




The drivers of high *Rhododendron* diversity in south-west China: Does seasonality matter?

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Funding information

National Natural Science Foundation of China, Grant/Award Number: #31650110471, #31522012, #31470564, #31621091

Editor: Hanno Schaefer

Abstract

Aim: Is high diversity in tropical and subtropical mountains due to topographical complexity alone or a combination of topography and temperature seasonality? Here, we aim to assess the contribution of these two factors on *Rhododendron* diversity in China. Specifically, we evaluate how low temperature seasonality in subtropical China jointly with heterogeneous environment accounts for increased species diversity across montane landscapes relative to those of the more seasonal temperate zone in north China.

Location: China.

Methods: We compiled distributional data for all *Rhododendron* species in China and then estimated the species richness patterns of rare versus common species, and of shrubs versus trees at spatial resolutions of 50 × 50 km. Bivariate regressions were performed to evaluate the effects of environmental variables on species richness followed by stepwise regression to select the best set of predictors.

Results: The variables of habitat heterogeneity and climate seasonality were consistently the strongest predictors of species richness for all species groups, while the contribution of water and energy variables was proportionately much lower. Winter coldness had very low predictive power, which indicated that unlike other woody plants, the northward dispersal of *Rhododendron* is not limited by cold winter temperature.

Main conclusions: High *Rhododendron* diversity in south-west China appears to be influenced jointly by the climatic gradients induced by topographical complexity and temperature seasonality as suggested by Janzen's hypothesis. The increased topographical complexity in combination with low temperature seasonality in south-west China might have promoted species accumulation by offering more niche space, preventing extinction and providing increased opportunities for allopatric speciation. While our findings strongly indicate the effect of habitat heterogeneity on species diversity, they also suggest the role of seasonal uniformity of temperature for increased diversity towards the tropics. The effect of seasonality may, however, be more pronounced in plants because of their limited ability to use behaviour to avoid environmental influences.

KEYWORDS

climate seasonality, habitat heterogeneity, Janzen's hypothesis, latitudinal diversity gradient, species richness, tropical mountains



1 | INTRODUCTION

The latitudinal gradient in species richness (high diversity in the tropics and low in the temperate) is a well-known biological phenomenon, which has puzzled ecologists since the early 19th century (O'Brien, 1993). The mechanism underlying this pattern has remained one of the most controversial issues in ecology and biogeography (Rosenzweig, 1995). Several hypotheses have been proposed to explain this unique diversity gradient (Currie et al., 2004), which can be broadly grouped into environment based hypotheses (e.g. water, energy, seasonality, heterogeneity, etc.) and those based on evolutionary history (e.g. niche conservatism hypothesis). For example the energy hypothesis states that the regions with higher energy availability, measured in terms of mean annual temperature or potential evapotranspiration, harbour more species (Currie, 1991), whereas the water–energy dynamics hypothesis states that species richness is determined by the combined effects of water and energy (Francis & Currie, 2003; O'Brien, 1998). The niche conservatism hypothesis (also known as freezing tolerance hypothesis), which integrates the effect of contemporary climate with the evolutionary history, states that species richness is primarily determined by winter coldness because most species evolved in tropical-like climate and hence have difficulties to colonize cold temperate regions due to niche conservatism (Latham & Ricklefs, 1993; Wiens & Donoghue, 2004; Wiens, Graham, Moen, Smith, & Reeder, 2006). Despite a number of theories, ecologists have, however, failed to arrive at a common consensus, partly because the primary forces driving species richness have been found to vary across taxa and regions (see Rahbek & Graves, 2001).

Among the many hypotheses, which regard contemporary climate as the primary determinant of species richness, Janzen's hypothesis (Janzen, 1967) states that the elevationally separated sites in tropical latitudes have little overlap in their thermal regimes at any given time, whereas in temperate latitudes the thermal regimes of lowlands and highlands overlap with each other due marked seasonal variation in temperature. Therefore, this hypothesis suggests that it is this uniformity in temperature at tropical localities that creates barrier between lowland and highland species, which ultimately leads to reduced gene flow and hence promote allopatric speciation (see Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006 for detailed discussion). It provides plausible explanation for high tropical diversity, though not explicitly stated. This hypothesis assumes that the magnitude of temperature gradient across the elevation acts as an effective barrier to species dispersal in tropical mountains (Ruggiero & Hawkins, 2008). Although it was proposed almost 50 years ago, this hypothesis is one of the least understood and barely tested hypotheses (but see Ruggiero & Hawkins, 2008; Wiens et al., 2006) and has remained at the centre of debates of latitudinal gradients in diversity since its publication (Schemske, 2002).

Another recently formalized environment based hypothesis is the habitat heterogeneity hypothesis (Stein, Gerstner, & Kreft, 2014; Stein & Kreft, 2015; Stein et al., 2015), which assumes that species'

existence largely depends upon available niche space. According to this hypothesis, heterogeneous habitats offer diverse niche space due to increased habitat types and hence promote co-existence of many species (Tews et al., 2004). Heterogeneous habitat is also believed to promote species persistence by providing shelter and refuges during period of climate change (Fjelds , Bowie, & Rahbek, 2012). There is widespread empirical evidence from many taxonomic and functional groups supporting positive heterogeneity–diversity relationship (Hortal, Triantis, Meiri, Th bault, & Sfenthourakis, 2009; Tews et al., 2004). However, there are several other studies, which have supported, either negative or non-significant relationship between heterogeneous habitat and species richness (e.g. August, 1983; Coyle & Hurlbert, 2016; Laanisto et al., 2013; Lundholm, 2009). Therefore, the role of habitat heterogeneity in determining species richness patterns is prone to controversy.

Rhododendron L. is one of the largest genera of flowering plant comprising ca. 1000 species globally (Milne, Davies, Prickett, Inns, & Chamberlain, 2010). It exhibits striking latitudinal gradients in species richness from tropics to the north. One of the interesting features of this group is its notable diversity and endemism in China (c. 60% of all species occur in China) and the Pacific islands (i.e. along the subtropical and tropical latitudes) (Irving & Hebda, 1993). Although the diversity is greater in the tropics and the subtropics, it is found only along the mountain slopes in these regions, which indicate the strong affinity of the genus for cooler temperatures. Therefore, unlike most other tropically diverse groups, the climatic preference of *Rhododendron* exhibits a striking pattern (groups with high tropical diversity usually have low preference for cool climates). The factors that may have contributed to a high diversity of this temperate adapted group in tropical and subtropical mountains, however, remain largely elusive. We do not know if high *Rhododendron* diversity in the mountains of south-west China is the result of increased topographical complexity (Stein et al., 2014) or a combination of topography and seasonal variation in temperature as proposed by Janzen (1967).

Here, we assess the relative importance of contemporary environment, particularly habitat heterogeneity and climate seasonality on the latitudinal gradient of species richness using species distributional data of *Rhododendron* in China. Specifically, we aim to evaluate if low temperature seasonality in subtropical China accounts for increased *Rhododendron* diversity across montane landscapes relative to those of the more seasonal temperate zone in north China. We do this by quantitatively assessing the associations among current climate, habitat heterogeneity and *Rhododendron* distributional patterns across China.

2 | MATERIALS AND METHODS

2.1 | Distributional data

The county-level distributional data were obtained from *Atlas of Woody Plants in China* (Fang, Wang, & Tang, 2011), which contains

the distribution of 11,405 native woody species. The species distributions in the atlas were compiled from all national-level floras including *Flora Reipublicae Popularis Sinicae* (126 issues of 80 volumes), *Flora of China* (Wu, Raven, & Hong, 1994–2013) and *Higher Plants of China* (Fu, 1999–2005), more than 120 volumes of provincial floras, and a great number of local floras and inventory reports across the country (Wang, Fang, Tang, & Lin, 2011). The atlas, therefore, provides the most comprehensive distributional records for all native woody species in China. We also compiled the county level distributional data from recently updated *Flora of China* (Wu, Raven, & Hong, 2005) as well as herbarium specimens deposited at Chinese National Herbarium (PE). In total, our database included the distributional records for 556 *Rhododendron* species out of 571 species occurring in China. The county-level distributional maps were then transferred into gridded distributions at a spatial resolution of 50 × 50 km (see Table S3.1 in Appendix S3) by overlaying the distributional map of each species with the grid in ArcGIS (ESRI, Redlands, CA) (see Wang, Brown, Tang, & Fang, 2009 for details).

We further divided our data into rare and common species, and three life-forms (i.e. dwarf shrubs, tall shrubs and trees) to evaluate effects of contemporary climate on different life-forms and categories. To classify species into rare and common, we first ranked all species into descending order of range size. Following previous studies (Araújo et al., 2008; Liu et al., 2017), we then categorized the top 25% and the bottom 50% as common and rare species, respectively. The rare species had range size of 1–36 grids, while the common species had range size greater than 81 grid cells. Our dataset included a total of 279 rare and 140 common species as well as 119 dwarf shrubs, 284 tall shrubs and 153 trees.

2.2 | Environmental variables

Climatic data used in the analysis included mean annual temperature (MAT), mean annual precipitation (MAP), mean temperature of the coldest quarter (MTCQ), mean temperature of the warmest quarter (MTWQ), precipitation of the driest quarter (PDQ), annual range of temperature (ART), temperature seasonality (TSN), precipitation seasonality (PSN), potential evapotranspiration (PET), annual actual evapotranspiration (AET), moisture index (MI), warmth index (WI) and water deficit (WD). TSN was defined as the standard deviation of monthly mean temperature, whereas PSN was defined as the coefficient of variation of monthly precipitation. ART was calculated as the mean difference between the maximum temperature of the warmest month and minimum temperature of the coldest month.

PET, AET, MI and WI were calculated using monthly mean temperature and monthly mean precipitation. MI and AET were calculated using the method of Thornthwaite and Hare (1955). WD measures the biological aridity of a region and was calculated as the difference between PET and AET (Francis & Currie, 2003). WI, which represents the annual accumulation of growing temperature, was calculated following Fang and Lechowicz (2006). The data for MAT, MAP, MTCQ, MTWQ, ART, TSN, PSN and monthly mean temperature and precipitation were downloaded from the WorldClim

database (<http://www.worldclim.org/>) at the spatial resolution of 30 arc second (c. 1 km at the equator). The value of a 50 × 50 grid cell for each climatic variable was estimated by averaging all 1 × 1 km cells in it.

Elevation range (ELER) was calculated as the difference between the maximum and minimum elevation of a grid cell using a GTOPO30 digital elevation model, and was used to represent topographical relief. Range of mean annual temperature (MATR) and mean annual precipitation (MAPR) were calculated as the difference between the maximum and minimum MAT and MAP in a grid, respectively, and were used to represent the heterogeneity of climatic conditions.

All the sixteen environmental variables were grouped into four categories, which represented (1) environmental energy (MAT, MTWQ, MTCQ, WI, PET), (2) water availability (MAP, PDQ, AET, MI, WD), (3) climate seasonality (ART, TSN, PSN) and (4) habitat heterogeneity (ELER, MATR, MAPR).

2.3 | Statistical analysis

We first performed correlation analyses to evaluate the concordance between the species richness patterns of all *Rhododendron* species and all other life-forms and categories. The underlying assumption was that high correlation among richness of different species groups indicates similar casual factors for the patterns observed. Next we performed simple regressions to evaluate the explanatory power of each predictor for the species richness of the six species groups. The aim was to evaluate which predictor or set of predictors best explain the richness pattern. Similarly, to compare the contribution of various environmental groups in predicting species richness, we performed multiple regressions using variance partition approach where we created four models for each species group, each model representing individual environmental category. This approach was adopted to compare which environmental factor (e.g. water availability, energy, heterogeneity or seasonality) accounts for highest variance in each group. Since different environmental categories had different number of variables, we did not use original variables as predictors in regression. Instead, we conducted principal component analysis (PCA) for each of the four environmental groups: energy, water availability, seasonality and habitat heterogeneity, respectively, using the principal() function in the R package 'psych' (Revelle, 2017). We then used Kaiser criterion (Kaiser, 1960) to select the extracted principal components to use in our regression analysis.

Stepwise regression was used to explore the combined effects of environmental factors on species richness and ultimately evaluate the best set of predictors with highest explanatory power and least multicollinearity. Because the predictors in each of the four environmental categories were highly correlated with each other (Table S1.3 in Appendix S3), we selected one variable from each environment category and built a model with four predictors to reduce the influence of multicollinearity on model performance (Faraway, 2005). We made all the possible combinations of predictors using five energy, five water, three habitat heterogeneity and three seasonality



variables, which yielded $5 \times 5 \times 3 \times 3 = 225$ models for each species group. We selected the model with the lowest Akaike information criterion (AIC) as the best model for each group. We also calculated variance inflation factors (VIFs) for all predictors within each model to evaluate the significance of multicollinearity (Legendre & Legendre, 2012). Generally multicollinearity between predictors is considered to be significant when VIF is greater than 5.

Because species richness values generally do not follow normal distributions, and are often over-dispersed where the variance exceeds the mean (Ver Hoef & Boveng, 2007), we used generalized linear models (GLMs) with 'quasi-Poisson' and 'negative binomial' residuals (McCullagh & Nelder, 1989) in preliminary analyses. Both methods have been widely used to analyse over-dispersed ecological count data like species richness (Ver Hoef & Boveng, 2007). To evaluate which model (quasi-Poisson or negative binomial) best fits our data, we created a diagnostic plot of the empirical fit of the variance to mean relationship (see Figure S2.1 in Appendix S2). The mean-root-square deviation between the observed and predicted species richness suggested that the negative binomial model provides a better description of our data than the quasi-Poisson model. Therefore, we used the negative binomial generalized linear models for all regressions in our study using the `glm.nb()` function in the R package 'MASS' (Venables & Ripley, 2002).

It is important to note that dependency of samples leads to high spatial autocorrelation of richness data which can significantly inflate type I errors and hence affect significance level of all our correlation analyses (Fortin & Dale, 2005). Therefore to normalize this, we performed modified *t* test (Dutilleul, Clifford, Richardson, & Hemon, 1993) to evaluate the significance level of all correlation coefficients and models. All statistical analyses were carried out using R version 3.1.3 (<http://www.r-project.org>).

3 | RESULTS

The patterns of species richness of all *Rhododendron* species and the five subcategories were highly consistent with the topographical structure of China. The mountainous region of south-western China had the highest species richness, whereas the richness for all categories was much lower in the Tibetan Plateau, Xinjiang and Inner Mongolia regions, which mostly include deserts and basins (Figure 1a). The rare species occurred only in southern China (Figure 1b), but common species in both northern and southern China (Figure 1c). Dwarf shrubs and trees showed similar pattern as the rare species (Figure 1d and f). On the contrary, tall shrubs were distributed throughout the northern as well as southern China (Figure 1e). The species richness per grid for all species ranged from 1 to 177. Similarly the ranges of richness per grid for other categories were 1–39 (rare), 1–78 (common), 1–43 (dwarf shrubs), 1–88 (tall shrubs) and 1–53 (trees). The species richness of all groups was highly right-skewed (see Table S1.1 in Appendix S1). The result of correlation analyses showed moderate to high concordance between all *Rhododendron* species and the five subcategories ($r = .76-.98$; see

Table S1.2 in Appendix S1) indicating that the potential factors driving species richness is possibly the same across different species groups.

Of the sixteen environmental variables, the variables of habitat heterogeneity particularly MATR and ELER were consistently the strongest predictors of species richness (Table 1). MATR explained 32%–55% of the total variation, whereas ELER explained 32%–51% of the total variation. Variables of climate seasonality particularly TSN and ART were the second best predictors of species richness and they contributed 17%–50% and 8%–45% respectively. The contribution of energy variables was much lower for all categories and life-forms. Interestingly MTCQ explained only 1%–22% of the total variation and its contribution was nearly two times less than that of MATR and ART for total species. The contribution of MTCQ was proportionately much lower than the variables of habitat heterogeneity and climate seasonality for all species groups (Table 1).

Comparison between contributions of individual environmental categories based on variation partition using extracted principal components showed significant role of habitat heterogeneity and climate seasonality in determining species richness (Figure 2). Habitat heterogeneity was by far the strongest predictor of species richness followed by climate seasonality for all species groups.

It is important to note the collinearity between variables of habitat heterogeneity and climate seasonality (see Table S1.3 in Appendix S1), which can influence the interpretation of our results. Therefore, to explore the effects of interaction among variables and to compare the independent effects of habitat heterogeneity and climate seasonality, we further conducted partial regression. Using partial regression we partitioned the total variation in species richness into independent components, covarying components and unexplained variation (Figure 3). The results showed that habitat heterogeneity and climate seasonality independently accounted for 10%–34% and 5%–24% of species richness, respectively (Figure 3).

The combined models developed using stepwise regression (GLM) selected consistent predictors of habitat heterogeneity and climate seasonality for all species groups (Table 2). MATR, ART and MI were consistently selected as significant predictors in most models representing habitat heterogeneity, climate seasonality and water availability, respectively. The variance inflation factors (VIF) for the predictors in all six models were less than 5, which indicates insignificant multicollinearity between predictors in the models. The models moderately predicted richness of *Rhododendron* species in China for all species groups. The R^2 of the models ranged between 47% and 70% (Table 2).

4 | DISCUSSION

Our results unequivocally supported the role of habitat heterogeneity and climate seasonality in predicting *Rhododendron* diversity in China. Habitat heterogeneity was, by far, the strongest predictor, explaining about 32%–55% of the total variation followed by climate seasonality, which accounted for about 8%–50% of the deviance. Although we partitioned our data into different categories, habitat

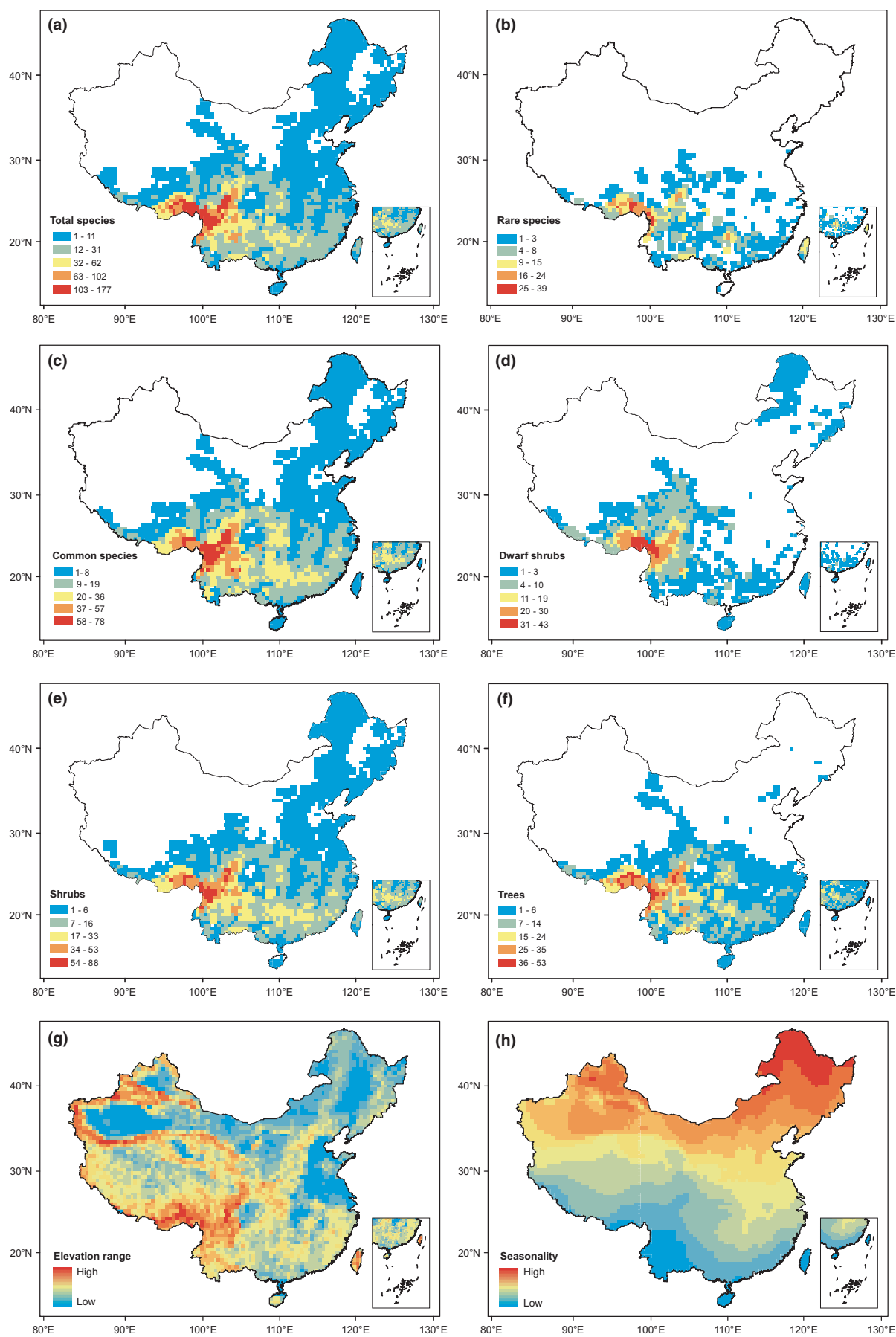


FIGURE 1 Spatial patterns of *Rhododendron* species richness in China estimated in 50 × 50 km equal-area grid cells. (a) All *Rhododendron* species (b) rare species (c) common species (d) dwarf shrubs (e) tall shrubs (f) trees. Elevation range and climate seasonality are shown in subfigures (g) and (h) respectively

heterogeneity and climatic seasonality variables were consistently the primary determinants of all species groups irrespective of differences in their distribution patterns. Our study supported a positive heterogeneity–diversity relationship (see Figure S2.1 in Appendix S2) that is consistent with the results of several other studies (e.g. Hortal et al., 2009; Stein et al., 2014; Tews et al., 2004) and a negative seasonality–diversity relationship, which has been barely

established (but see Chan et al., 2016; Ruggiero & Hawkins, 2008). The effect of energy was weak, whereas water variables (MI and WD) showed moderate effects for all species groups. These findings contradict the hypothesis that the availability of environmental energy limits regional species richness (Currie, 1991; Hawkins, Porter, Diniz-Filho, & Alexandre, 2003; Turner, Lennon, & Lawrenson, 1988).

TABLE 1 Explanatory power (R^2 , %) of the predictors for the species richness patterns of all *Rhododendron* species, rare species, common species, dwarf shrubs, tall shrubs and trees in China evaluated by negative binomial generalized linear model. Stronger predictors are in bold font face and non-significant values are marked with an asterisk (*). All other values are significant at $p < .05$

| Environmental categories | Predictors | All | Rare | Common | Dwarf shrubs | Tall shrubs | Trees |
|--------------------------|------------|--------------|--------------|--------------|--------------|--------------|--------------|
| Environmental energy | MAT | 3.71 | 3.58 | 5.94 | 0.62 | 5.52 | 0.44 |
| | MTWQ | 2.21 | 8.67 | 0.84 | 13.49 | 1.33 | 5.15 |
| | MTCQ | 19.92 | 0.67 | 22.15 | 2.39 | 21.62 | 0.72 |
| | WI | 0* | 6.54 | 0.31 | 9.17 | 0.17 | 3.06 |
| | PET | 0* | 6.73 | 0.21 | 7.92 | 0.1* | 4.02 |
| Water availability | MAP | 12.75 | 0.19* | 15.35 | 0.29 | 14.28 | 0.69 |
| | PDQ | 0.25 | 1.23 | 1.24 | 5.60 | 1.06 | 4.95 |
| | AET | 1.65 | 5.56 | 3.49 | 4.69 | 2.07 | 1.15 |
| | MI | 40.36 | 12.5 | 41.07 | 21.83 | 37.01 | 16.54 |
| | WD | 22.56 | 3.28 | 22.81 | 6.56 | 18.62 | 11.79 |
| Climate seasonality | ART | 44.82 | 8.43 | 43.84 | 18.27 | 42.63 | 20.67 |
| | TSN | 49.79 | 17.41 | 47.44 | 27.85 | 45.39 | 27.66 |
| | PSN | 2.54 | 5.01 | 5.84 | 1.89 | 4.22 | 3.73 |
| Habitat heterogeneity | ELER | 45.08 | 34.86 | 39.14 | 51.08 | 42.42 | 32.44 |
| | MATR | 44.04 | 34.38 | 38.33 | 55.03 | 40.95 | 31.77 |
| | MAPR | 19.28 | 18.3 | 13.37 | 14.75 | 18.16 | 11.11 |

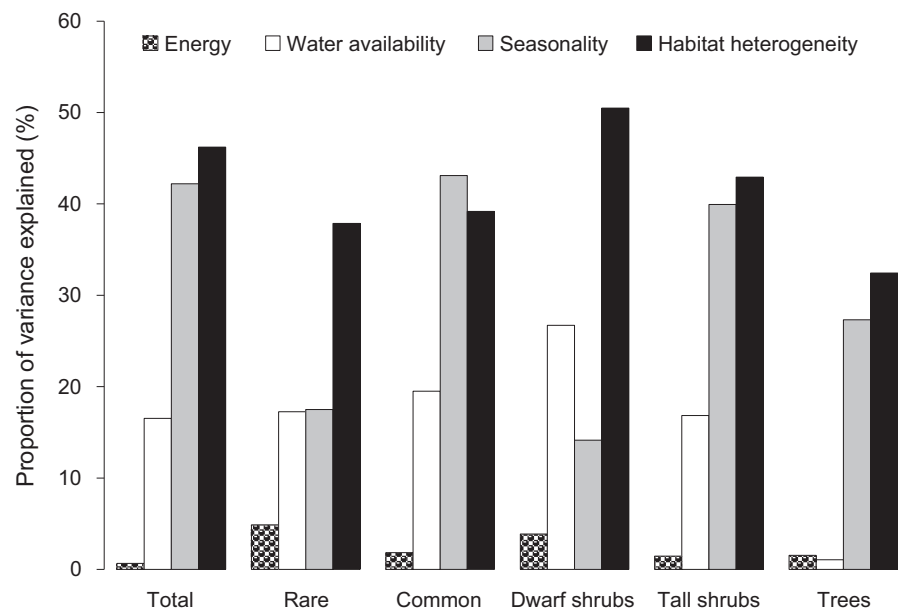


FIGURE 2 Proportion of variance (R^2 , %) explained by individual environmental categories

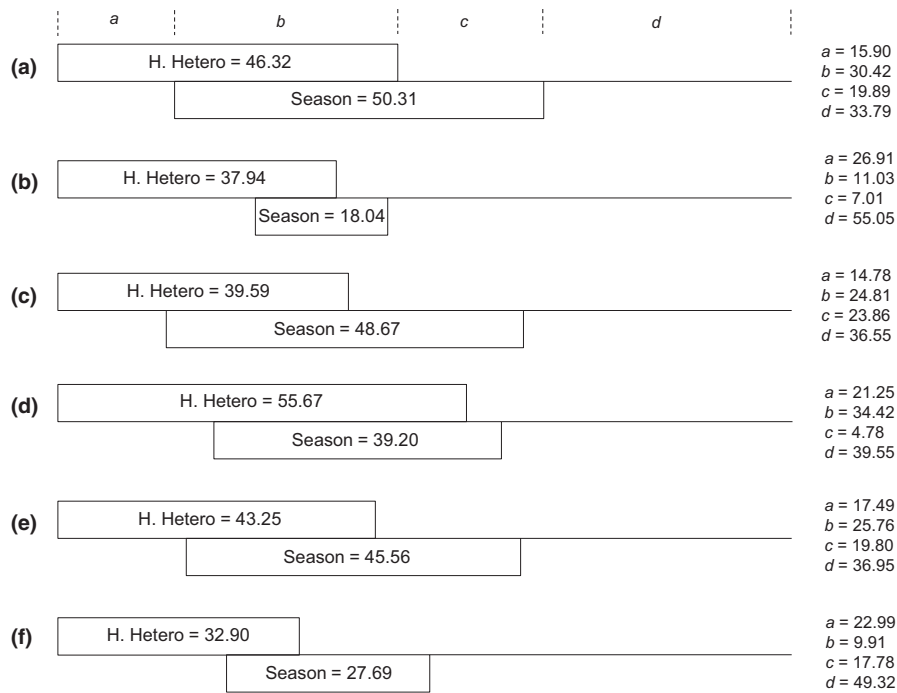


FIGURE 3 Comparison of the effect of habitat heterogeneity and climate seasonality on *Rhododendron* species richness in China using partial regression. (a) All *Rhododendron* species (b) rare species (c) common species (d) dwarf shrubs (e) tall shrubs (f) trees. The variation in each category is partitioned as independent component, covarying component and unexplained variation represented by (a) & (c), (b) and (d) respectively

TABLE 2 The best combinations of variables for each *Rhododendron* species group in China evaluated using stepwise regression and their coefficients of determination (R^2). The best models for each group were selected from 225 models based on the lowest Akaike information criterion. Numbers in parentheses are coefficients of respective variables. The variance inflation factors for all predictors were less than 5 indicating insignificant multicollinearity

| Groups | Energy | Water availability | Seasonality | Habitat heterogeneity | R^2 (%) |
|----------------|---------------|--------------------|---------------|-----------------------|-----------|
| All species | MAT (0.0164) | MI (0.0083) | ART (−0.0362) | MATR (0.1165) | 69.93 |
| Rare species | WI (−0.0059) | PDQ (0.0037) | ART (−0.1059) | ELER (0.0004) | 47.73 |
| Common species | MAT (0.0196) | MI (0.0078) | ART (−0.0286) | MATR (0.0963) | 66.12 |
| Dwarf shrubs | WI (−0.0053) | MI (0.0059) | TSN (−0.0009) | MATR (0.0874) | 64.60 |
| Tall shrubs | MTWQ (0.0305) | MI (0.0058) | ART (−0.0333) | MATR (0.1107) | 64.83 |
| Trees | PET (−0.0007) | MI (0.0038) | ART (−0.0908) | ELER (0.0004) | 51.93 |

Habitat heterogeneity is believed to be one of the main factors affecting diversity and has been supported by studies on a wide range of faunal groups (e.g. Ricklefs & Lovette, 1999; Van Rensburg, Chown, & Gaston, 2002). A recent meta-analysis by Stein et al. (2014) supported generality of positive heterogeneity–richness relationship across heterogeneity components, habitat types, taxa and spatial scales and our result is in the line of this theory. Heterogeneous habitat promotes coexistence and diversification of species (Stein et al., 2014) by offering increased niche spaces (Tews et al., 2004), and providing increased opportunities for reproductive isolation (Rosenzweig, 1995). Heterogeneous habitats, therefore, increase species number by increasing speciation and reducing extinction.

As the global diversity centre of *Rhododendron* species, southwest China is characterized by a unique geomorphological heterogeneity. Nowhere on earth are so many mountains and deep valleys clustered so closely together. This unique feature gives rise to a very complex topography and hence creates wider diversity of habitats thereby supporting large number of species (Rosenzweig, 1995).

Majority of seed plants including *Rhododendron* are relatively younger (<15 Ma) in this region (Liu, Wang, Wang, Hideaki, & Abbott, 2006; Milne et al., 2010), which potentially indicate that plants here might have undergone rapid radiation during the middle to late Miocene (Wen, Zhang, Nie, Zhong, & Sun, 2014). Interestingly, the rapid radiation of seed plants coincides with the period of mountain formation in this region (Harrison, Copeland, Kidd, & Yin, 1992) and this potentially suggests that development of heterogeneous topography might have promoted diversification of *Rhododendron* here by offering increased niche space. It is highly likely that the population fragmentation following the period of mountain formation might have triggered speciation events in the southern part of Qinghai-Tibetan Plateau (QEP) by isolation through elevation changes, hybridization and adaptation to diverse environmental conditions (Antonelli & Sanmartín, 2011; Hughes & Eastwood, 2006). These series of events have particularly been hypothesized to be important for spectacular radiation of species of subgenus *Hymenantes* in the southern part of QEP (Milne et al., 2010). This speciation



mechanism has also been found for other groups in this area (Mao & Wang, 2011). For example a recent study (Xing & Ree, 2017) evaluated the modes and rates of plant diversification in south-west China using the molecular phylogenies of 19 clades, and found that most clades experienced elevated diversification in late Cenozoic due to topographical isolation. These findings suggest that topographically induced allopatric divergence is likely a general driver of high plant diversity in south-west China.

In addition, habitat heterogeneity may also influence species diversity by providing refuge for species during climate change events (Fjelds  et al., 2012). For example species distributed in topographically heterogeneous landscapes do not require strong dispersal abilities to track climate (Sandel et al., 2011). As a result, they experience low climate change velocities and less extinction than those living in lowlands (Bertrand et al., 2011). Studies have confirmed that south-west China, which is the diversity centre of *Rhododendron* species, was less severely affected by quaternary glaciations (Li, Chen, & Wan, 1991). This region might have, thus, acted as refuge during glacial periods and prevented extinction of many species (Zhang, Boufford, Ree, & Sun, 2009).

Strong correlation between variables of climate seasonality (represented by ART and TSN) and species richness further suggests that seasonal variation in temperature is an important indicator of *Rhododendron* diversity. We found that moderately low climate seasonality favours high species diversity (see Figure S2.2 in Appendix S2). This pattern has been supported by recent analysis on terrestrial vertebrates at global scale (Chan et al., 2016), and tree frogs from the New World (Wiens et al., 2006). Our result together with previous findings provides evidence for climate seasonality-richness hypothesis. However, it is important to note that the effect of seasonality was more pronounced in regions of high topographical relief. For example although southeast China has equivalent seasonality as south-west China (see Figure 1h for comparison), diversity was much higher in the latter which is characterized by unique geomorphological heterogeneity. This suggests that the effects of seasonality, jointly with those of topography, contribute to higher *Rhododendron* diversity in south-west China.

These findings are consistent with the prediction of Janzen's hypothesis (Janzen, 1967), which explains why we encounter more species in tropical and subtropical mountains. According to this hypothesis, the seasonal variation in temperature in tropical and subtropical mountains is almost uniform and this creates physiological barrier between species growing in valleys and mountain passes. This, in turn, enhances allopatric speciation and therefore results in accumulation of higher species diversity along the elevation gradients (Ghalambor et al., 2006; Janzen, 1967). The high correlation of *Rhododendron* richness with both habitat heterogeneity and seasonality variables observed in our analyses provides strong evidence for Janzen's hypothesis as a mechanism for the accumulation of high *Rhododendron* diversity in south-west China. Although rapid radiation of plants in south-west China may have been driven by a number of processes (see Wen et al., 2014), allopatric divergence induced by both topographical and thermal isolations may be a

dominant causal factor for high plant diversity in this area. A recent study analysed the topographically derived thermal gradient and found that the thermal barrier between low and high elevation areas may also occur in the temperate mountains (Currie, 2017), which may have influenced the turnover in the assemblages of amphibians and mammals along elevational gradients in the Americas (Zuloaga & Kerr, 2017). Together these findings suggest an important role of thermal barrier on allopatric speciation and species accumulation in the mountains. In addition, previous studies have also shown the influence of large temperature gradient along elevation on species richness. For example using richness data of birds from the New World, Ruggiero and Hawkins (2008) showed that the richness of montane species is strongly influenced by range in temperature along elevation gradient and not topographical heterogeneity *per se*. Consistent with this finding, our results showed that the effects of spatial temperature variation on species richness were higher or comparable with those of topographical relief for most species groups, suggesting that the magnitude of the climatic gradient along elevation induced by topographical relief contribute to the species richness patterns of *Rhododendron*. Recent analyses on richness pattern of bird species at continental and global scales (e.g. Hawkins, Diniz-Filho, Jaramillo, & Soeller, 2007; Rahbek & Graves, 2001) have found similar effects of local climatic gradient and topography.

It has previously been hypothesized that extreme winter temperature strongly limits the northward dispersal of tropical clades (see Latham & Ricklefs, 1993; Wiens & Donoghue, 2004). However, our results did not show significant contribution of MTCQ. Previous studies showed that some *Rhododendron* species have relatively good adaptation to frost. For example some Himalayan species living in sub-alpine to alpine habitat exhibit winter hardiness of -20°C to -30°C (Sakai & Malla, 1981). The good adaptation of *Rhododendron* to cold winter temperature suggests that this group might have originated in temperate regions at high palaeo-latitudes (Irving & Hebda, 1993; Xing & Ree, 2017) from where they acquired the coldness adaptive trait. More studies involving phylogenetic comparative methods are, however, needed to fully understand the evolutionary history of this group. Despite their cold tolerance, most *Rhododendron* species live in narrow elevational belts and hence have narrow thermal requirement. More than 100 species live in an elevational belt narrower than 200 m, and c. 200 species in a belt narrower than 500 m (Fang et al., 2011). The narrow distributions may have facilitated the allopatric speciation induced by topography and thermal isolation.

In summary, our results provide evidence supporting Janzen's hypothesis and suggest that the high *Rhododendron* diversity in south-west China is likely due to the combined effects of increased topographical complexity and seasonal uniformity in temperature on allopatric speciation. Our findings are consistent with the recent molecular studies on plant diversification for different clades in the Hengduan mountains (Xing & Ree, 2017). As plants have limited ability to use behaviour to avoid environmental influences, they may experience stronger selection for physiological tolerance and greater population isolation (Bradshaw, 1965; Ghalambor et al., 2006; Huey

et al., 2002). Therefore, the effect of seasonality may be more pronounced in plants than in animals, which are more buffered from climatic concerns (Porter & Gates, 1969). The generality of Janzen's hypothesis, however, may be further tested by linking climatic variation with physiology, ecology and evolution of other plant groups in this region.

ACKNOWLEDGEMENTS

We thank Carsten Rahbek for useful discussions. This work was supported by the National Natural Science Foundation of China (NSFC) (#31650110471), National Key Research Development Program of China (#2017YFA0605101) and NSFC (#31522012, #31470564, #31621091). X.X. was also supported by the Fundamental Research Funds for Central Universities (#YJ201721).

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BIOSKETCHES

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Author contributions: N.S. and Z.W. conceived the idea and designed the study; N.S., X.S., X.X. and Z.W. collected the data; N.S., X.S. analysed the data; N.S., Z.W. led the writing. All authors approved the submission.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Shrestha N, Su X, Xu X, Wang Z. The drivers of high *Rhododendron* diversity in south-west China: Does seasonality matter? *J Biogeogr*. 2018;45:438–447. <https://doi.org/10.1111/jbi.13136>