LETTER

Richness patterns of endemic and threatened conifers in south-west China: topographic-soil fertility explanation

Mohammed A Dakhil1,2,3,*, Jiangrong Li4,5, Bikram Pandey1,2,*, Kaiwen Pan1, Ziyan Liao1,*, Olusanya Abiodun Olatunji1,*, Lin Zhang1, Ebrahem M Eid6,7, and Mohamed Abdelaal8

1 CAS Key Laboratory of Mountain Ecological Restoration and Biodiversity Conservation Key Laboratory of Sichuan Province, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, People's Republic of China
2 University of Chinese Academy of Sciences, Beijing 100039, People's Republic of China
3 Botany and Microbiology Department, Faculty of Science, Helwan University, Cairo 11790, Egypt
4 Key Laboratory of Forest Ecology in Tibet Plateau (Tibet Agricultural and Animal Husbandry University), Ministry of Education, Nyingchi, Tibet 860000, People's Republic of China
5 National Forest Ecosystem Observation & Research Station of Nyingchi Tibet, Nyingchi, Tibet 860000, People's Republic of China
6 Biology Department, College of Science, King Khalid University, Abha 61321, P.O. Box 9004, Saudi Arabia
7 Permanent address: Botany Department, Faculty of Science, Kafr El-Sheikh University, Kafr El-Sheikh 33516, Egypt
8 Department of Botany, Faculty of Science, Mansoura University, 35516 Mansoura, Egypt

E-mail: mohamed_dakhil@science.helwan.edu.eg and pankw@cib.ac.cn

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Abstract

Understanding the relationships between species richness patterns and environment constitutes a key issue in biogeography and conservation strategies. To our knowledge, this is the first integrative study that incorporates soil and human-influence data into species richness modelling. Our aims were to (a) estimate the richness patterns of four conifers groups (all conifers species, endemics, threatened, and endemic-threatened species) in south-west China, (b) assess the relative importance of environmental predictors (energy, water, climate, topography, and soil) and the human-influence on the conifers richness patterns and (c) identify hotspot ecoregions, nature reserves, or important plant areas as priority conservation areas. Generalized linear models and hierarchical partitioning were used by correlating 8962 distributional records of 97 conifer species with different environmental drivers. Results indicated that central Sichuan, northern Sichuan, northern Yunnan, and the southern areas of the Hengduan mountains were identified as distinct centres of conifers richness in China. Topographic heterogeneity and soil fertility were the strongest drivers of conifer richness patterns, while climate, energy, water, and human drivers were contributed to a lower degree. The identified conifers’ important areas were mostly located outside of the existing nature reserves but inside the ecoregions. Our findings emphasize that incorporating soil data into spatial modelling provides great insights for the conservation of conifers species. We recommend conservationists to use soil variables and other environmental data to generate a comprehensive understanding of the key drivers underlying the patterns of conifer diversity and distribution.

1. Introduction

Species richness can positively affect community stability and ecosystem functions such as nutrient cycling (Maestre et al. 2012), resilience (Oliver et al. 2015), productivity, and carbon storage (Liang et al. 2016, Chen et al. 2018, Liu et al. 2018). Also, species richness of the rare, threatened, or endemic plants play a central role in identifying important plant areas (IPAs) that are used to determine the best sites for plant conservation (Anderson 2002).

Understanding the relationship between species richness and the environment is a key issue in ecology and biogeography. Although climate is one of
the major factors driving species composition, habitat characteristics are also strongly associated with forest structure and composition (Zellweger et al 2015). In forestry, ensuring species diversity has become one of the important goals which require an understanding of the impacts of disturbance on species diversity and its management concerning other natural drivers (Schmiedinger et al 2012). Multiple drivers like climate, soil conditions, and human influence interact to affect the patterns of species diversity and composition (Urbach et al 2014). Several hypotheses, such as climatic seasonality, environmental energy, water, and habitat heterogeneity (Currie et al 2004, Shrestha et al 2018), have been suggested to explain the diversity gradient. For example, the water-energy hypothesis suggests that an area with high energy and water availability will promote high species diversity (O’Brien 1998, Francis and Currie 2003). Human disturbance is known to cause habitat fragmentation. It may have a stronger impact on the loss of species than global warming (Schmiedinger et al 2012, Venter et al 2016). The habitat heterogeneity hypothesis attempts to explain species richness through space niches and diversification (Moeslund et al 2013, Stein et al 2014).

In addition, on the basis of geological and topographical characteristics for pertaining biodiversity, geodiversity has an effect on biodiversity at landscape and subnational scales (Hjort et al 2012, Gray 2013, Bailey et al 2017). Gray (2013) defined ‘geodiversity’ as the variability of geological, soil, and geomorphological characteristics and the physical processes that lead to these characteristics. Furthermore, terminology or definitions for describing the geodiversity has not been standardized (Anderson et al 2015). Geodiversity in this article is defined as the variability of geo-traits of morphological, physical, and chemical components representing three hypotheses of topographic heterogeneity, soil texture type, and soil fertility (Keith 2011, Räsänen et al 2016, Bailey et al 2017, Lausch et al 2019). The approach to compile geodiversity information was highly simplified in the current study, but the previous studies e.g. Hjort and Luoto (2012) and Hjort et al (2012) have described geodiversity as the variability in the Earth’s surface materials, geomorphological and hydrological variability. Several studies recommend incorporating geodiversity quantitative data such as topographic heterogeneity or soil nutrients into spatial modelling and conservation studies (Mod et al 2016, Bailey et al 2017, Tukiainen et al 2017).

Several studies have neglected some meaningful variables directly or indirectly affect species distributions and ecosystem functions, such as available soil water, nutrients, carbon, potential evapotranspiration (PET), and solar radiation (SR) (Piedade and Gégoût 2008, Mod et al 2016). Studies have either reported negative or positive relationships between soil nutrients and species richness (e.g. Huston 1980, van der Sande et al 2018, Yuan et al 2020), which has resulted in the drivers of plant species richness being controversial. As a result, recent studies recommend the integration of biodiversity, geodiversity, and anthropogenic factors into conservation planning (Tukiainen et al 2017, Xu et al 2017, Tripathi et al 2019).

Conifer forests constitute terrestrial biomes present in tropical, subtropical, boreal, and temperate climates worldwide (Olson et al 2001). Globally, more than 50% of the temperate conifer forests are located in Asia and primarily in China (Farjon and Filer 2013, Wan et al 2017, Dakhil et al 2019). Nearly 50% of conifer species are threatened due to anthropogenic activities (López-Pujol and Zhao 2004, Farjon et al 2019). Woody species have been predicted to decline due to climate change (Zhang et al 2014, Dakhil et al 2019). Also, the nature reserve system of China has primarily focused on protecting mammals, while plant diversity and its habitats have not been well captured (Xu et al 2017).

We hypothesized that important conifer areas might be located outside the nature reserve system, which would indicate that they require protection. Therefore, our objectives were to (a) estimate the richness patterns of four conifer groups (all conifer species, endemics, threatened, and endemic-threatened species), (b) determine the relative importance of environmental predictors (environmental energy, climatic seasonality, water availability, and soil factors) and the human-influence on the species richness patterns, (c) determine the set of predictors that best explains the richness patterns, and (d) identify the boundaries of the identified IPAs.

2. Methods

2.1. Species distribution data and richness estimation

We downloaded occurrence data from the Global Biodiversity Information Facility (www.gbfif.org), Chinese Virtual Herbarium (www.cvh.org.cn), National Specimen Information Infrastructure (www.nsii.org.cn/), and appropriate literature (Ying et al 2004). We cleaned the records by removing synonyms and unresolved names using the conifer database (Farjon et al 2019). Occurrence records from outside the study area and the duplicates were removed using ArcGIS v. 10.3 (ESRI 2014). Finally, we compiled 8962 occurrence records of 97 taxa, including 59 endemics, 63 threatened species, and 41 endemic-threatened species (see appendix A, table S1 (available online at stacks.iop.org/ERL/16/034017/mmedia)). As a conservative approach, we divided the species into four categories (all 97 conifers, endemics, threatened, and endemic-threatened species), and then estimated the richness based on the total number of species per grid cell (50 × 50 km²) using SDM toolbox in ArcGIS v. 10.3 (Brown 2014). Several similar studies have used
the same grid size (e.g. Wang et al 2010, Shrestha et al 2018, Liu et al 2019). The generated richness maps were projected to WGS 1984 UTM zone 48° N, which included 740 grid cells (see appendix B). To explore the conifer richness inside each ecoregion, we have used the shapefile of the five terrestrial conifer ecoregions in the study area, that were downloaded from the World Wildlife Fund (Olson et al 2001, WWF 2018).

### 2.2. Environmental and human-influence drivers

We used 23 predictor variables of seven hypotheses (table 1) to explain the patterns of conifer richness. Mean annual temperature (MAT), mean temperature of the coldest quarter (MTCQ), SR, and PET pertain to the environmental energy (Wang et al 2018). Mean annual precipitation (MAP), the aridity index (AI), and water deficit (WD) pertain to the water availability hypothesis. The WD is a measure of biological aridity and is calculated as the difference between PET and actual evapotranspiration (AET; Francis and Currie 2003). Temperature seasonality (TS) and precipitation seasonality (PS) pertain to climatic seasonality (Shrestha et al 2018).

The climatic variables (MAT, MTCQ, MAP, TS, and PS) were obtained from the WorldClim database (www.worldclim.org, Fick and Hijmans 2017) at a resolution of 30 arc-seconds. The PET, AET, and AI data were downloaded from the CGIAR-CSI Global database (www.cgiar-csi.org, Trabucco et al 2008, Fisher et al 2011) at the same resolution. As topographic heterogeneity is an important driver of species richness in China and particularly southwestern China (Shrestha et al 2018, Liu et al 2019), we represented it by two metrics; elevation range (ELER) and elevation standard deviation (ELE-SD) were extracted from the GTOP030 digital elevation model using ArcGIS. ELER is defined as the difference between the maximum and minimum elevation of a grid cell while ELE-SD is the standard deviation of the elevation within each geographical unit (Bailey et al 2017, Shrestha et al 2018).

We downloaded the Human Influence Index (HII) (https://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic) at a resolution of 30 arc-seconds, which represents human pressures (Wildlife Conservation Society-WCS 2005). The HII was created from nine layers of global data covering human population density, land use, built-up areas, night-time lights, land use/land cover, roads, coastlines, navigable rivers, and railroads (Xu et al 2014). Eight soil variables

| Hypothesis                        | Predictor | All conifers | Endemics | Threatened | Endemic-threatened |
|-----------------------------------|-----------|--------------|----------|------------|--------------------|
| Environmental energy              | MAT       | 5.56 (—)     | 9.69 (—) | 6.43 (—)   | 19.29 (—)          |
|                                  | MTCQ      | 3.51 (—)     | 7.67 (—) | 3.78 (—)   | 17.1 (—)           |
|                                  | SR        | 0.85 (—)     | 3.84 (—) | 0.73 (—ns) | 4.44 (—)           |
|                                  | PET       | 4.37 (—)     | 9.22 (—) | 4.28 (—)   | 18.68 (—)          |
| Water availability                | WD        | 0.08 (—)     | 0.76 (—) | 0.25 (—ns) | 0.73 (—)           |
|                                  | MAP       | 4.17 (—)     | 6.87 (—) | 3.23 (—)   | 12.1 (—)           |
|                                  | AI        | 1.42 (+)     | 1.64 (+) | 1.94 (+)   | 0.82 (+)           |
| Climatic seasonality              | PS        | 1.99 (+)     | 3.49 (+) | 3.68 (+)   | 8.08 (+)           |
|                                  | TS        | 3.2 (—)      | 0.96 (—) | 5.45 (—)   | 0.04 (—)           |
| Topographic heterogeneity         | ELE-SD    | 33.2 (+)     | 30.07 (+) | 29.9 (+)   | 29.89 (+)          |
|                                  | ELER      | 36.01 (+)    | 32.79 (+) | 32.31 (+) | 31.77 (+)          |
| Soil texture type                 | CRF       | 7.58 (+)     | 8.07 (+) | 9.5 (+)    | 11.56 (+)          |
|                                  | SND       | 10.77 (+)    | 12.74 (+) | 15.09 (+) | 23.01 (+)          |
|                                  | SET       | 2.42 (—)     | 1.54 (—) | 7.36 (—)   | 2.18 (—)           |
|                                  | CLY       | 9.93 (—)     | 13.73 (—) | 10.49 (—) | 26.39 (—)          |
| Soil fertility                    | AW        | 7.8 (+)      | 11.67 (+) | 10.5 (+)   | 24.68 (+)          |
|                                  | AN        | 13.6 (+)     | 17.91 (+) | 16.49 (+) | 28.8 (+)           |
|                                  | AP        | 18.34 (+)    | 19.16 (+) | 20.53 (+) | 25.44 (+)          |
|                                  | C_stock   | 19.23 (+)    | 20.83 (+) | 21.1 (+)   | 26.42 (+)          |
|                                  | C_content  | 23.87 (+)    | 25.16 (+) | 25.79 (+) | 30.71 (+)          |
|                                  | C_N_ratio | 1.82 (+)     | 0.73 (+ns)| 0.60 (+ns)| 0.16 (+)           |
|                                  | CEC       | 23.55 (+)    | 24.7 (+) | 20.99 (+) | 26.39 (+)          |
| Human influence                  | HII       | 2.75 (—)     | 3.64 (—) | 3.64 (—)   | 6.98 (—)           |

*Predictors include MAT: mean annual temperature, MTCQ: mean temperature of the coldest quarter, SR: solar radiation, PET: potential evapotranspiration, MAP: mean annual precipitation, AI: aridity index, WD: water deficit; calculated as the difference between PET and the actual evapotranspiration (AET) (Francis and Currie 2003). TS: temperature seasonality, PS: precipitation seasonality. ELE-SD: standard deviation of elevation, ELER: elevation range, CLY: clay fraction, CRF: coarse fragments, SET: silt fraction, SND: sand fraction. AW: available water, AN: available nitrogen, AP: available phosphorus, C_stock: organic carbon stock, C_content: organic carbon content, C/N_ratio: carbon/nitrogen ratio, and CEC: cation exchange capacity.
Figure 1. Flowchart showing statistical and spatial modelling analyses.

(see appendix A, table S4) at depth (0–2 m) with 1 km resolution were obtained from the ISRIC-World database, in which a high density of the sampled points was located in south-west China (ftp://ftp.soilgrids.org/data/aggregated; Hengl et al 2014). Soil nitrogen and phosphorus data were downloaded from http://globalchange.bnu.edu.cn/research/soil2d.jsp (Shangguan et al 2013). The means of the raster-layer depths (0–2 m) were generated using the raster calculator in ArcGIS v. 10.3 (ESRI (Environmental Systems Research Institute) 2014). The values of all environmental and human-influence layers were estimated using 50 × 50 km² grid cells in ArcGIS (zonal statistics tool) by averaging all 1 × 1 km grid cells (ESRI (Environmental Systems Research Institute) 2014; Shrestha et al 2018; see appendix B).

2.3. Statistical and model analyses

Descriptive statistics (variance, mean, skewness, and kurtosis) and Spearman correlation analyses were applied among the four richness groups using SPSS v. 21.0 (IBM 2012). Given that the species richness values of all groups were abnormally distributed and often over-dispersed with variance-mean ratios greater than 1 (Ver Hoef and Boveng 2007; see appendix A, table S2), we used generalized linear models with negative binomial residuals (GLM-NB) to analyse the relationships between conifer richness and environmental-human variables (figure 1). The GLM-NBs could better compensate for over-dispersed data compared to that of the Poissonian residuals, and this method has been widely used for ecological count data (Ver Hoef and Boveng 2007.).

For each predictor, we performed a GLM to evaluate the explanatory power ($R^2$, %) of each predictor individually, which was calculated according to (Panda et al 2017, Shrestha et al 2018, Wang et al 2018) as follows:

$$R^2 = \frac{\text{null deviance} - \text{residual deviance}}{\text{null deviance}} \times 100.$$

The glm.nb() function was used for GLMs in the ‘MASS’ R package (Venables and Ripley 2013) followed by stepwise regression to explore the combined effect of predictor variables on richness pattern and determine the best group of predictors with the highest explanatory power (Shrestha et al 2018). Due to high correlation, one variable from each predictor category was selected to build a model, and finally, seven predictors were selected (Faraway 2016) (see appendix A, table S4). We used all possible combinations of predictors using four energy, three water, two seasonality, two topographic heterogeneity, one
human influence, four soil-texture types, and seven soil fertility variables, which yielded 1344 models ($4 \times 3 \times 2 \times 2 \times 1 \times 4 \times 7$) for each richness category. We selected the best model based on the lowest Akaike information criterion (AIC) for each richness group. Within each selected model, we calculated the variance inflation factor (VIF) for all predictors using the ‘car’ package in R v. 3.6.1 to evaluate the significance of multicollinearity (Legendre and Legendre 2012, Fox et al. 2016), where collinearity is considered to be significant when VIF > 5. Next, we compared the explanatory power of each predictor individually using GLM, and their combined effect using stepwise regression. Similarly, we used a hierarchical partitioning model to compare the proportion of variance explained by each predictor category (Liu et al. 2019). We first conducted a principal component analysis (PCA) with the varimax rotation in SPSS v. 21.0 (IBM 2012) within each of the predictor categories. We then extracted the first axis to represent each category (hypothesis). We standardized the human influence variable because the PCA cannot be applied to a group containing only one variable (Liu et al. 2019). Then, we used the PCA-extracted first axes to apply hierarchical partitioning analysis using the ‘hier.part’ R package (Walsh and Mac Nally 2013).

3. Results

3.1. Conifer species richness patterns and hotspot ecoregions

Four distinct centres of conifer richness were identified based on the output maps produced (figure 2(a)). These centres were central Sichuan, northern Sichuan, northern Yunnan, and the southern areas of Hengduan Mountains. The conifer richness ranged from 1 to 30 (figure 2(a)) for all species. Two endemic conifer centres were identified central Sichuan and the northern Qionglai-Minshan ecoregion (figure 2(b)), in which richness ranged from 1 to 24. Regarding threatened species richness (1–17 species per grid), two centres in central Sichuan and northern Yunnan were identified (figure 2(c)). Furthermore, one richness centre (central Sichuan) for endemic-threatened species was detected with a range from 1 to 14 (figure 2(d)). The species richness of all categories was highly right-skewed (see appendix A, table S2). Four canters of species richness (proposed nature reserves) were located outside the national nature reserve system (figure 2(e)). Out of 34 non-threatened species, 18 species are endemic. Consequently, the total number of threatened or endemic conifer species is 81 (i.e. 18 (endemic non-threatened) + 63 (all threatened)). Thus, 81 species endemic or threatened and represent 84% of the total studied conifer species. This percentage (84%) is high enough to represent the map of total species to represent the priority conservation areas for either endemic or threatened conifer species.

The results of the correlation analysis showed moderate to high concordance between conifer richness and the three remaining richness groups ($r = 0.68–0.90$, appendix A, table S3), implying that the factors driving conifer richness are possibly the same among the different species richness groups.

3.2. Relationship between different predictors/hypothesis and richness patterns

The GLMs showed that the explanatory variables of environmental energy, particularly MAT and PET, were stronger predictors than climatic seasonality and water availability, and these showed negative relationships (table 1). The MAT explained 6%–19%, while PET explained 4%–19% of the total variance in species richness. The proportion of variance also indicated that environmental energy determines conifer endemic-threatened richness (figure 3). Environmental energy, climatic seasonality, and water availability showed much lower contributions to the variation in species richness compared to that of topographic and soil predictors (figure 3).

Of the 23 variables, the explanatory variables of topographic heterogeneity were the strongest predictors of species richness and showed positive relationships with all richness groups (table 1). Most of the soil fertility variables showed positive and stronger relationships than those of soil texture variables (table 1). The contribution of the human-influence variable was low for all groups and showed negative relationships among groups (table 1). The proportion of variance using the extracted principal components explained by the individual environmental and human-influence predictors highlighted the significant roles of topographic heterogeneity and soil fertility in determining species richness (figure 3).

Hierarchical partitioning modelling showed similar results to those of the GLM models, suggesting that topographic heterogeneity and soil fertility had the highest independent effects on all conifer-richness groups. In contrast, these variables had the highest joint effect on the richness of endemic-threatened species (see appendix A, figures S1a and S1b). The output of the stepwise GLM combined models showed that three models of the all conifer richness group, were rejected due to multicollinearity (i.e. VIF > 5), while for threatened richness group, only one model with the lowest AIC was rejected due to multicollinearity. For endemic or endemic-threatened richness groups, there was no model rejected because the predictor variables, of the model with the lowest AIC, has no multicollinearity. The combined models produced using stepwise regression (GLM) showed that ELER and soil nitrogen were consistently significant predictors (table 2).
Figure 2. Spatial patterns of conifer richness in south-west China are estimated in 50 × 50 km² grid cells. (A) All conifer species; (B) endemics, (C) threatened, (D) endemic-threatened species and (E) national nature reserves, and total conifer richness.
Figure 2. (Continued.)
developed models moderately predicted the conifer richness for all groups (table 2).

4. Discussion

4.1. Conifer richness and conservation priorities

Our results showed that the major centers of conifers richness and endemism were located in Sichuan and Yunnan (Farjon and Filer 2013), including the Qionglai-Minshan ecoregion. This finding supports the critically endangered WWF conservation status of these areas (López-Pujol and Zhao 2004, Ye et al 2015, WWF 2018). It includes threatened conifers growing in these areas, e.g. *Picea likiangensis*, *Picea aurantiaca*, *Picea brachytyla*, *Larix potaninii*, *Abies recurvata*, *Abies fabri*, *Abies forrestii*, *Abies squamata*, *Juniperus spp.*, *Pinus henryi*, and *Pseudotsuga sinensis* (Dakhil et al 2019, Farjon et al 2019, Threatened Conifers of the World 2019). This finding supports making these areas priority conservation regions (López-Pujol et al 2011, Huang et al 2016). Similarly, the Nujiang Langcang Gorge ecoregion harbours high richness of endemic and threatened conifers, e.g. *Abies delavayi*, *Taxus wallichiana*, *Pinus densata*, *Pinus yunnanensis*, *Taiwania cryptomerioides*, and *Cupressus duclouxiana* (Ye et al 2015, Farjon et al 2019, Threatened Conifers of the World 2019).

The highest conifer richness was found in latitudes ranging from 28° to 33° N, indicating a Sichuan-Yunnan hotspot (Farjon 2010, Farjon and Filer 2013). This result strongly agrees with the results of Fragniere et al (2015), who studied the global latitudinal distribution of 607 conifer species. Moreover, the highest elevation was also found in the same latitudinal range, indicating that high levels of endemism are also present in these high elevations (Fragniere et al 2015). Hence, the findings of Fragniere et al (2015) can be used to validate our richness outputs.

Similar studies have used the same spatial resolution as that of our study. They have found that the geographic area of central Sichuan is rich in ~1000–1500 woody species per grid cell (50 km²) with a total of 11 405 studied species, while the Hengduan Mountains in northern Yunnan have high woody species diversity (>1500 species per 50 km²; Wang et al 2010). These hotspot areas could be assumed as priority conservation areas for woody species, particularly conifers (Wang et al 2010, Huang et al 2016).

4.2. The effects of energy, climatic seasonality, and water availability on conifer richness

The effects of water availability and climatic seasonality were relatively weak compared to those of environmental energy, and this due to the differences among conifer species with regard to the demand for water (Liu et al 2019). Generally, this finding supports the hypothesis that environmental energy limits regional species richness (Hawkins et al 2003, Pandey et al
Table 2. The best combinations of variables for each conifer group in south-west China evaluated using stepwise regression and their coefficients of determination ($R^2$). The best models for each group were selected from 1344 models based on the lowest Akaike information criterion (AIC). The numbers in parentheses are coefficients of respective variables from GLM. The variance inflation factors (VIF) for all predictors were less than 5, indicating insignificant multicollinearity.

| Groups           | Environmental energy | Water availability | Climatic seasonality | Topographic heterogeneity | Soil type | Soil fertility (quality) | HII       | $R^2$ (%) |
|------------------|----------------------|--------------------|----------------------|---------------------------|-----------|--------------------------|-----------|-----------|
| All conifers spp.| PET (0.0004)         | ARI (0.00001)      | TS (−0.0012)         | ELER (0.0005)             | SLT (0.0446) | AN (0.0035)              | HII (0.0121) | 62.90     |
| Endemics         | Solar_rad (−0.0002)  | MAP (−0.0052)      | PS (−0.0108)         | ELER (0.0004)             | CLY (0.0255) | AN (0.0045)              | HII (0.0083) | 63.23     |
| Threatened       | Solar_rad (−0.0001)  | AI (0.0000)        | TS (−0.0014)         | ELER (0.0003)             | CR (−0.0123) | AN (0.0035)              | HII (0.0095) | 61.53     |
| Endemic-threatened | Solar_rad (−0.0002) | MAP (−0.0061)      | PS (−0.0091)         | ELER (0.0003)             | SLT (−0.0153) | AN (0.0044)              | HII (0.0114) | 69.50     |
The energy variables (PET) explained the richness patterns better than water variables (AI), and this agrees with the findings of Panda et al. (2017), who studied plant species richness in western Himalaya. Furthermore, PET saturates at an elevation above 900 m with no significant variations, and this highlights the influence of elevation on the patterns of species richness (Zellweger et al. 2015). Moreover, in eastern Himalaya and the Alxa Plateau in China, species richness has been found to show a significant negative relationship with temperature (Sharma et al. 2019, Wang et al. 2019), which supports our findings of MAT and MTCQ, as cool climates at high elevations favour the distribution of conifers (Fang et al. 2011). The seedlings (early developmental stages of trees) are more susceptible to environmental constraints, with warming or heat stress that decreases the species richness of emerging seedlings (Robinson et al. 2018). Also, the adverse effects of energy on conifer richness indicate that endemic-threatened conifers may face a high risk of extinction in the future due to global warming (Ye et al. 2015). This indication supports the findings of conifer forest range dynamics under climate change conditions (Dakhil et al. 2019). It confirms the suggestion of Rosenblad et al. (2019) of species currently being restricted to particular environments, e.g. alpine areas being at risk of extinction due to climate change. It is important to note that the relationships between species richness and climate can be influenced by soil fertility in forest ecosystems (Zhang et al. 2014). The different combined effects of these drivers support the suggestion that the relative effects of these drivers vary among common and threatened taxa (Shrestha et al. 2018, Liu et al. 2019).

4.3. The effect of topographic heterogeneity and human-influence factors on conifer richness

Our results support strong positive topographic heterogeneity-diversity relationships (see table 1 and figure 3) that promote the coexistence and diversification of species by offering niche spaces, which agrees with the findings of several studies (e.g. Stein et al. 2014, Lee and Chun 2016, Shrestha et al. 2018, Sharma et al. 2019, Wang et al. 2019). Topographic heterogeneity was the principle and key driver affecting conifer richness patterns. This result has been reported in several studies for Rhododendron tree species in south-west China (Shrestha et al. 2018), rare woody plant species in the Inner Asian drylands (Liu et al. 2019), and conifer species in southeast Alaska (Bisbing et al. 2016). The high richness of endemic conifers in Qionglai-Minshan and the Hengduan Mountains may be rooted in the complex topography that creates a wide range of habitats and provides more resources that support a high number of species (Bisbing et al. 2016, Shrestha et al. 2018). Furthermore, historically high rates of plant diversification in south-west China have been due to
topographical isolation based on a recent study of molecular phylogeny (Xing and Ree 2017). Hence, heterogeneity is thought to have a significant effect on the structure and dynamics of plant communities (Moeslund et al 2013, Lee and Chun 2016). Moreover, topographic heterogeneity can be used as a proxy of habitat heterogeneity through the control of temperature, the distribution of soil water, and nutrient availability, particularly at high elevations, thereby controlling the occurrence and distribution patterns of species (Bisbing et al 2016, Tashi et al 2016). These results support our findings that temperature was negatively correlated with conifer richness. At the same time, topographic heterogeneity and soil fertility were greatly correlated with species richness (see tables 1 and 2).

The negative correlation between human influence and conifer richness was comparatively weak and explained by 4%. This finding supports the results of Wang et al (2010), who studied the tree species richness in China. On the other hand, the human influence was comparatively strong for endemic-threatened species (Schmiedinger et al 2012, Venter et al 2016). Anthropogenic activity in south-west China is lower than that of Europe or North America. This may be because most of our study conifers were distributed at higher elevations compared to those of Europe and America (Schmiedinger et al 2012, Threatened Conifers of the World 2019).

4.4. The effects of soil texture type and soil fertility on conifer richness

Our findings support the assumption that site-specific habitat factors (e.g. topography and soil) determine the patterns of species richness in addition to climate at the regional scale (Zellweger et al 2015). Soil texture has played a significant role in shaping plant richness patterns along the elevation gradient in eastern Himalaya (Sharma et al 2019), and this agrees with our findings (see figure 3). Furthermore, Sharma et al (2019) also found that soil type was the second strongest predictor explaining 36.4% of the variance in conifer richness. Soil texture and fertility also explained a notable portion of the variance, and similar findings were found in boreal conifer forests in Europe (Germany) and North America (Canada; Schmiedinger et al 2012).

Our results support the finding that explains the importance of sandy soils in the presence of high soil carbon, which leads to an increase in the water-holding capacity and aggregate stability with a greater number of macro pores which are vital to soil functions such as cycling and storing of nutrients, based on their influence on water and air exchange, plant root exploration and habitat for soil biota (Soil Quality Institute 1999). The improvement of macro pores and soil stability will increase soil infiltration capacity and enhance root penetration, subsequently boosting germination and growth of the seedlings of various species (Stein et al 2014, Quesada and Lloyd 2016, Yao et al 2019). Moreover, soil water variables contributed to species richness patterns more than climatic water predictors. This result verifies that soil water balance variables performed better than climatic water variables in tree species distribution modelling (Piedallu et al 2013).

Cation exchange capacity is an ecological indicator of soil fertility, explaining the variation in plant species richness in China (Zhang et al 2016), and this confirms our results. Soil fertility has direct and indirect effects on the growth of plant species, potential distributions, and thereby species composition (Mod et al 2016, Quesada and Lloyd 2016, van der Sande et al 2018). In addition, soil physical properties correlated with soil fertility and directly influence forest disturbance levels (Quesada et al 2012). This effect ultimately determines the turnover rates of tree species with differences in stand level floristic composition (Quesada et al 2012, Quesada and Lloyd 2016). Also, soil fertility including the nutrient availability, increases the species diversity or the competitive advantage of certain species (Yuan et al 2020). Moreover, the finding that nitrogen and phosphorus positively contributed to the variation in species richness through increasing the soil biota, which increases decomposition. The diverse forms of such nutrients may promote plant diversity through resource partitioning when species differ in their preferences for different forms of these nutrients, leading to rapid forest regeneration (Laliberté et al 2014, van der Putten et al 2016). Soil organic carbon is one of the most important constituents of the soil due to its capacity to affect plant growth as both a source of energy and a trigger for nutrient availability through mineralization. Consequently, this provides aggregate stability and water holding capacity, and consequently, enhance seed germination and ecosystem multifunctionality (Soil Quality Institute 1999, Quesada and Lloyd 2016).

4.5. Geodiversity and Conservation implications

Geodiversity components (topography, soil texture and soil fertility) are the main strongest variables shaping the patterns of conifer richness. The soil fertility variables had strong positive effects on the richness patterns, which supports that, rarity may be more related to reduced soil fertility than climatic factors (Ulrich et al 2014, Quesada and Lloyd 2016). Thus, areas with high richness and characteristic geodiversity features are key priority areas for conservation and provide greater insights into the distinctive soil conditions that support conifer diversity and ecosystem functioning and should be considered in afforestation planning (Hjort et al 2015, Knudson et al 2018) with multi-species plantations that increase forest productivity, carbon stocks, and ecosystem resilience (Oliver et al 2015, Liang et al 2016, Chen et al 2018).
Plant habitats with high species richness hasn’t been well captured by the national nature reserve system in comparison to mammalian habitats (Xu et al 2017). Accordingly, the IPAs with the high richness of endemic or threatened conifers (84% of the total conifer species) were found around giant panda and alpine forest nature reserves (see figure 2(e)) and require the establishment of new nature reserves for their protection, and this agrees with the findings of Xu et al (2017) and Dakhil et al (2019).

4.6. Limitations

Broad-scale environment–richness associations are stronger when the grain size increases (Xu et al 2014). On the other hand, some studies have found that landscape attributes may be significant at relatively small scales (e.g. 10–20 km grain sizes (Luoto et al 2007, Reino et al 2013)). Moreover, the model contribution of geodiversity was quite similar in the case of the 25 km² and 50 km² resolutions, providing better model fits than that of the 100–250 km² resolution in native species richness (Bailey et al 2017).

Hence, future studies should include different resolution scales (i.e. fine 5, or 10 km²; coarse 25, or 50 km²). It is important to note that we observed a suitable number of species in each 50 km² grid cell for all groups of conifer richness; hence, if this resolution becomes finer, the number of endemic threatened species in each grid cell will be fewer, and the variation between grid cells will be less so may will not enough to evaluate the relationship with the predictor variables.

5. Conclusions

Geodiversity, including topographic heterogeneity and soil fertility, was the main driver of conifer richness patterns. The Qionglai-Minshan, Hengduan Mountains, and Nujiang Langcang Gorge ecoregions were the major centres of threatened and endemic conifers in south-west China. Compared to all conifer species. Endemic-threatened conifers were more strongly affected by soil fertility, MAT, and topographic heterogeneity, and this indicates that endemic-threatened conifers may face a high risk of extinction in the future due to climate change and habitat destruction which induced by human activities that may reduce soil fertility. Also, this finding is a promising tool for afforestation planning of the threatened-endemic conifers, as soil fertility increase species diversity or the competitive advantage of certain species. The areas of central Sichuan, with a high richness of endemic-threatened conifers, could be considered to be priority areas for conservation because they were positively correlated with geodiversity, including soil fertility. Carbon, nitrogen, and topographic heterogeneity showed the highest contributions and strongest positive relationships with the richness of all conifer groups. This finding would help in afforestation planning. Climate, energy, and water availability were influenced by topographic-soil fertility. Accordingly, we recommend global researchers to incorporate soil fertility variables into the spatial modelling at community levels, and this will provide greater insights into conservation and management of the ecosystem multifunctionality.

The four proposed nature reserves or areas around the giant panda and alpine forest nature reserves in central Sichuan and northern Yunnan (see figure 2(e)) could be suggested as priority conservation areas. These areas should be protected to rescue all conifers of the endemic or threatened communities and their habitats.

The conifers in the current study may serve as a proxy for other plant or conifer taxa living in similar topo-geographical areas in Europe, America, or Canada. However, human influence should be taken into consideration because this is high in Europe. While the Chinese government has banned logging in south-west China, human disturbances in the region could be the result of urbanization, tourism activities, and agricultural expansions, which promote the growth of invasive species. As such, these human influences should be taken into consideration, along with the recent data of these disturbances.

Finally, logical directions of future research include a spatial conservation assessment of endemic-threatened conifer species under various scenarios of climate change, taking into account the findings of the current study when planning future conservation and ecosystem management strategies.

Data availability statement

The data that support the findings of this study are openly available.

All data that support the findings of this study are included within the article (and any supplementary files).

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Statement of authorship

Dakhil MA and Pan K conceived the idea. Dakhil MA performed statistical, spatial and modelling analysis. Pandey B and Liao Z helped Dakhil MA in R scripts. Dakhil MA wrote the manuscript. All authors contributed substantially to collect the data and revise the manuscript.

ORCID iDs

Mohammed A Dakhil https://orcid.org/0000-0002-5140-1360
Bikram Pandey https://orcid.org/0000-0003-2592-1466
Ziyaan Liao https://orcid.org/0000-0001-9354-2009
Ebrahim M Eid https://orcid.org/0000-0003-2452-4469
Mohamed Abdelaal https://orcid.org/0000-0003-2162-7630

References

Anderson M G, Conner P J, Beier D, Lawler J J, Schluss C A, Buttrick S, Albano C M and Faith D P 2015 Case studies of conservation plans that incorporate geodiversity Conserv. Biol. 29 680–91
Anderson S 2002 Identifying Important Plant Areas (London: Plantlife International)
Bailey J, Boyd D S, Hjort J, Luoto M and Field R 2017 Modelling native and alien vascular plant species richness: at which scales is geodiversity most relevant? Glob. Ecol. Biogeogr. 26 763–76
Bissing S M, Cooper D J, Amore D V D and Marshall K N 2016 Determinants of conifer distributions across peatland to forest gradients in the coastal temperate rainforest of southeast Alaska Ecolhydrology 367 354–67
Brown J L 2014 SDM toolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses Methods Ecol. Evol. 5 694–700
Chen S, Wang W, Xu W, Wang Y, Wan H, Chen D, Tang Z, Tang X, Zhou G and Xie Z 2018 Plant diversity enhances productivity and soil carbon storage Proc. Natl Acad. Sci. 115 4027–32
Currie D J, Mittelbach G, Cornell H V, Field R, Guégan J, Hawkins B A, Kaufman D M, Kerr J T, Oberdorff T and O’Brien E M 2004 Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness Ecol. Lett. 7 1121–34
Dakhil M A, Xiong Q, Farahat E A, Zhang L, Pan K, Pandey B, Olatunji O A, Tarig A, Wu X and Zhang A 2019 Past and future climatic indicators for distribution patterns and conservation planning of temperate coniferous forests in southwestern China Ecol. Indic. 107 105559
ESRI (Environmental Systems Research Institute) 2014 ArcGIS® Desktop Help 10.3 Geostatistical Analyst (available at: https://desktop.arcgis.com/en/arcmap/10.3)
Fang J, Wang Z and Tang Z 2011 Atlas of Woody Plants in China: Distribution and Climate vol 1 (Berlin: Springer Science & Business Media)
Faraway J 2016 Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models (Boca Raton, FL: Chapman and Hall)
Farjon A 2010 A Handbook of the World’s Conifers (2 Vols.) Vol. 1 (Leiden: Brill)
Farjon A and Filer D 2013 An Atlas of the World’s Conifers: An Analysis of Their Distribution, Biogeography, Diversity and Conservation Status (Leiden: Brill)
Farjon A, Gardner M and Thomas P 2019 Conifer Database (version Jan 2014) Species 2000 ITIS Cat. Life, 2019 Annu. Checkl. (ed Roskov Y, Ower G, Orrell T, Nicolson D, Bailly N, Kirk P M, Bour尹n T, DeWalt R E, Decoock W, Nieuwerken E van, Zarucchi J, Pener L) (http://www.catalogueoflife.org/annual-checklist/ 2019/details/database/id/45)
Fick S E and Hijmans R J 2017 WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas Int. J. Climatol. 37 4302–15
Fishner J B, Whittaker R J and Malhi Y 2011 ET come home: potential evapotranspiration in geographical ecology Glob. Ecol. Biogeogr. 20 1–18
Fox J, Weinberg S, Adler D, Bates D, Baud-Bovy G and Ellison S and Zeileis A R-Core 2016 Car: companion to applied regression package version 2.1-2
Fragi niere Y, Bétrisey S, Cardinaux L, Stoffel M and Kozlowski G 2015 Fighting their last stand? A global analysis of the distribution and conservation status of gymnosperms J. Biogeogr. 42 809–20
Francis A P and Currie D J 2003 A globally consistent richness-climate relationship for angiosperms Am. Nat. 161 323–36
Gray M 2013 Geodiversity: Valuing and Conserving Abiotic Nature 2nd edn (New York: Wiley)
Hawkins B A, Field R, Cornell H V, Currie D J, Guégan J-F, Kaufman D M, Kerr J T, Mittelbach G, Obergordorff T and O’Brien E M 2003 Energy, water, and broad-scale geographic patterns of species richness Ecology 84 3105–17
Heng T, de Jesus J M, Macmillan R A, Batjes N H, Heuvelink G B M, Ribeiro E, Samuel-Rosa A, Kempen B, Leenaars J G B and Walsh M G 2014 SoilGrids1km—global soil information based on automated mapping PLoS One 9 e105992
Hjort J, Gordon J E, Gray M and Hunter Jr M L 2015 Why geodiversity matters in valuing nature’s stage Conserv. Biol. 29 630–9
Hjort J, Heikkinen R K and Luoto M 2012 Inclusion of explicit measures of geodiversity improve biodiversity models in a boreal landscape Biodivers. Conserv. 21 3487–506
Hjort J and Luoto M 2012 Can geodiversity be predicted from space? Geomorphology 153 74–80
Huang J, Lu X, Huang J and Ma K 2016 Conservation priority of endemic Chinese flora at family and genus levels Biodivers. Conserv. 25 23–35
Huston M 1980 Soil nutrients and tree species richness in Costa Rican forests J. Biogeogr. 7 147–57
IBM 2012 IBM SPSS statistics version 21 Boston, Mass Int. Bus. Mach. Corp 126
Keith D A 2011 Relationships between geodiversity and vegetation in southeastern Australia. Proc. of the Linnean Society of New South Wales 132 5–26
Knudson C, Kay K and Fisher S 2018 Appraising geodiversity and cultural diversity approaches to building resilience through conservation Nat. Clim. Change 8 678
Laliberté E, Zemunik G and Turner B L 2014 Environmental filtering explains variation in plant diversity along resource gradients Science 345 1602–5
Lausch A et al 2019 Linking remote sensing and geodiversity and their traits relevant to biodiversity—part I: soil characteristics Remote Sens. 11 2356
Lee C-B and Chun J-H 2016 Environmental drivers of patterns of plant diversity along a wide environmental gradient in Korean temperate forests Forests 7 19
Legendre P and Legendre L 2012 Numerical Ecology 3rd English edn (Amsterdam: Elsevier)
Liang J, Crowther T W, Picard N, Wiser S, Zhou M, Alberti G, Schulze E-D, Mcguire A D, Bozzato F and Pretzsch H 2016 Positive biodiversity-productivity relationship predominant in global forests Science 354 718957
Liu X, Trogisch S, He J-S, Niklaus P A, Brulleheide H, Tang Z, Erfmeier A, Scherer-Lorenzen M, Pietsch K A and
Yang B 2018 Tree species richness increases ecosystem carbon storage in subtropical forests Proc. R. Soc. B 285 20181240

Liu Y, Su X, Shrestha N, Xu X, Wang S, Li Y, Wang Q, Sandanov D and Wang Z 2019 Effects of contemporary environment and Quaternary climate change on drylands plant diversity differ between growth forms Ecography 42 334–45

López-Pujol J and Zhao A 2004 China: a rich flora needed of urgent conservation Ovni Org. 19 49–89

López-Pujol J, Zhang F, Sun H, Ying T and Ge S 2011 Centres of plant endemism in China: places for survival or for speciation? J. Biogeogr. 38 1267–80

Luoto M, Virkkala R and Heikkinen R K 2007 The role of land cover in bioclimatic models depends on spatial resolution Glob. Ecol. Biogeogr. 16 54–42

Maestre F T, Quero J I, Gotelli N J, Escudero A, Ochoa V, Delgado-Baquerizo M, García-Gómez M, Bowker M A, Soliveres S and Escolar C 2012 Plant species richness and ecosystem multifunctionality in global drylands Science 335 214–8

Mod H K, Scherrrer D, Luoto M and Guisan A 2016 What we use is not what we know: environmental predictors in plant distribution models J. Veg. Sci. 27 1308–22

Moeslund J E, Arge L, Bøcher P K, Dalgaard T and Svenning J 2016 What we use is not what we know: environmental predictors in plant distribution models J. Veg. Sci. 27 1308–22

O’Brien E 1998 Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model J. Biogeogr. 25 379–98

Oliver T H, Heard M S, Isaac N J B, Roy D B, Procter D, Eigenbrod F, Freckleton R, Hector A, Orme C D L and Pentchey O J 2015 Biodiversity and resilience of ecosystem functions Trends Ecol. Evol. 30 673–84

Olson D M, Dinerstein E, Wikramanayake E D, Burgess N D, Powell G V N, Underwood E C, D’Amico J A, Ioula I, Strand H E and Morrison J C 2001 Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity Bioscience 51 933–8

Panda R M, Behera M D, Roy P S and Biradar C 2017 Energy determines broad pattern of plant distribution in Western Himalaya Ecol. Evol. 7 10850–60

Pandey B, Nepal N, Tripathi S, Xu X, Wang S, Li Y, Wang Q, Sandanov D and Wang Z 2019 Effects of contemporary environment and Quaternary climate change on drylands plant diversity differ between growth forms Ecography 42 334–45

Piedallu C and Géorgot J 2008 Efficient assessment of topographic solar radiation to improve plant distribution models Agric. For. Meteorol. 148 1096–760

Piedallu C, Géorgot J, Perez V and Lebougeois F 2013 Soil water balance performs better than climatic water variables in tree species distribution modelling Glob. Ecol. Biogeogr. 22 470–82

Quesada C A et al 2012 Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate Biogeosciences 9 2203–46

Quesada C A and Lloyd J 2016 Soil–vegetation Interactions in Amazonia Interactions between Biosphere, Atmosphere and Human Land Use in the Amazon Basin (Berlin: Springer) pp 267–99

Räsänen A, Kuitunen M, Hjort J, Vaso A, Kuitunen T and Lensu A 2016 The role of landscape, topography, and geodiversity in explaining vascular plant species richness in a fragmented landscape Boreal Environ. Res. 21 53–70

Reino L, Beja P, Araújo M B, Dray S and Segurado P 2013 Does local habitat fragmentation affect large-scale distributions? The case of a specialist grassland bird Divers. Distrib. 19 423–43

Ren H et al 2020 Progress of implementation on the global strategy for plant conservation in (2011–2020) China Biol. Conserv. 230 169–78

Robinson S J, McLaughlin Ó B, Marteinsdóttir B and O’Gorman E J 2018 Soil temperature effects on the structure and diversity of plant and invertebrate communities in a natural warming experiment J. Anim. Ecol. 87 634–46

Rosenblad K C, Perret D L and Sax D F 2019 Niche syndromes reveal climate-driven extinction threat to island endemic conifers Nat. Clim. Change 9 627–31

Schimd M, Alexe B, Redgley J, Steinbauer M J, Macdonald S E, Jentsch A and Beierkuhnlein C 2012 A continental comparison indicates long-term effects of forest management on understory diversity in coniferous forests Can. J. For. Res. 42 1239–52

Shanggwan W, Dai Y, Liu B, Zhu A, Duan Q, Wu L, Ji D, Ye A, Yuan H and Zhang Q 2013 A China data set of soil properties for land surface modeling J. Adv. Model. Earth Syst. 5 212–24

Sharma N, Behera M D, Das A P and Panda R M 2019 Plant richness pattern in an elevation gradient in the Eastern Himalaya Biodivers. Conserv. 28 1–20

Shrestha N, Su X, Xu X and Wang Z 2018 The drivers of high Rhododendron diversity in south-west China: does seasonality matter? J. Biogeogr. 45 438–47

Soil Quality Institute 1999 Soil Quality Test Kit Guide USDA (available at: www.nrcs.usda.gov/wps/portal/nrcs/main/sols/health/resource/)

Stein A, Gerstner K and Krell H 2014 Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales Ecol. Lett. 17 866–80

Tashi S, Singh B, Keitel C and Adams M 2016 Soil carbon and nitrogen stocks in forests along an altitudinal gradient in the eastern Himalayas and a meta-analysis of global data Glob. Chang. Biol. 22 2255–69

Threatened Conifers of the World 2019 Threatened Conifers of the World (available at: https://threatenedconifers.rbge.org.uk)

Trabucco A, Zomer R J, Bossio D A, van Straaten O and Verchot L V 2008 Climate change mitigation through afforestation/reforestation: a global analysis of hydrologic impacts with four case studies Agric. Ecosyst. Environ. 126 81–97

Tripathi P, Behera M D and Roy P S 2019 Spatial heterogeneity of climate explains plant richness distribution at the regional scale in India PLoS One 14 e0218322

Tukiainen H, Bailey J, Field R, Kangas K and Hjort J 2017 Combining geodiversity with climate and topography to account for threatened species richness Conserv. Biol. 31 364–75

Ulrich W, Soliveres S, Maestre F T, Gotelli N J, Quero J I, Delgado-Baquerizo M, Bowker M A, Elderidge D J, Ochoa V and Gozalo B 2014 Climate and soil attributes determine plant species turnover in global drylands J. Biogeogr. 41 2307–19

van der Putten W H, Bradford M A, Pernilla Brinkman E, van de Voorde T F J and Veen G F 2016 Where, when and how plant–soil feedback matters in a changing world Funct. Ecol. 30 1109–20

van der Sande M T, Arets E J M, Peña-Claros M, Hoosbeek M R, Trabucco A, Zomer R J, Bossio D A, van Straaten O and Verchot L V 2008 Climate change mitigation through afforestation/reforestation: a global analysis of hydrologic impacts with four case studies Agric. Ecosyst. Environ. 126 81–97

Venables W N and Ripley B D 2013 Modern Applied Statistics with S-PLUS (Berlin: Springer Science & Business Media)

Venter O et al 2016 Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation Nat. Commun. 7 1–11

Ver Hoef J M and Boveng P L 2007 Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? J. Ecol. 88 2766–72

Walsh C and Mac Nally R 2013 hier. part: hierarchical partitioning R package version 1.0-4 Part R software, R Found. Stat. Comput. Vienna, Austria
Wan J Z, Wang C J and Yu F H 2017 Spatial conservation prioritization for dominant tree species of Chinese forest communities under climate change Clim. Change 144 303–16

Wang J, Cui P, Zhong Y, Li J and Chu J 2019 Biogeographic patterns and environmental interpretation of plant regional species richness in Alxa Plateau of northern China J. Beijing For. Univ. 41 14–23

Wang Q et al 2018 Niche conservatism and elevated diversification shape species diversity in drylands: evidence from Zygophyllaceae Proc. R. Soc. B 285 20181742

Wang Z, Fang J, Tang Z and Lin X 2010 Patterns, determinants and models of woody plant diversity in China Proc. R. Soc. B 278 2122–32

Wildlife Conservation Society-WCS 2005 Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic) (Palisades, NY: NASA Socioeconomic Data and Applications Center) (https://doi.org/10.7927/h4bp00qc)

WWF 2018 Terrestrial ecoregions: temperate coniferous forest (available at: www.worldwildlife.org/biomes/temperate-coniferous-forest) (Accessed March 2018)

Xing Y and Ree R H 2017 Uplift-driven diversification in the Hengduan mountains, a temperate biodiversity hotspot Proc. Natl Acad. Sci. 114 E3444–51

Xu C, Huang Z Y, Chi T, Chen B J, Zhang M and Liu M 2014 Can local landscape attributes explain species richness patterns at macroecological scales? Glob. Ecol. Biogeogr. 23 436–45

Xu W, Xiao Y, Zhang J, Yang W, Zhang L, Hull V, Wang Z, Zheng H, Liu J and Polasky S 2017 Strengthening protected areas for biodiversity and ecosystem services in China Proc. Natl Acad. Sci. 114 1601–6

Yao R, Palmer D, Hock B, Harrison D, Payn T and Monge J 2019 Forest investment framework as a support tool for the sustainable management of planted forests Sustainability 11 3477

Ye X, Liu G, Li Z, Wang H and Zeng Y 2015 Assessing local and surrounding threats to the protected area network in a biodiversity hotspot: the Hengduan Mountains of Southwest China PLoS One 10 e0138533

Ying J, Chen M and Zhang H 2004 Atlas of the Gymnosperms of China (Beijing: China Science and Technology Press)

Yuan Z et al 2020 Above- and below-ground biodiversity jointly regulate temperate forest multifunctionality along a local-scale environmental gradient J. Ecol. 108 2012–24

Zellweger F, Braunisch V, Morsdorf F, Baltensweiler A, Abeg M, Roth T, Bugmann H and Bollmann K 2015 Disentangling the effects of climate, topography, soil and vegetation on stand-scale species richness in temperate forests For. Ecol. Manage. 349 36–44

Zhang M G, Slik J W F and Ma K P 2016 Using species distribution modeling to delineate the botanical richness patterns and phytogeographical regions of China Sci. Rep. 6 1–9

Zhang M, Zhou Z, Chen W, Cannon C H, Raes N and Slik J W F 2014 Major declines of woody plant species ranges under climate change in Yunnan, China Divers. Distrib. 20 405–15