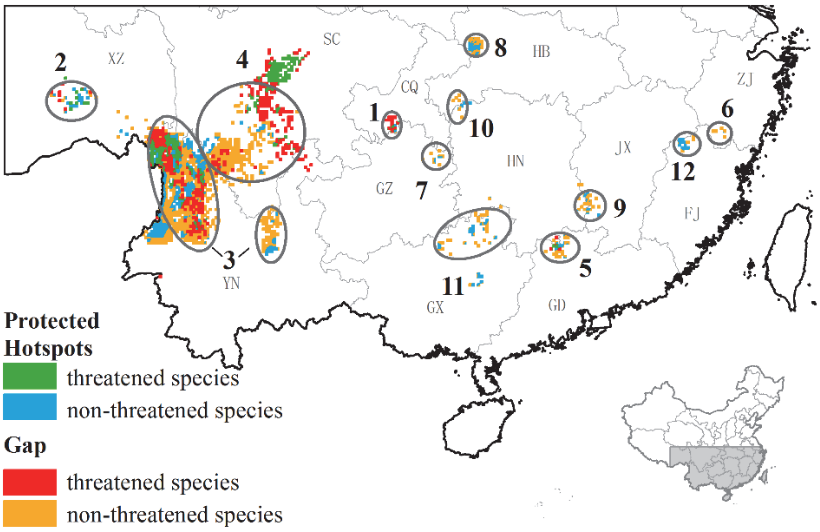


Figure 6.2 Hotspots and gap areas of threatened and non-threatened Rhododendron species. Hotspots are defined as the congruence of the richest 50% of grid cells of species richness, β-diversity, and weighted endemism of Rhododendrons. (1) southern CQ (Mt Jinfo), (2) south-eastern XZ, (3) Mt Hengduan (YN) and north-eastern YN, (4) southern SC (Mt Shaluli, Mt Daxue and Mt Qionglai), (5) northern GD (Mt Danxia), (6) southern ZJ, (7) north-eastern GZ (Mt Fanjing), (8) western HB (Mt Daba), (9) south-eastern JX, (10) south-western HB and northern HN, (11) northern GX (Mt Maoer and Mt Yuanbao), and (12) northern FJ

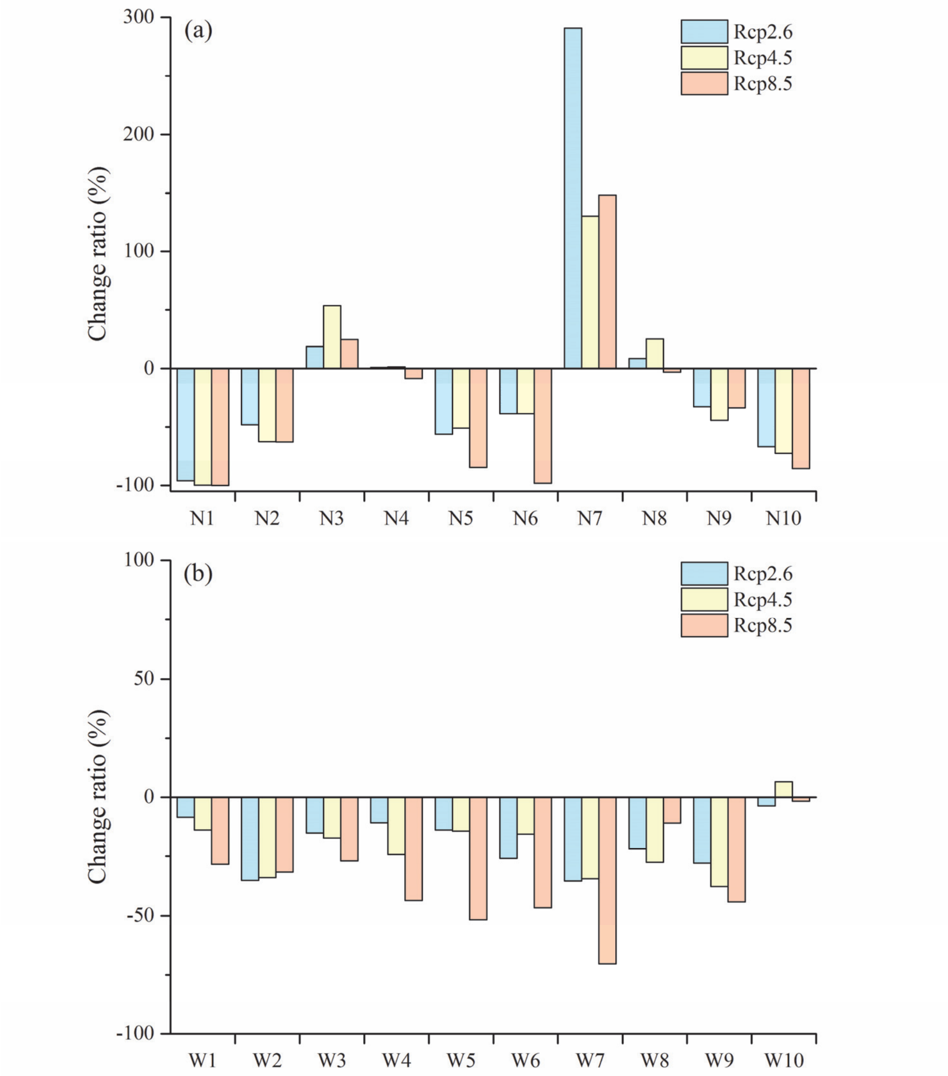


Figure 6.3 Change ratios of distribution areas for narrow-ranging (a) and wide-ranging (b) Rhododendron species under RCP 2.6, RCP 4.5, and RCP 8.5 for 2070. Species codes N1 to N10, and W1 to W10 are explained in Table 5.1

6.5 How does this thesis inform on biodiversity indicators?

This thesis examined drivers of the distribution of Rhododendron species, presented the state of Rhododendron diversity, and predicted the response of geographically narrow- and wide-ranging Rhododendron species under pressure of climate and land use change. The findings enable conservation efforts for Rhododendrons to be prioritized, but also contribute to two biodiversity indicators (i.e. The Red List Index and Protected Areas coverage) which are most important and commonly used for achieving the 'Aichi Biodiversity Targets', with a perspective of biogeography. The Red List Index and Protected Areas coverage are not only important indicators for measuring biodiversity loss for the CBD, but also to track Sustainable Development Goals (SDGs). SDG 15 proposes to protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss.

The Red List Index is found to be of particular value due to its ability to be disaggregated to report against various targets of the CBD (McOwen et al., 2016). The use of SDMs to quantify geographical range size as an alternative measure to extent of occurrence (EOO) and area of occupancy (AOO) is increasing in IUCN assessments (Breiner et al., 2017). EOO and AOO are measured in horizontal direction. Our results show that Rhododendron species with narrow geographical ranges do not necessarily have narrow elevational ranges. Both geographically and elevationally narrow-ranging species are more vulnerable to environmental change. But it is possible that geographically narrow-ranging species are positively affected by global environmental change, whilst a species with both a narrow geographical and elevational range may face a high risk of extinction. Therefore, elevational range should be taken into account for assessing the distribution of alpine and subalpine plant species. Lenoir and Svenning (2015) also advocated using multi-faceted approaches of at least two geographical gradients (horizontally and vertically) simultaneously to assess distribution shifts or abundance change either at the leading edge, the trailing edge or the optimal position.

To design robust protected area networks, the commonly used diversity metrics, species richness and weighted endemism, measure the richness and endemism (rarity) of hotspots (Laffan & Crisp, 2003). However, an important principle of systematic conservation planning is complementarity, which maximizes the total number of species saved with least effort required. This means identifying sites that complement one another rather than simply designating sites that are individually most diverse (Jepson et al., 2011). β-diversity measures the extent of change in community composition and provides a complementary analysis for assessing optimal reserve locations (Marsh et al., 2010; Socolar et al., 2016). Incorporating β-diversity into management decision-making can maximize the conservation effort (Karp et al., 2012) and investigate the placement of protected areas (Gering et al., 2003; Wiersma & Urban, 2005). Therefore, as the results shown in Chapter 4 advocate, a combination of species richness, weighted endemism, and β-diversity should be used in establishing and managing protected areas, because together they can provide a more comprehensive assessment of species diversity, as well as utilize the resources and conservation efforts optimally.

6.6 Future research

Future research may be undertaken with respect to species, spatial scale, and temporal scale.

Species: in view of the very few studies existing on such a large genus as Rhododendron, this thesis used Rhododendrons as indicator taxa to explore existing data using different types of analyses to generate new biogeographical knowledge for plant conservation. With the increasing availability of occurrence records of many species, harmonized and mobilized remote sensing based data (e.g. net primary productivity, land surface temperature, and vegetation height), and the development of cutting-edge modelling techniques (e.g. process-based range models), it will be possible to undertake further study based on geographical and elevational gradients, which may be more representative and robust.

Spatial scale: the spatial extent for the studies in this thesis has been China as a whole. Given that Rhododendrons cover a vast section of south-eastern Asia, including Nepal, Sikkim, and Bhutan, future research may be extended to Asia to verify the findings of this thesis.

Temporal scale: ensuring the survival of species in the long term is always a main aim of conservation. It is important to understand the temporal dynamics of biogeographical processes and predict species distribution and diversity for their conservation in a changing word. Future research may include exploring and understanding the Rhododendron - environment relationship in the past and making predictions for the future, including different dispersal scenarios.

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Summary

Global biodiversity continues to be lost, especially in face of rapid climate and land use change. Rhododendrons form a major biodiversity component of the montane ecosystem in the Himalayan subalpine and alpine zone. However, the Rhododendron genus is one of the most neglected groups of plants in terms of scientific inquiry. The Rhododendrons of China exhibit great diversity, however, knowledge of their spatial distribution at the national level are still poor, especially about narrow-ranging species which are usually endemic and tend to be threatened. Rhododendrons display a great variation in range size, some Rhododendron species occur throughout most of the northern hemisphere, while others are highly restricted to small regions. Therefore, examining and understanding determining factors of spatial distribution, diversity patterns, and potential response to environmental change of Rhododendrons can provide a sound base for the comprehensive conservation strategy for Rhododendrons which required to maintain the sustainable alpine and subalpine ecosystem, as well as expand our knowledge of biogeography for plant conservation.

The main goal is to investigate the biogeographical patterns and the underlying mechanisms of distribution and diversity of Rhododendrons for their conservation in a changing world. The research in this thesis firstly examined the correlations between eight topographic complexity indices and Rhododendron species richness in China at seven spatial scales, the results showed that topographic complexity has positive correlation with Rhododendrons species richness. Secondly, this thesis examined the relationship between geographical and elevational range sizes for 80 endemic Rhododendron species in China, and investigates the importance of basic factors (i.e. climate, topography, and soil) in shaping the distribution of Rhododendrons with various geographical and elevational range sizes. The results showed that climatic niche breadth, especially the range of seasonal temperature variability relative to diurnal temperature variability, can explain variation in geographical range size of Rhododendrons. Thirdly, this thesis predicted Rhododendron diversity patterns, and identified hotspots and priority areas for

Rhododendrons in China. Based on a combination of species richness, β-diversity, and weighted endemism, 12 general hotspots and five endangered species hotspots were detected. Lastly, this thesis predicted distribution of geographically narrow- and wide-ranging Rhododendron species under climate and land use change, which demonstrated Rhododendron species generally will be negatively affected by the climatic and land use change, narrow-ranging and threatened Rhododendron species are facing a high risk of extinction in the near future, but some geographically narrow-ranging species may be positively influenced.

This thesis demonstrates one of the Essential Biodiversity Variables (EBVs) - species occurrence, used to build distribution maps and calculate diversity information - provides fundamental data for biodiversity indicators that measure the progress of halting biodiversity loss which is the aim of Convention on Biological Diversity(CBD). Meanwhile, this thesis highlights that elevational range size should be taken into account for assessing the distribution shift of alpine and subalpine plant species. Species richness, β-diversity, and weighted endemism are complementary metrics of diversity, which can represent biodiversity and facilitate the optimal spatial arrangement of conservation areas. Balancing of the selected diversity metrics, the level of spatial congruence of diversity metrics, and spatial scale (both extent and grain) are critical as it may lead to diverging results of hotspots detection and protected areas design when used in isolation.

Samenvatting

Biodiversiteit blijft wereldwijd teruglopen, helemaal in het licht van snelle klimaat- en landgebruiksveranderingen. In de alpine en subalpine zones van de Himalaya vormen Rhododendrons een belangrijk onderdeel van het bergecosysteem. Rhododendrons zijn echter in zeer beperkte mate wetenschappelijk onderzocht. De Rhododendron soorten in China bestrijken een grote diversiteit, maar kennis over hun ruimtelijke verspreiding op nationaal niveau is beperkt, vooral wat betreft soorten met een beperkt verspreidingsgebied. Deze soorten zijn vaak endemisch en hebben een verhoogd risico om bedreigd te zijn. Rhododendron soorten laten een grote variatie zien in verspreidingsbereik. Sommige soorten kunnen over bijna het gehele noordelijk halfrond gevonden worden terwijl andere soorten beperkt zijn tot kleine leefgebiedjes. Het begrijpen van de factoren die de ruimtelijke verspreiding van Rhododendrons bepalen en studies naar de patronen in hun diversiteit en hun mogelijke respons op veranderingen in omgevingsomstandigheden kunnen een basis vormen voor wetenschappelijk gefundeerde beschermingsmaatregelen. Deze zijn nodig om duurzaame alpine en subalpine ecosystemen te behouden. Daarnaast vergroten zulke studies onze kennis over het gebruik van biogeografische kennis voor de bescherming van plantensoorten.

Het hoofddoel van dit proefschrift is om de biogeografische patronen en onderliggende mechanismen voor de verspreiding en diversiteit van Rhododendrons in een veranderende wereld in kaart te brengen om ze te kunnen beschermen. Als eerste zijn de correlaties tussen acht topografische complexiteits indicatoren en Rhododendon soortenrijkdom onderzocht op zeven verschillende ruimtelijke schalen. Dit liet zien dat er een positief verband is tussen topografische complexiteit en soortenrijkdom van Rhododendrons. Ten tweede is in dit proefschrift de relatie tussen het verspreidings- en hoogtebereik van 80 endemische Rhododendron soorten in China onderzocht, en hoe basis factoren (klimaat, topografie en bodem) een rol spelen in de verspreiding van soorten met een uitgebreid en beperkt bereik (zowel geografisch als qua hoogtebereik). De resultaten lieten zien dat de klimatologische "nichebreedte" van een soort, en dan vooral variatie in temperatuur tussen seizoenen in verhouding tot de dagelijkse temperatuursvariatie, de variatie in geografisch bereik van soorten kan verklaren. Ten derde geeft dit proefschrift een schatting van de ruimtelijke patronen van Rhododendron diversiteit. Op basis van deze patronen zijn diversiteits hotspots en gebieden met beschermingsprioriteit in China geïdentificeerd. In totaal zijn op basis van een combinatie van soortenrijkdom, β-diversiteit en gewogen endemisme, 12 algemene hotspots en vijf hotspots voor bedreigde Rhododendron soorten geïdentificeerd. Ten slotte wordt in dit proefschrift een schatting gemaakt van de toekomstige verspreiding van soorten met een uitgebreide of een beperkte verspreiding als gevolg van klimaats- en landgebruiksverandering. Dit liet zien dat soorten over het algemeen negatief worden beïnvloed door deze veranderingen. Vooral bedreigde soorten en soorten met een beperkte verspreiding lopen het risico uit te sterven in de nabije toekomst vanwege habitatverlies, hoewel een enkele soort ook baat lijkt te hebben bij de geprojecteerde veranderingen.

Dit proefschrift laat zien dat een van de Essentiele Biodiversiteits Variabelen (EBV's) – het voorkomen van een soort, welke gebruikt werd om verspredingskaarten te maken en diversiteits informatie te bepalen – fundamentele informatie geeft voor biodiversiteitsindicatoren. Deze zijn nodig om de voortgang van het beteugelen van biodiversiteitsverlies te bepalen, wat een van de doelen van het Verdrag inzake Biologische Diversiteit (CBD) is. Tegelijkertijd laat dit proefschrift zien dat het hoogtebereik van een soort belangrijk is om de verschuiving in de verspreiding van alpine en subalpine plantensoorten te bepalen. Ook laat het proefschrift zien dat soortenrijkdom, β-diversiteit en gewogen endemisme complementaire indicatoren voor diversiteit zijn, die gebruikt kunnen worden om biodiversiteit aan te geven en kunnen helpen bij de ruimtelijke planning van beschermde gebieden. Het is belangrijk om deze diversiteitsindicatoren te balanceren en op de juiste ruimtelijke schaal (zowel qua omvang als resolutie) de overlap van deze indicatoren te overwegen omdat ze individueel tot verschillende resultaten kunnen leiden wat bereft het identificeren van hotspots en het aanwijzen van beschermde gebieden.

Biography

Fangyuan Yu was born on 18 October, 1985 in Xinjiang, China. She received the BSc degree in Geographic Information System from Northwest A&F University in 2007. She worked as a research assistant from July of 2007 to August of 2008 at Institute of soil and water conservation, Northwest A&F University. She started her Msc in Land Resources and Spatial Information Technology at Northwest A&F University from September of 2008, and got the MSc degree in June of 2011. In the same year, she was awarded a four-year doctorial scholarship from the China Scholarship Council (CSC), and started to pursue her PhD at the Faculty of Geo-Information Science and Earth Observation (ITC), University of Twente. Her research interest lies in spatial ecology, biogeography, and biodiversity conservation.

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