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Biogeographic Patterns and Richness of the *Meconopsis* Species and Their Influence Factors across the Pan-Himalaya and Adjacent Regions

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Abstract: Understanding the potential habitat of *Meconopsis*, their species richness distribution patterns, and their influencing factors are critical for the conservation and rational exploitation of this valuable resource. In this study, we applied the MaxEnt model to predict their potential distribution, mapped the distribution pattern of species richness, and analyzed the variation of species richness along environmental gradients. Finally, we calculated the landscape fragmentation indices between the five subregions. Our results found that: (1) the medium- and high-suitable habitats of *Meconopsis* were mainly distributed in the central and eastern Himalaya, the Hengduan Mountains, and the southeast edge of the plateau platform, with suitable habitats ranged from 3200 m to 4300 m, whose most important factor is precipitation of the warmest quarter; (2) species richness showed a hump pattern along the environmental gradients except for longitude that showed an increasing trend, mainly concentrated in the south and southeast; and (3) the subregions are in the descending order of species richness: plateau platform, Hengduan Mountains, central, eastern, and western Himalaya; the highest and lowest degree of landscape fragmentation were in the western Himalaya and eastern Himalaya, respectively. Our study provides a theoretical background for the conservation and sustainable exploitation of *Meconopsis* in the wild.

Keywords: *Meconopsis*; potential distribution; species richness; environmental factors; landscape fragmentation; Himalaya; Qinghai-Tibet Plateau; Hengduan Mountains

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1. Introduction

Climate change is an indisputable reality today, evidenced by glacial melting from mountain areas, greening of alpine tundra or arctic, upward shifting of alpine tree lines, and shrub encroachment into alpine grassland [1–3]. Many scientists believe that mountains act as early warning systems and can provide direct evidence to understand potential changes in the lowland environment [4,5]. Mountains around the world vary in terms of shape, extension, elevation, climate change impact, and biodiversity because of the differences in their geographic locations coupled with the complex region-specific hydrothermal condition [5,6]. Most studies have shown that the Qinghai-Tibet Plateau sensu lato (QTPsl) is not a natural tectonic association, but rather comprises a "plateau platform" (i.e., Qinghai-Tibet Plateau sensu stricto; QTPss) [7,8], the Himalaya, and the Hengduan Mountains [9,10]. Together these three regions are also referred to as the pan-Himalayan region [10,11] which boasts of complex topography, diverse geomorphological types, a wide altitudinal range, and different soil textures and geological conditions. This region, where one can observe diverse habitats within a short distance, supports a variety of endemic and endangered species [11,12]. The pan-Himalayan region is an important biodiversity hotspot with the world's highest diversity of alpine plants, attracting extensive scientific attentions [10,13,14].

Biodiversity, especially plant diversity, plays an important role in regulating climate, stabilizing the structure and functions of ecosystems, and providing ecosystem services for humans [15,16]. However, this diversity of plant resources has been constantly threatened by climate change and excessive anthropogenic disturbance since the last century [17,18]. As one of the most severe threats to global biodiversity, climate change has interfered with the composition, structure, and functioning of many mountainous ecosystems, resulting in an ecosystem imbalance that eventually affects human well-being [19–21]. Climate variables can determine the geographic distribution patterns of plant species [22] in addition to several non-climatic factors, such as topography, soil types, and land use, which equally impact species distribution [23]. The geographical distribution of alpine plants, in particular, is sensitive to the interaction between climate and topography [11,24]. Furthermore, human disturbances in mountainous landscapes not only accelerate climate change but also cause severe habitat loss and fragmentation and support the invasion of alien species, which are often directly or indirectly related to the loss of biodiversity [18,25–27]. Many native plant habitats have suffered habitat loss and fragmentation [23,25,27] that leads to the creation of isolated habitat patches resulting in an eventual decline in species viability across the landscape and ultimately reduction of species diversity across the ecosystem [18,28]. Numerous studies have shown the negative impact of fragmentation at the landscape scale on species diversity; however, the ecological effects of fragmentation at larger macroscopic scales are not clearly demonstrated [29,30]. Habitat loss and fragmentation are the primary drivers for the extinction of plant species [31]. Maintaining plant diversity while ensuring their sustainable utilization for human well-being is a common global concern [32]. Species richness is a fundamental scale for measuring regional diversity and the basis for constructing evolutionary and ecological models and conservation strategies [33]. Species diversity at the local scale is influenced by habitat heterogeneity such as geographic differences, climate, topography (elevation, slope, slope direction, etc.), and latitude and longitude, among other factors [34,35]. Thus, understanding the geographic distribution patterns of species richness in a particular area is of great scientific significance for the conservation, development, and sustainable utilization of plant resources.

The genus *Meconopsis* (Himalayan or blue poppies) belongs to the Papaveraceae family and contains over 70 species [36]. These plants are mainly localized in the Qinghai-Tibet Plateau, Hengduan Mountains, and Himalaya between the elevational range of 2000 m to 5800 m, where habitat changes from temperate forests to alpine meadows to screes and nival zones [37,38]. The East Himalaya-Hengduan Mountains region is the center of diversity for *Meconopsis* genus. *Meconopsis* plays a unique role in the alpine ecosystem. It is an important component of the regional biodiversity and participates in primary production, which is critical for ecosystem functioning [39]. *Meconopsis* is well-known for its colorful, attractive, and gracefully postured flower with high ornamental value and is widely used in horticultural gardening [40]. Species of this genus are symbols of tenacious vitalities since they bloom with beautiful flowers despite the extremely cold and harsh environment, inspiring those who live in the same extreme conditions [41]. These flowers are often shown in frescoes and thangkas, being closely related to Tibetan Buddhism, being the prototype of the ubala flower held by the *Green Tara* for relieving suffering [42]. *Meconopsis* is valued for its medicinal properties with a long clinical history in China and other Asian countries. The medicinal properties of the genus were first recorded in the Tibetan medicine book *Yue Wang Yao Zhen*. Famous masterpieces of traditional Tibetan herbal medicine such as

The Four Medical Tantras and *Jing Zhu Materia Medica* have described the use of *Meconopsis* for its anti-inflammatory or analgesic properties [41]. For instance, the flowers or whole plant of *M. integrifolia* can be used for curing hepatitis, pneumonia, liver heat, lung heat, and edema [41]. Recently, a variety of isoquinoline alkaloids with bioactivities have been isolated from *Meconopsis*, which partly explains its unique therapeutic effects [41]. However, only a few species of this genus have been cultivated for floriculture successfully in a controlled environment [41,43]. With the development of the pharmaceutical economy in these regions, overexploitation and anthropogenic habitat destruction are increasingly threatening the survival of many wild *Meconopsis* species, and some *Meconopsis* species have been placed under protection by law [41,42]. Hence, it is of great necessity to map the habitat distribution and ensure the sustainable development of *Meconopsis* from both natural and social perspectives for their habitat conservation and sustainable development.

Predicting the potential species distribution is a significant step toward habitat protection, and the species distribution model (SDM) has become one of the most widely used tools for simulating the potential distribution of organisms [44,45]. The basic principle of SDM is to correlate current species distribution with corresponding environmental variables to estimate the ecological requirements of a species based on ecological niches, thus predicting the suitable habitat [46,47]. The MaxEnt model is the most widely used among the many SDMs because it not only provides stable and reliable prediction results even with small sample data sizes but can work with presence-only data unlike some other models [42,48,49]. Due to the high prediction accuracy, it has been widely used in studies on the spatial distribution of species in response to climate change [9], suitable planting areas for important economic crops, and priority conservation areas for endangered and rare species [50–52]. The screening of suitable habitats and identifying priority conservation areas is critical for habitat management. However, to develop effective landscape management plans, the role of landscape fragmentation in determining the distribution and survival of species cannot be ignored.

Landscape fragmentation is the process by which the surface of a landscape is transformed from a regular homogeneous entity into smaller, complex, and poorly connected patches, mainly as a result of human activities and environmental disturbances [53]. The landscape index can reflect the landscape information well and is a common method to study landscape fragmentation quantitatively. Landscape indices are generally calculated using FragStats (Fragment Statistic), a software program for calculating indices of different types of landscape patterns in classified map patterns or patch mosaics, and analysis of spatial patterns for quantifying landscape structure (i.e., composition and configuration) [54]. It offers a comprehensive choice for the calculation of landscape pattern indices, and three levels (individual patch, patch class, and landscape) of the landscape index can be obtained after the calculation [54]. It is of practical significance to clarify the relationship between landscape pattern and species richness for the conservation and sustainable development of diversity.

In this study, we used MaxEnt to predict the potential distribution pattern of *Meconopsis* and used regression analysis to explore the geospatial pattern of species richness for *Meconopsis* in the pan-Himalaya and its adjacent regions. In addition, we divided the study area into five subregions and used landscape index as a variable to measure landscape fragmentation, and compared the species richness of *Meconopsis* in each subregion (Figure 1). This paper aimed to: (1) predict the potential distribution of *Meconopsis* and determine the key factors affecting the distribution of these species in the pan-Himalaya and adjacent regions; (2) clarify the species richness pattern of *Meconopsis* and analyze the distribution characteristics of species richness under different altitude, latitude and longitude, and other topographical factors (aspect and slope); and (3) assess the degree of landscape fragmentation and species richness *Meconopsis* in five subregions. The results will contribute to identifying the appropriate geographical space available for *Meconopsis* species and help in ensuring sustainable utilization and management of the genus.

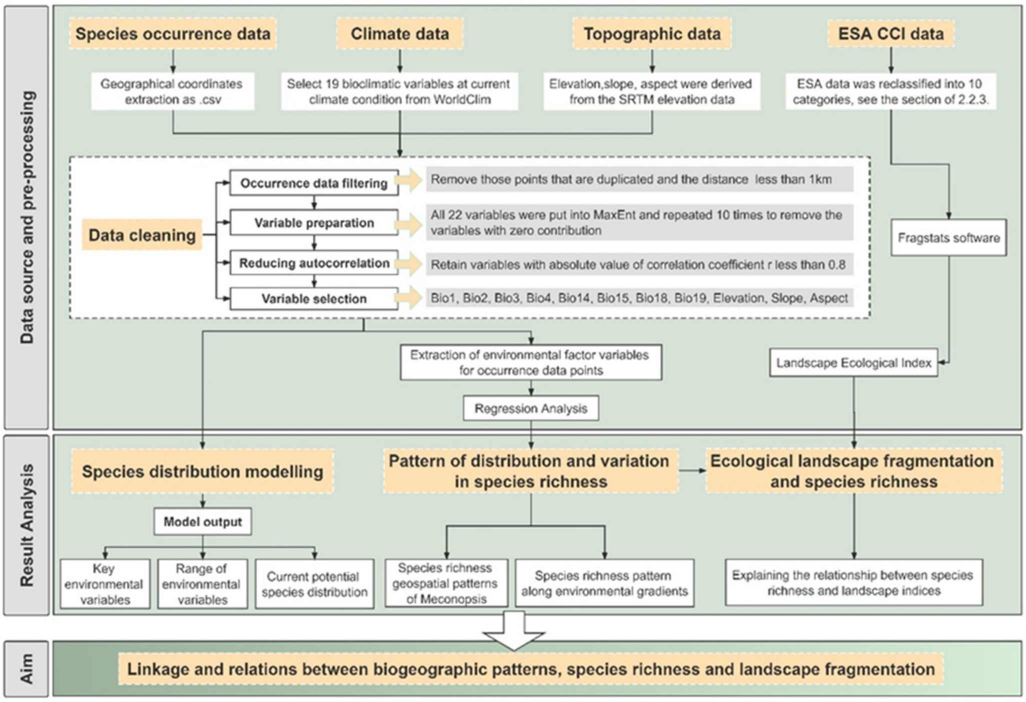


Figure 1. The conceptual framework of the study.

2. Materials and Methods

2.1. Study Area

The study area lies between 68°04′00″~104°40′00″ E and 27°25′30″~40°08′00″ N (Figure 2), which extends from the southern margin of the Himalaya to the northern margin of the Kunlun and Qilian Mountains, and the Pamirs Plateau and Karakorum Mountains in the west to the Hengduan Mountains in the east [55]. This area has the highest elevation (more than 4000 m above sea level) and diverse topography, which support a variety of vegetation types at different elevations. From low to high elevations, these vegetation types include dry and hot river valley scrubs, broadleaved forests, mixed coniferous broadleaved forests, coniferous forests, shrubs, meadows, cold subnival belts, and nival belts (glaciers). This region harbors the world's most species-rich temperate alpine flora driven by orogenetic movements and climate change (monsoon intensification) [56]. It is currently home to approximately 12,000 species of vascular plants belonging to 1500 genera, of which more than 20% are endemic [57]. The mountain region is a diversity center for many species-rich genera, such as rhododendron, gentiana, saussurea, and pedicularis, all of which contain numerous endemic species [14]. We divided the entire study area into five subregions based on the boundaries of the Qinghai-Tibet Plateau, Hengduan Mountains, and Hindu-Kush Himalaya: plateau platform, Hengduan Mountains, eastern Himalaya, central Himalaya, and western Himalaya (Figure 2) [10,11,55]. Of these, the alpine plant biota in Hengduan Mountains is the richest [56].

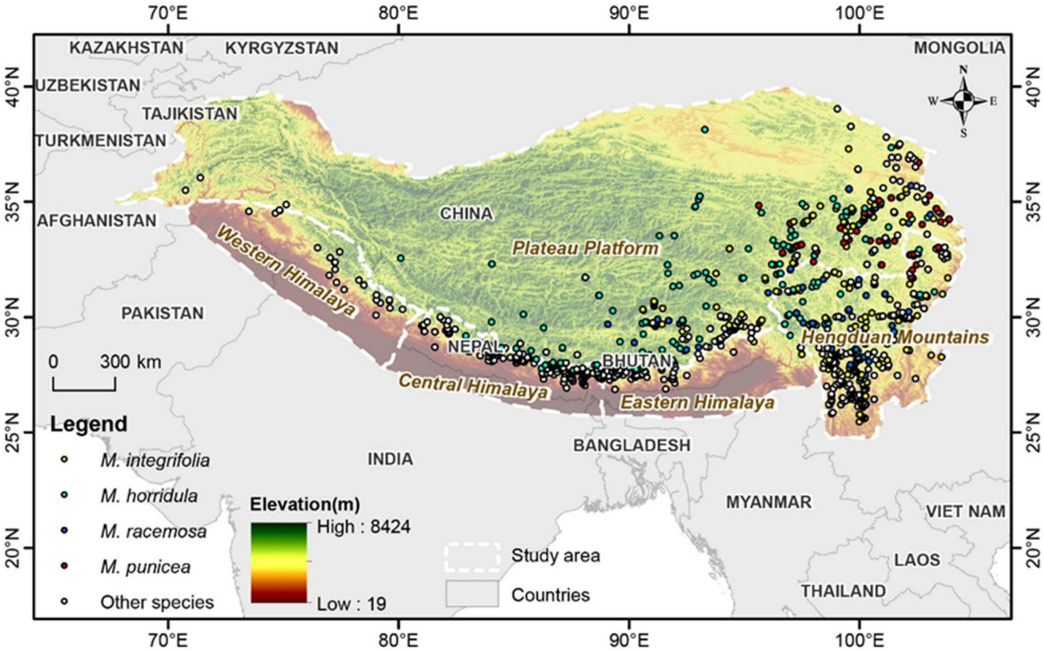


Figure 2. The presence points of *Meconopsis* species in the study area.

2.2. Data Sources and Preprocessing

2.2.1. Species Occurrence Data

We collected the occurrence data for *Meconopsis*, *M. integrifolia*, *M. horridula*, *M. racemosa*, and *M. punicea* from the following three sources: (1) Chinese Virtual Herbarium (CVH, http://www.cvh.ac.cn/; accessed on 22 December 2021), (2) Global Biodiversity Information Facility (GBIF.org, https://www.gbif.org/; accessed on 22 December 2021), and (3) published literature (China National Knowledge Infrastructure, CNKI, https://www.cnki.net/; Web of Science, https://www.webofscience.com/; accessed on 22 December 2021). All data points were carefully evaluated to exclude duplicate data points and then validated via Google Earth to eliminate possible errors; finally, ArcGIS 10.8 was used to remove points that were not in the study region. We also ensured that the selected presence data points were evenly distributed throughout the study area to avoid sampling bias. Following this selection and elimination criteria, the selected presence locations of each species involved in our study are as follows: *Meconopsis* (1445), *M. integrifolia* (296), *M. horridula* (304), *M. racemosa* (111), and *M. punicea* (90) (Figure 2, Table S1).

2.2.2. Bioclimatic and Topographic Data

Bioclimatic data used for the study included 19 bioclimatic variables with the spatial resolution of 30 arc-seconds (~1 km at the equator) representing current climatic conditions (average for 1950–2000) [45], obtained from the WorldClim dataset (https://www.worldclim.org; accessed on 5 January 2022). Besides, three topographic variables (elevation, slope, and aspect) derived from digital elevation model (DEM) data downloaded from WorldClim were also used in the study. To improve the prediction accuracy by eliminating multicollinearity, we performed a Pearson correlation analysis on all environmental variables and retained the environmental factors with low correlation coefficients ($|r| < 0.8$) [58]. Among the environmental factors with high correlation coefficients ($|r| > 0.8$), we retained only one factor of the two variables [58]. Finally, a total of 11 environmental variables, including 8 bioclimatic variables and 3 topographic variables, were obtained to simulate the current potential habitat of *Meconopsis* (Table 1).

Table 1. Environmental variables for modelling the habitat suitability for *Meconopsis* species and four typical species.

Type	Variable Name	Code	Data Source	Unit	Resolution
Bio-Climatic	Annual Mean Temperature	Bio1	WorldClim	°C	30″
	Mean Diurnal Range	Bio2	WorldClim	°C	30″
	Isothermality (Bio2/Bio7) (×100)	Bio3	WorldClim	°C	30″
	Temperature Seasonality (Standard Deviation × 100)	Bio4	WorldClim	°C	30″
	Precipitation of Driest Month	Bio14	WorldClim	mm	30″
	Precipitation Seasonality (Coefficient of Variation)	Bio15	WorldClim	1	30″
	Precipitation of Warmest Quarter	Bio18	WorldClim	mm	30″
	Precipitation of Coldest Quarter	Bio19	WorldClim	mm	30″
Topographic	Elevation	Elevation	WorldClim	m	30″
	Slope	Slope	DEM	°	30″
	Aspect	Aspect	DEM	°	30″

2.2.3. Land Type Data

ESA CCI-LC land use/cover data (300 m spatial resolution, 1992–2015) were downloaded from the European space agency (http://maps.elie.ucl.ac.be/CCI/viewer/; accessed on 11 January 2022). The ESA data (including 22 categories) were reclassified into 10 categories: agriculture, forest, grassland, wetland, settlement, shrubland, sparse vegetation, bare area, water, and permanent snow and ice (Figure 3).

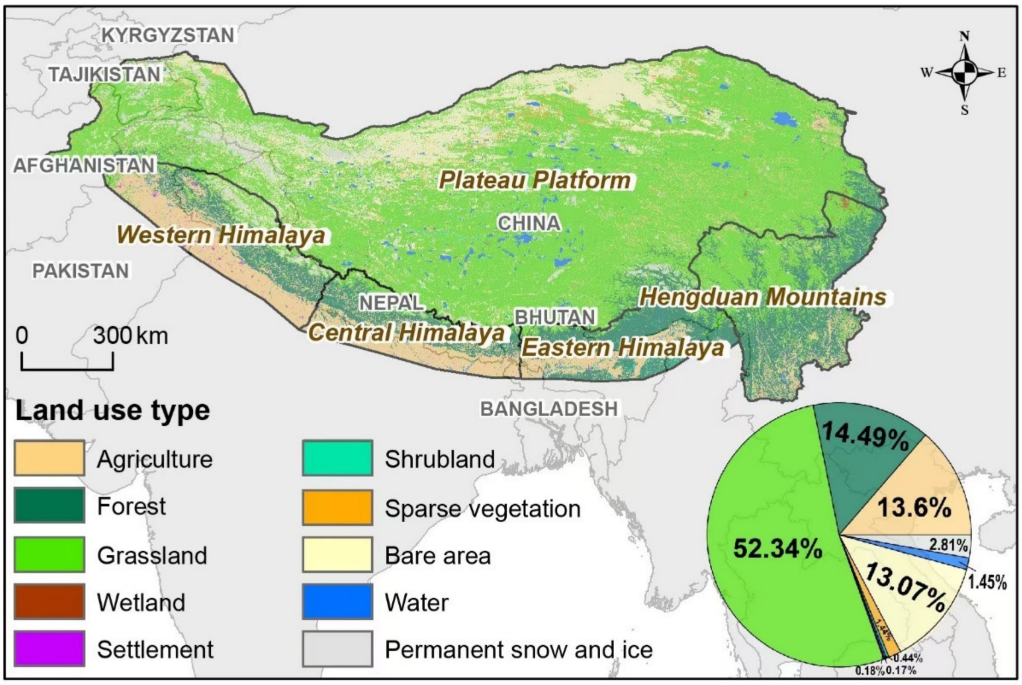


Figure 3. The land-use type maps in the study area.

2.3. Methods

2.3.1. MaxEnt Modeling

MaxEnt is a popular open-access species distribution model. It employs the maximum entropy algorithm and species occurrence points to predict the probability of species occurrence in potential distribution areas. In the study, we used MaxEnt 3.4.4 to model the current habitat distribution of typical *Meconopsis* species and the whole genus. Species occurrence data were divided into two data sets, 75% of total occurrence records were used for training the model, while the remaining 25% were used for validating the model. The number of iterations to run the algorithm is set to 1000 and the model was repeated for 10 runs, which allows adequate time for the model to converge [59], and the rest of the settings were the default settings.

Receiver operating characteristic (ROC) analysis was used to calibrate and validate the robustness of the evaluation of the MaxEnt model [58]. The area under the curve (AUC) of the ROC curve was used to estimate the model performance, which varies from 0 to 1 and is a diagnostic evaluation index with high recognition at present. Generally, the model performance can be categorized according to the value of AUC as fair (0.6–0.7), good (0.7–0.8), very good (0.8–0.9), and excellent (>0.9) [58]. A jackknife test was applied to identify variables that made a significant contribution to model output. The results of this test showed the training gains of each variable when the model was run in isolation and was compared with the training gains of all variables. Additionally, species response curves were created to explore the relationships between the probability of occurrence and environmental variables.

A threshold value of 25% was set based on the logistic output from the Maxent model, below which the probability of species occurring can be considered almost negligible. The final suitable habitat predictions were regrouped into three classes: low suitable (25–50%), medium suitable (50–75%), high suitable (>75%), and the values below 25% as nonsuitable.

2.3.2. Spatial Pattern Distribution of Species Richness

A total of 62 *Meconopsis* species were included in this study, which represents the species richness of *Meconopsis* genus in the study area. The species distribution pattern was affected by different spatial scales or areas, and to eliminate their influence, when calculating the species richness, the fishnet tool was used to divide the study area according to the equal area grid of 50 km × 50 km, and a total of 1314 grids were obtained. Then, the species distribution points of *Meconopsis* were associated with the grids, and the number of species in each equal-area grid was counted based on the actual recorded points of *Meconopsis*, and this value was taken as the species richness value of each grid. Finally, the species richness was divided into 15 levels using the classification function of ArcGIS 10.8, and the spatial pattern of species richness was visualized.

2.3.3. Distribution Pattern of Species Richness along Environmental Gradients

We extracted the topographic factor data of 1445 occurrence data points for 62 species of the genus *Meconopsis* in the study area, including elevation, slope, and aspect, and explored the relationship among topographic factors, longitude and latitude, and species richness. In this study, elevation was divided into 32 bands, each with an interval of 100 m, and the species richness was counted according to the altitudinal band. In terms of slope, aspect, longitude, and latitude, we divided them into 30, 36, 33, and 14 bands at 1° intervals, and calculated the species richness of each band in turn. The influence of environmental factors on *Meconopsis* plant species richness geospatial patterns were determined by running polynomial regression or nonlinear regression (GaussMod) models.

2.3.4. Landscape Fragmentation

Four landscape indices were used to measure landscape fragmentation in this paper (Table 2). Based on the reclassified land cover data grid-by-grid, the landscape indices in the grid based on the landscape scale were calculated, the spatial data were processed in ArcGIS 10.8, and the landscape indices were calculated by software Fragstats 4.2.1.

Table 2. Selected landscape indices and their ecological significance.

Landscape Indices	Range of Value	Ecological Significance
Patch density index (PD)	PD > 0	It can reflect the degree of fragmentation of the landscape. The higher the value, the higher the degree of fragmentation.
Patch richness index (PR)	PR >= 1	It indicates the total number of all patch types in the landscape and is one of the key indicators of landscape components, as well as spatial heterogeneity, and has implications for many ecological processes.
Contagion index (CONTAG)	0 < CONTAG <= 100	It describes the degree of clustering or extension trend of different patch types in the landscape. Since this indicator contains spatial information, it is one of the most important indices to describe the landscape pattern. Generally, high spreading values indicate that some dominant patch types in the landscape form a good connectivity; conversely, it indicates that the landscape is a dense pattern with multiple elements and a high degree of fragmentation in the landscape.
Shannon's diversity index (SHDI)	SHDI >= 0	An increase in SHDI indicates an increase in patch types or an equalizing trend in the distribution of each patch type in the landscape.

3. Results

3.1. Model Performance and Key Variables to Predict Typical *Meconopsis* Species

Models for the *Meconopsis*, *M. integrifolia*, *M. horridula*, *M. racemosa*, and *M. punicea* performed better than random, with the given set of training and test data. The average AUC values for *Meconopsis*, *M. integrifolia*, *M. horridula*, *M. racemosa*, and *M. punicea* were 0.847, 0.888, 0.852, 0.914, and 0.951, respectively, indicating these five models performed well and generated very good (excellent) evaluations.

The results showed that precipitation of warmest quarter (Bio 18, 43.8%), temperature seasonality (Bio 4, 20%), elevation (13.5%) and annual mean temperature (Bio 1, 7.8%) made the greatest contributions to the distribution model for *Meconopsis* relative to other variables (Table 3), and the cumulative contributions of these factors reached values as high as 85.1%. Among the 11 environmental variables, precipitation of the warmest quarter (Bio 18, 59.2%), annual mean temperature (Bio 1, 18.9%), precipitation seasonality (Bio 15, 8.3%), and precipitation of the coldest quarter (Bio 19, 5.5%) made a greater contribution to the species distribution model for *M. integrifolia* than other environmental variables (Table 2), accounting for 91.9% of variation in total. For *M. horridula*, the most important factors were precipitation of the warmest quarter (Bio 18, 36%), elevation (11.8%), temperature seasonality (Bio 4, 11.5%), and isothermality (Bio 3, 10.2%) (Table 2); the cumulative contribution value accounted for 69.5% of the total contribution value of all environmental factors to the model. As for *M. racemosa*, precipitation of the warmest quarter (Bio 18, 37.7%), temperature seasonality (Bio 4, 24.4%), annual mean temperature (Bio 1, 16.7%), and precipitation of the coldest quarter (Bio 19, 4.4%) totally contributed 83.2% in the model (Table 2), which means these four variables contain the most significant and useful information to predict species distribution. Similarly, precipitation of the warmest quarter (Bio 18, 43.6%) had the highest contribution in the *M. punicea* model and, followed by precipitation seasonality (Bio 15, 15.8%), temperature seasonality (Bio 4, 8.6%), and elevation (8.5%) (Table 3), they totally accounted for 76.5% of the contribution value and were identified as main factors influencing the species' spatial distribution.

The thresholds (presence probability > 0.25) of the main environmental parameters were obtained from the response curve (Figure 4). The presence probability of all species is the greatest with 300–400 mm precipitation of the warmest quarter (Figure 4). In *Meconopsis*, temperature seasonality (>500) and annual mean temperature (>8 °C) beyond thresholds affect the habitat suitability, and the most suitable elevation was about 3700 m (Figure 4a). *M. integrifolia* had the highest probability of existence when the annual mean temperature was about 10 °C and precipitation seasonality was 60–95. With the maximum probability of species occurrence when precipitation value reached 20 mm in the coldest quarter for *M. integrifolia* (Figure 4b). *M. horridula* was most likely to occur at elevations between 3200 and 4800 m, with the most suitable temperature seasonality ranging from 500 to 800, and isothermality had a sigmoid trend with the maximum species presence probability when its value up to 54 (Figure 4c). For *M. racemosa*, the optimum ranges of temperature seasonality, annual mean temperature, and precipitation of the coldest quarter were 540–690, 0–13 °C, and 10–30 mm, respectively (Figure 4d). The response curves of *M. punicea* indicated that precipitation seasonality, temperature seasonality and elevation followed a Gaussian shape, and they were within a certain range when the probability of species occurrence was higher (Figure 4e).

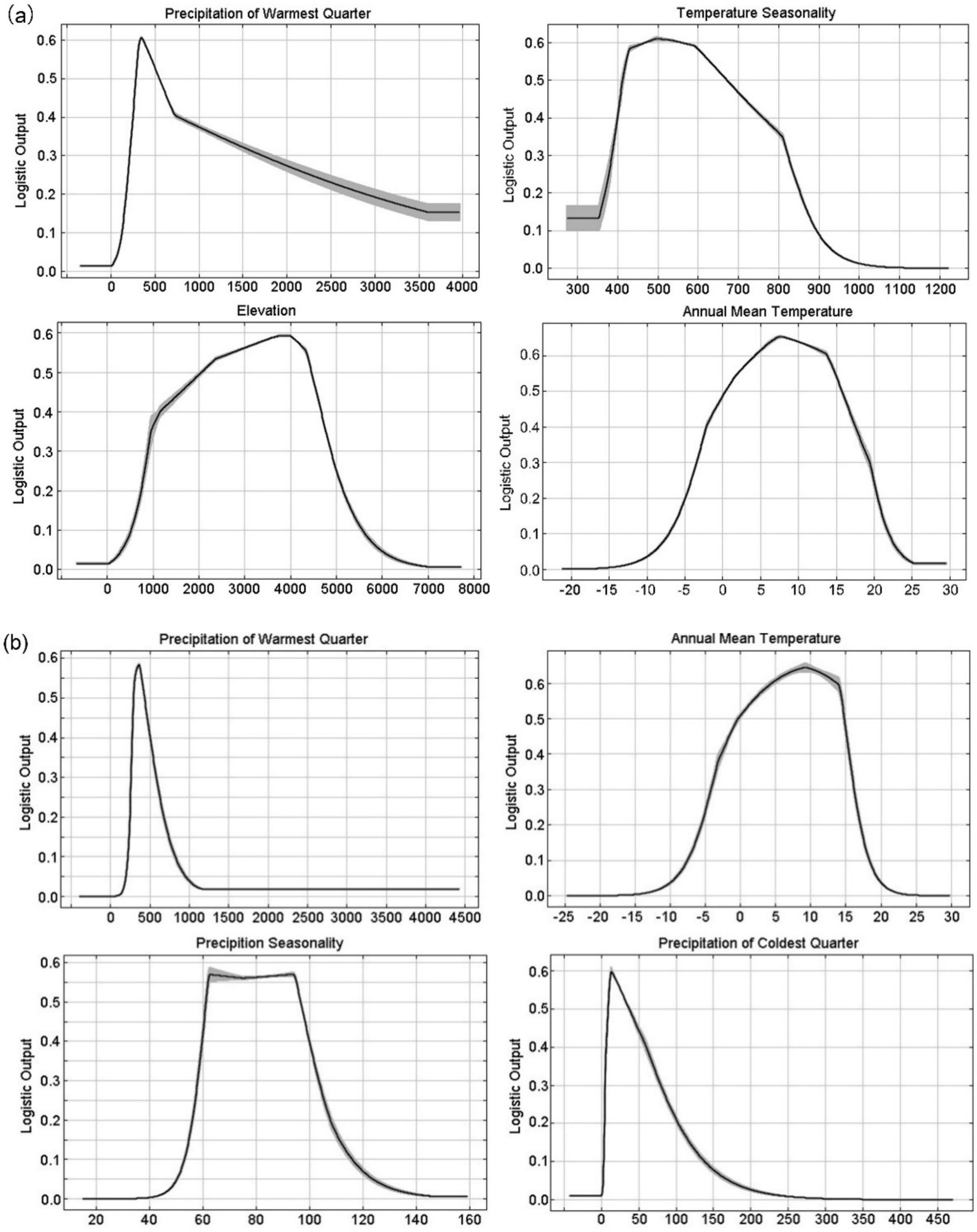
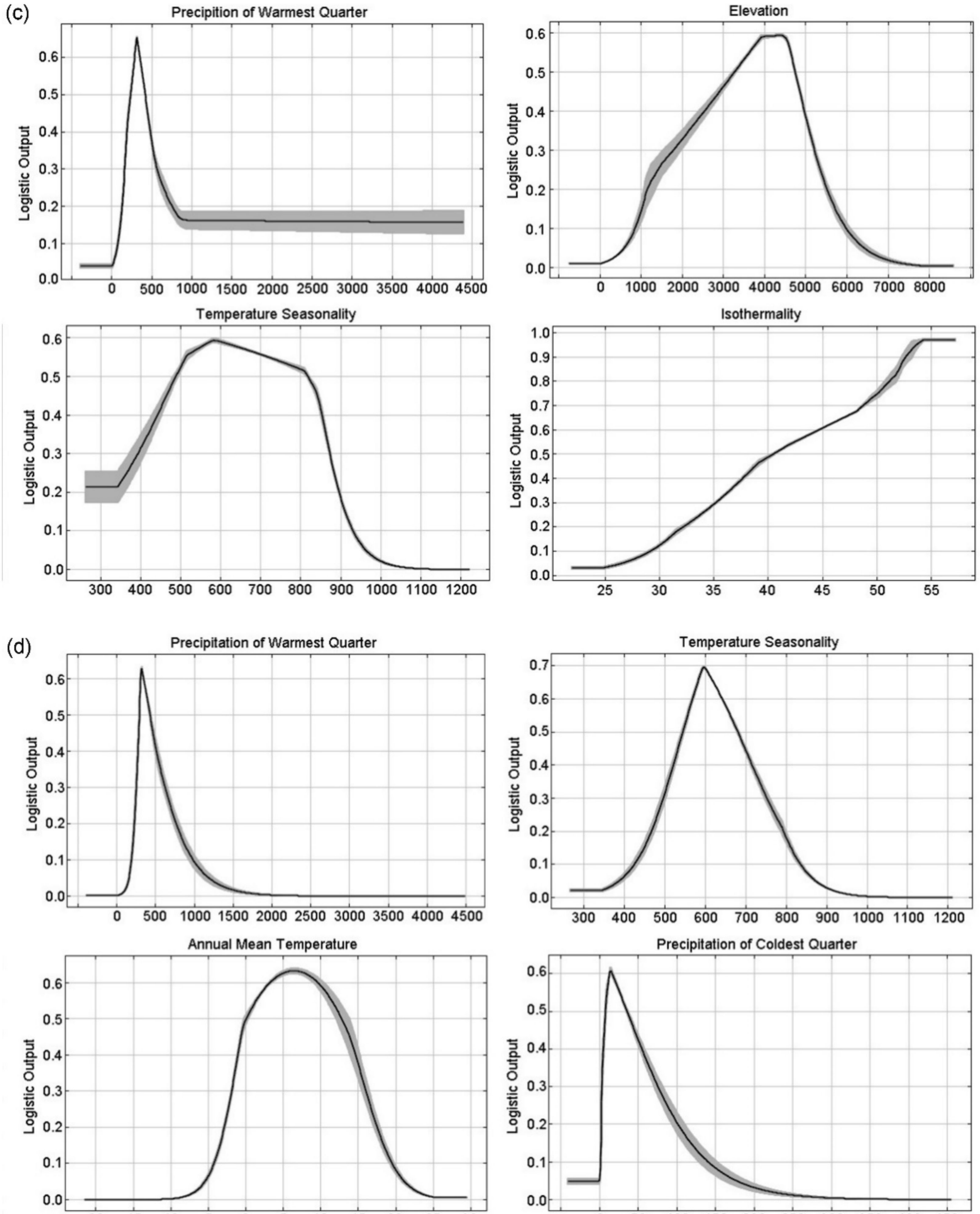


Figure 4. *Cont.*



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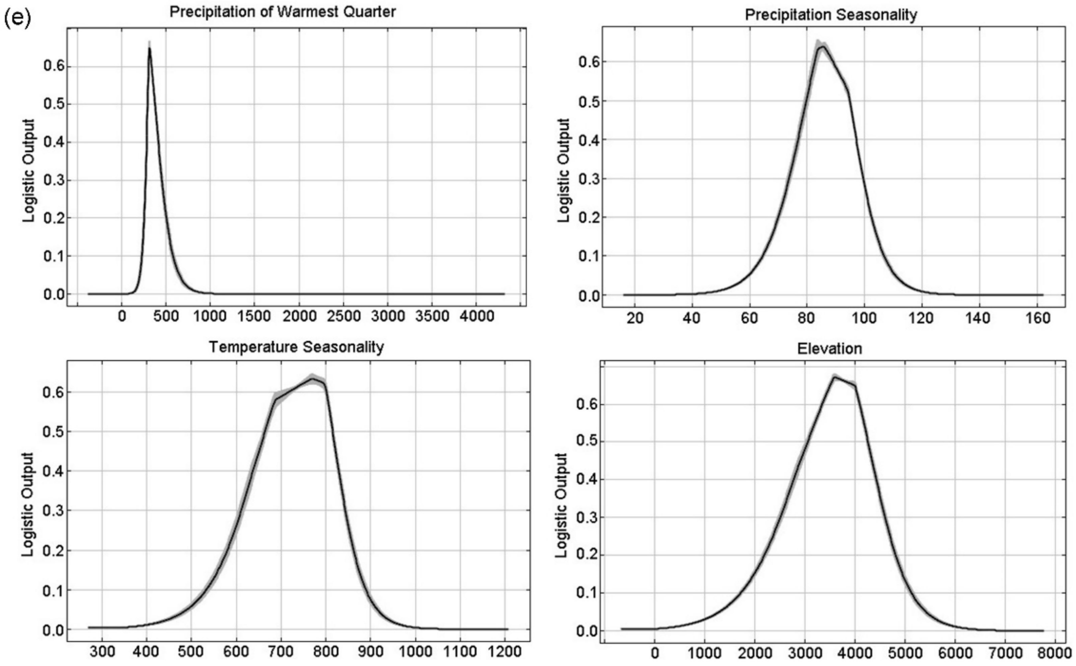


Figure 4. Relationships between key predictor variables and probability of presence of (**a**) *Meconopsis* species, (**b**) *M. integrifolia*, (**c**) *M. horridula*, (**d**) *M. racemose*, and (**e**) *M. punicea*.

Table 3. Relative contribution (%) of environmental variables to the MaxEnt model output for (a) *Meconopsis* species, (b) *M. integrifolia*, (c) *M. horridula*, (d) *M. racemosa*, and (e) *M. punicea*.

Variable	Code	a	b	c	d	e
Precipitation of Warmest Quarter	Bio18	43.8	59.2	36	37.7	43.6
Temperature Seasonality	Bio4	20	2.7	11.5	24.4	8.6
Elevation	Elevation	13.5	1.8	11.8	4.4	8.5
Annual Mean Temperature	Bio1	7.8	18.9	10	16.7	7.5
Precipitation Seasonality	Bio15	5.3	8.3	4.9	1.4	15.8
Isothermality	Bio3	3.9	0.2	10.2	4.3	1.4
Slope	Slope	2.6	2.3	5.4	2.4	2.3
Mean Diurnal Range	Bio2	1.5	0.6	3.7	1.6	3.2
Precipitation of Driest Month	Bio14	1.1	0.4	4	0.3	4.9
Precipitation of Coldest Quarter	Bio19	0.3	5.5	1.6	4.4	2.6
Aspect	Aspect	0.1	0.3	1	2.4	1.6

3.2. *Current Potential Geographical Distribution Patterns of Species*

The grade of the suitability zone of species has been presented in Figure 4 under the current climatic conditions across the whole study area. The potentially suitable habitats of *Meconopsis* are mainly distributed in the Himalaya and Hengduan Mountains, with an area of 1417.92 × 10^3 km^2, 31.74% of the total area. The high-suitability area accounted for only 0.23% of the study area, which is mainly distributed in the central Himalaya and the Nujiang and Jinsha River Basins in Yunnan Province (Figure 5a, Table 4). The potentially suitable distribution area of *M. integrifolia* extended from the western Himalaya to the east of Hengduan Mountains, with 1105.33 × 10^3 km^2 in total, accounting for 24.74% of the study area. Among these areas, the low and medium suitable areas were dominant, while the high suitable regions were concentrated in the Jinsha River Basins in Yunnan Province, with an area of only 9.14 × 10^3 km^2, accounting for 0.2% of the total study area (Figure 5b, Table 4). The most suitable region for *M. horridula* was located from the central Himalaya to the Hengduan Mountains, including the Minshan and Qilian Mountains, with a total area of 1428.40 × 10^3 km^2, accounting for 31.98% of the study area, while the area of the middle- and low-suitability zone (31.52%) was much larger than that of high suitable area

(0.46%) (Figure 5c, Table 4). Unlike *M. integrifolia* and *M. horridula*, the potentially suitable habitat area for *M. racemosa* was much smaller, accounting for only 15.78% of the study area, but with a slightly larger high suitable area than *M. integrifolia* and *M. horridula* (0.55%, 24.51 × 10^3 km^2), mainly scattered in the eastern Himalaya and the Hengduan Mountains (Figure 5d, Table 4). The suitable habitat for *M. punicea* covered an area of 407.19 × 10^3 km^2, accounting for less than 10% of the study area, and it was concentrated in the eastern part of the Hengduan Mountains, while regions with middle and high suitability for this species were mainly concentrated in the East Kunlun Mountains (Figure 5e, Table 4).

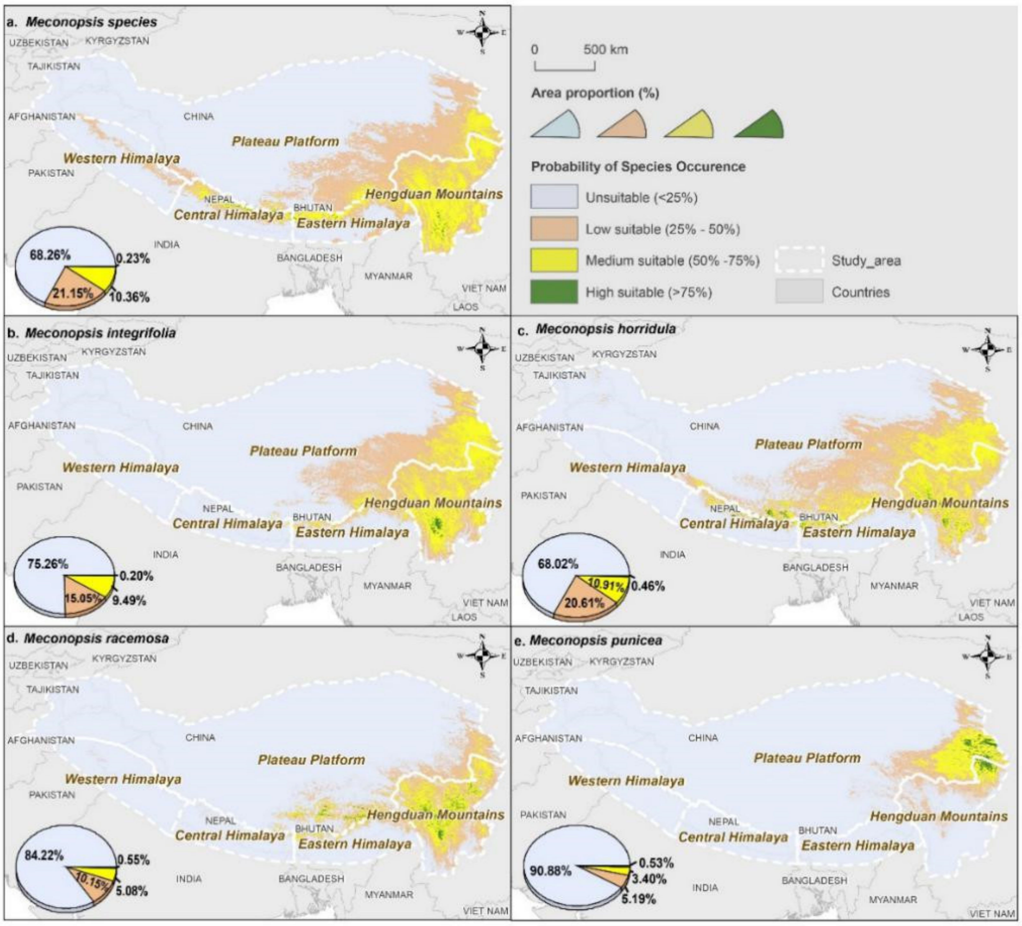


Figure 5. Potential geographic distributions of (**a**) *Meconopsis* species, (**b**) *M. integrifolia*, (**c**) *M. horridula*, (**d**) *M. racemosa*, and (**e**) *M. punicea* under current climate conditions in the study area. In this case, the probability of occurrence of *Meconopsis* species is categorized as low-, medium-, and high-suitable areas based on results of niche modeling.

Table 4. The areas of different suitable habitat of *Meconopsis* species based on model predictions under current climate scenario. (Unit: 10^3 km^2).

Probability of Occurrence	*Meconopsis*	*M. integrifolia*	*M. horridula*	*M. racemosa*	*M. punicea*
Unsuitable (<25%)	3049.07	3361.65	3038.57	3761.98	4059.79
Low suitable (25–50%)	944.89	672.12	920.74	453.50	231.63
Medium suitable (50–75%)	462.92	424.07	486.94	226.99	152.11
High suitable (>75%)	10.11	9.14	20.72	24.51	23.45

We found that the mean elevation distribution of suitable habitats for all species ranged from 3200 m to 4300 m (Table 5). For the genus *Meconopsis*, the distribution elevation range of the middle- and high-suitable zones was narrower than that of the low-suitable zones, and the elevation range of the high suitable zone was only 381 m, distributed in the area over 4000 m above sea level. The elevation widths of the low-suitable habitats of *M. integrifolia*, *M. horridula*, *M. racemosa*, and *M. punicea* were larger than those of the medium- and high-suitable habitats. In the high-suitable habitats, the elevational width of *M. integrifolia* was the narrowest at 843 m. In the medium-suitable habitats, the elevation width of *M. punicea* was 2320 m, which was the narrowest among them. *M. punicea* still had the narrowest elevation width of 2777 m in the low suitability habitat, and *M. horridula* had the widest in all suitability habitats, which means that it was better adapted than the other three species.

Table 5. Elevational pattern in species potential distribution in climate change scenarios under current climate conditions, in regions exhibiting high, medium, and low probability of species occurrence. All values in meters above mean sea level. (a: *Meconopsis*, b: *M. integrifolia*, c: *M. horridula*, d: *M. racemosa*, e: *M. punicea*).

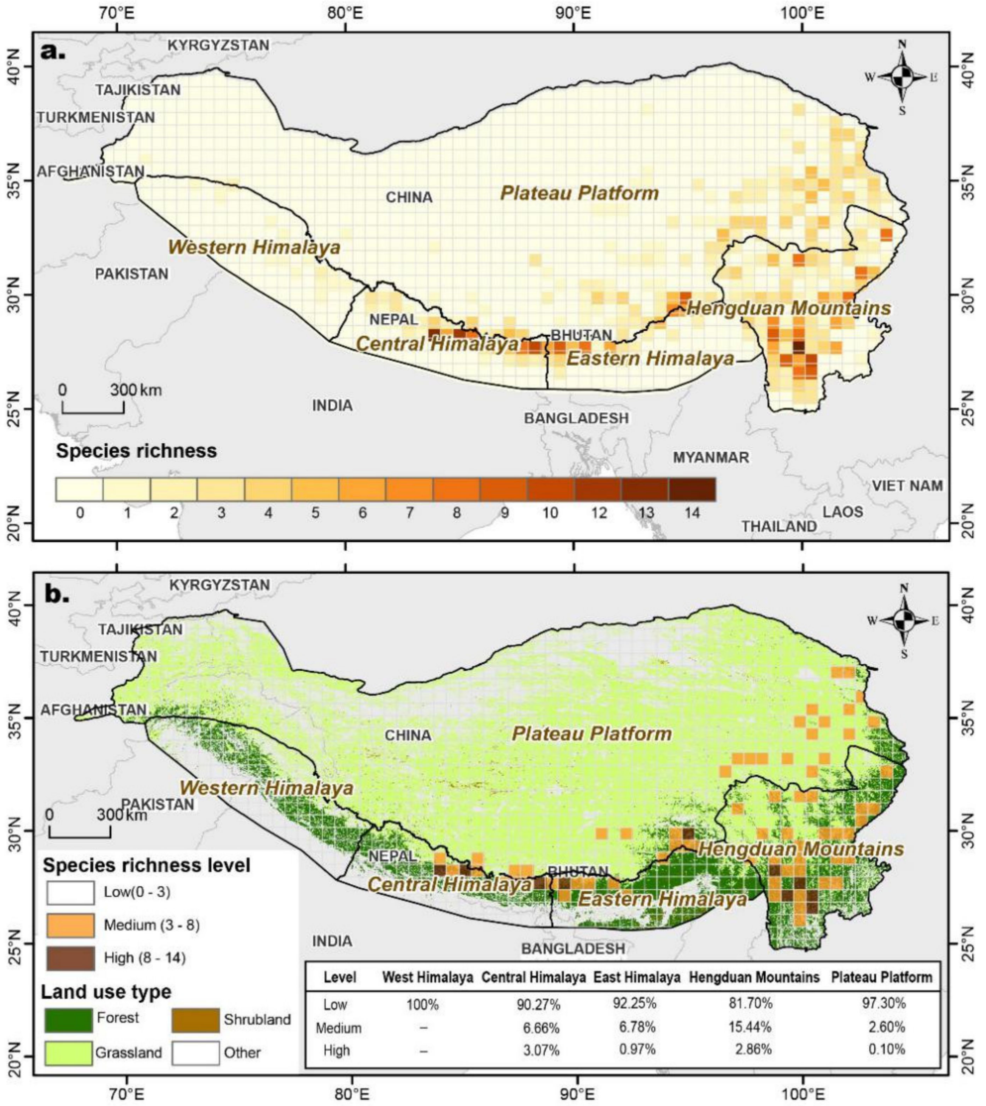
Species	**Low Suitable (25–50%)**			**Medium Suitable (50–75%)**			**High Suitable (>75%)**		
	Mean ± SD	**Min**	**Max**	**Mean ± SD**	**Min**	**Max**	**Mean ± SD**	**Min**	**Max**
a	4111 ± 791	2014	5983	3586± 737	2049	4988	4194 ± 142	4043	4424
b	4139 ± 760	2033	5983	3628 ± 713	2049	4925	3620 ± 367	3279	4122
c	4265 ± 807	2049	5953	4027 ± 643	2126	5406	4118 ± 540	2599	4617
d	3877 ± 766	2049	5142	3718 ± 647	2058	4707	3697 ± 391	2928	4259
e	4084 ± 565	2180	4958	3817 ± 454	2326	4646	3234 ± 484	2237	3677

3.3. Species Richness Geospatial Patterns of Meconopsis

We found an uneven spatial distribution of *Meconopsis*, with species richness ranging from 0 to 14 species per grid; most of the species were concentrated in the southeastern and southern regions of the study area (Figure 6a), i.e., the Hengduan Mountains, the central and eastern Himalaya, and the southeastern part of the plateau platform adjacent to the Himalaya and Hengduan Mountains, with relatively higher the species richness than other parts. According to the number of species per grid, we divided species richness into three categories: low (0–3), medium (3–8), and high (8–14). From Figure 6b, we could find that the areas with high species richness were mainly forests, while the areas with moderate species richness were forests and grasslands. In the Hengduan Mountains, central and eastern Himalaya, the areas with high and medium species richness were mainly forests, and in the plateau were mainly grasslands. The area with medium–high species richness in all subregions accounted for less than 10%, except for 18.3% in the Hengduan Mountains. Particularly, there was no area with medium–high species richness.

3.4. Species Richness Pattern along Environmental Gradients

The species richness gradient in the study area exhibited a hump-shaped pattern with increasing richness with elevation, peaking at around 3900–4100 m and declining toward the ends of the elevational gradient (Figure 7a). The pattern of *Meconopsis* plant richness along the latitudinal gradient increased remarkably to the maximum and gradually decreased with Gaussian shape fitted (R^2 = 0.96, Figure 7b). The richness of *Meconopsis* species showed a more or less monotonous increasing trend along the longitudinal gradient and was found absent beyond 104° (Figure 7c). In our study area, their richness varied strongly with the slope gradient with peaks occurring between 6° and 11°, and decreasing in both directions (Figure 7d). The *Meconopsis* plant richness presented a clear hump-shaped pattern along the aspect gradient, reaching its peak at the range of 150° to 200° (south slope or sunny slope), and it was similar at both the highest (north and northwest slopes) and lowest (north and northeast slopes) aspect belts (Figure 7e). In a word, the polynomial curve fitted precisely for richness patterns of *Meconopsis* plant along the elevation, longitude, slope, and aspect, with reasonable R^2 values ($R^2 > 0.5$).



Level	West Himalaya	Central Himalaya	East Himalaya	Hengduan Mountains	Plateau Platform
Low	100%	90.27%	92.25%	81.70%	97.30%
Medium	–	6.66%	6.78%	15.44%	2.60%
High	–	3.07%	0.97%	2.86%	0.10%

Figure 6. Spatial distribution of species richness of *Meconopsis* per 50 km × 50 km grid cell. (**a**) species richness distribution of each grid in the study area; (**b**) the distribution of species richness of *Meconopsis* in different vegetation.

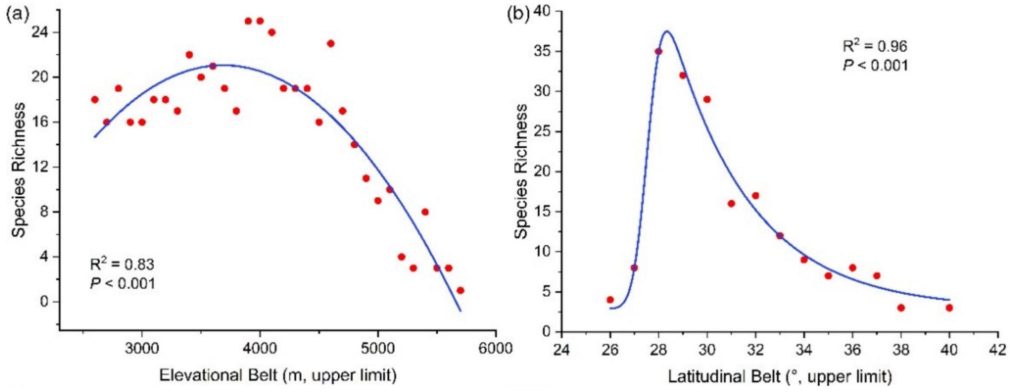


Figure 7. *Cont*.

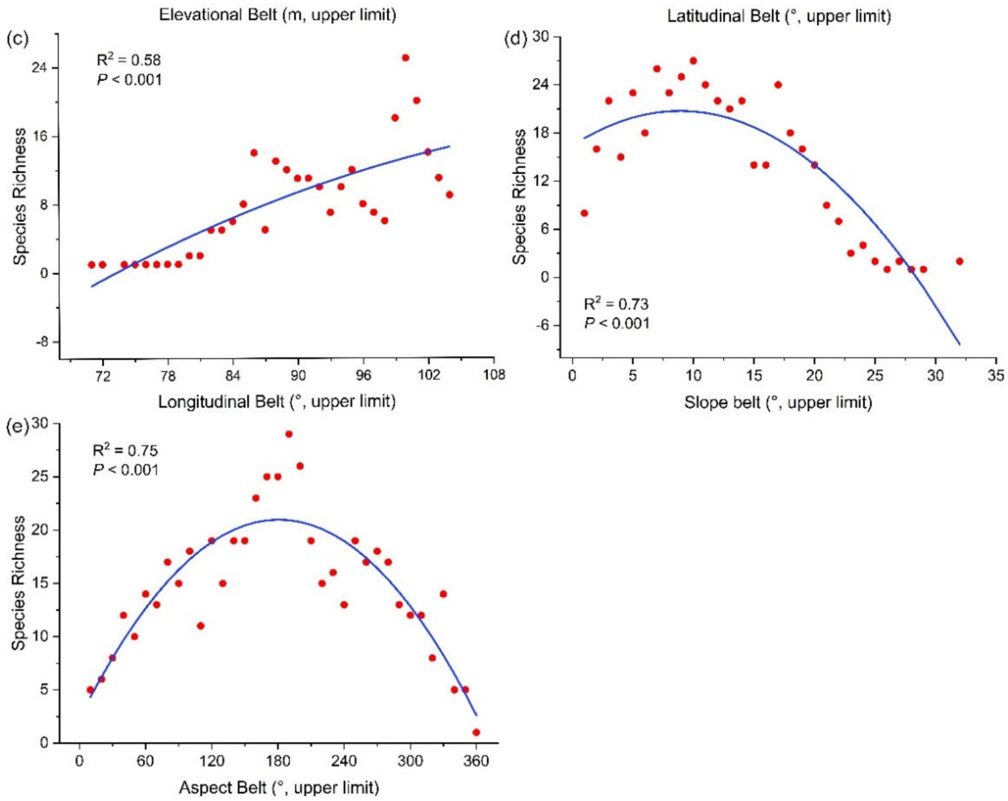
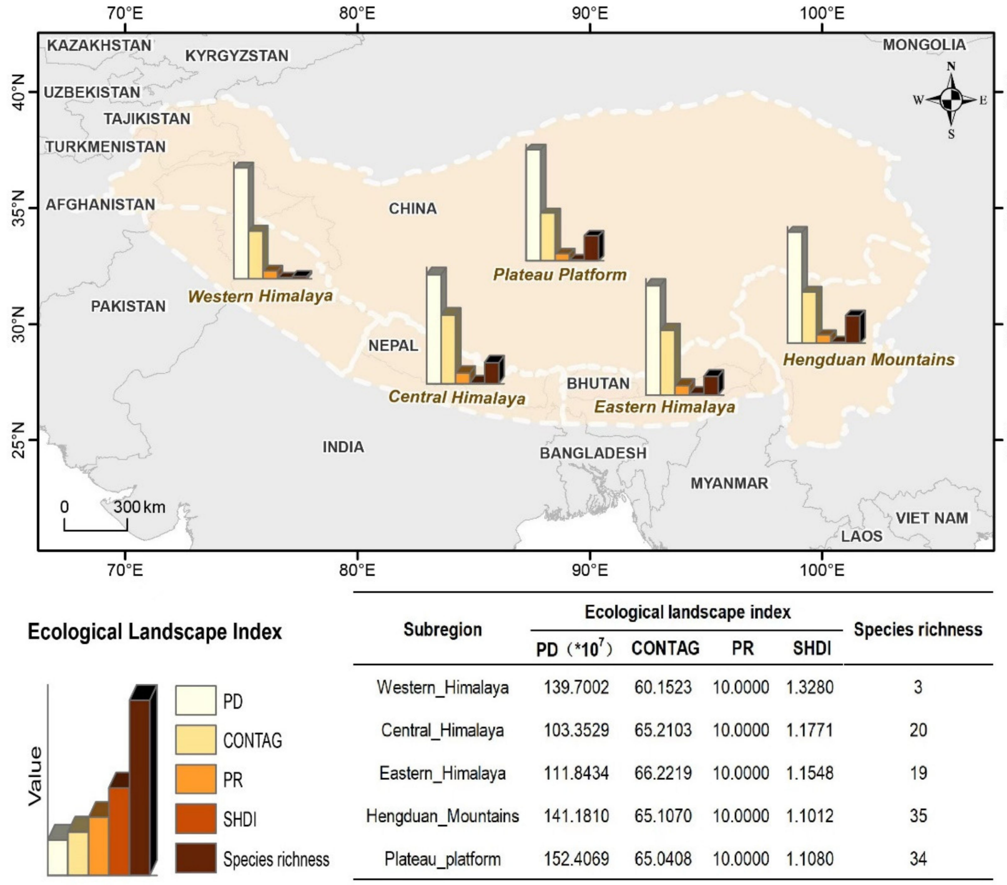


Figure 7. Species richness pattern of *Meconopsis* along the studied slope (**a**), latitudinal (**b**), longitudinal (**c**), elevational (**d**), and aspect (**e**) gradient.

3.5. Ecological Landscape Fragmentation and Species Richness

High PD in all subregions indicated a relatively large degree of landscape fragmentation across the pan-Himalaya that was quite similar in all subregions (Figure 8). Specifically, the plateau platform occupied the largest proportion of the study area with the highest PD (152.4069), while the central Himalayan region had the lowest PD (103.3529). In terms of the CONTAG, the value was the highest in eastern Himalaya (66.2219), indicating better connectivity between dominant patches in the landscape, while the CONTAG of the western Himalaya was the lowest (60.1523). The results of PR illustrated that each subregion covered all land-use types. For SHDI, all subregions were greater than 0.8, indicating high landscape heterogeneity in the study area, and the highest SHDI value was in the western Himalayan region (1.3280). According to the four landscape indices, the degree of landscape fragmentation in each subregion from high to low was the western Himalaya, plateau platform, the Hengduan Mountains, the Central Himalaya, and eastern Himalaya. Areas with the highest species richness were the Hengduan Mountains (35) and plateau platform (34); the central Himalaya (20) and eastern Himalaya (19) had similar richness, while the lowest richness was in the western Himalaya.



Subregion	Ecological landscape index				Species richness
	PD（*10^7）	CONTAG	PR	SHDI	
Western_Himalaya	139.7002	60.1523	10.0000	1.3280	3
Central_Himalaya	103.3529	65.2103	10.0000	1.1771	20
Eastern_Himalaya	111.8434	66.2219	10.0000	1.1548	19
Hengduan_Mountains	141.1810	65.1070	10.0000	1.1012	35
Plateau_platform	152.4069	65.0408	10.0000	1.1080	34

Figure 8. Ecological landscape index and species richness in each sub-region.

4. Discussion

4.1. Divergent Environmental Factors Affect the Spatial Distribution of *Meconopsis* Species

The long-term joint influence of several factors resulted in the geographical distribution of plants. Climate is the most important factor determining the geographical distribution of plants on a regional scale [60,61]. The findings for MaxEnt indicated that the precipitation of the warmest quarter (Bio 18) had the greatest effect on the distribution of all *Meconopsis* species amongst the 11 environmental variables involved in modeling, and this is consistent with our previous study in Minjiang headwater region [42]. Since precipitation can affect plant growth, morphology, phenology, and biomass accumulation [62–66], in particular for seedling emergence and establishment [67], an appropriate degree of precipitation can supply sufficient water and promote plant growth; however, excessive rainfall can deteriorate the soil permeability [68], creating an anaerobic environment that inhibits the regular respiration of roots [69], and limits plant growth and development by influencing their metabolism [70]. Moreover, waterlogging can also cause stomata to close and photosynthesis to decrease, and increases the energy consumption for respiration, affecting the accumulation of organic matter [71]. In addition, high humidity caused by excess water favors the rapid multiplication of pathogens and the formation of serious diseases that not only threaten the survival of plants but also their distribution patterns on a geographical scale [72]. The species response curves demonstrated that the ecological amplitude of precipitation is small, indicating the narrow tolerance range of *Meconopsis* to precipitation and limiting the geographical distribution range.

Temperature variation affects plant distribution by influencing their germination, water absorption, photosynthesis, transpiration, respiration, reproduction, and growth [73]. Our results showed that temperature seasonality (Bio4) and mean annual temperature (Bio1) were the two dominant temperature-related factors affecting the habitat suitability of *Meconopsis* species. Elevation was another key variable that had a strong indirect impact on the distribution of *Meconopsis* species. It integrates the effect of temperature, humidity, light, and other indicators to make secondary allocation of resources for influencing species composition and distribution [74,75]. Under the current climate, a potentially suitable area for *Meconopsis* was mainly distributed in the southeast Qinghai-Tibet Plateau and Hengduan Mountains where have similar climate conditions, particularly in terms of hydrothermal coupling. Monsoons, with sufficient rainfall with suitable temperature conditions, bolster the growth and development of alpine vegetation [76], accumulating assimilation products for overwintering and reproduction. Furthermore, high mountains and valleys are distributed in tandem with tremendous elevation variation, which creates a unique climate with cold temperatures at the mountain top and dry-hot conditions at the foot of the mountain. The suitable habitats of *Meconopsis* are mostly distributed in the alpine regions above 3500 m, consistent with their preference for cold and cool ecological habits [77,78]. This comprehensive analysis found that elevation and variables related to precipitation and temperature were the key factors restricting the distribution of *Meconopsis*.

4.2. The Richness of Meconopsis Species Varies along Geospatial Gradients

The decline of plant species richness from the equator to the poles is one of the most striking ecological patterns on Earth [79]. However, along the longitudinal gradient, from west to east, plant species richness increases with increasing wetness in different regions of the study area [80–83]. The highest species richness of *Meconopsis* was founded in Hengduan Mountain, which stands at the intersection of latitudinal and longitudinal curves (Figure 5) providing appropriate hydrothermal conditions, high habitat heterogeneity, and complex terrain [84,85] for the growth of *Meconopsis* species. Interestingly, many areas with medium and high species richness were forests. This contradicted our common knowledge that their favorable habitats are shrublands or grasslands, which might be due to scale variations or spatial resolution since shrub and grassland patches in forests are often classified as forests at a 300 m spatial resolution. Moreover, it is generally accepted that forests, shrubs, deserts, and other plant communities with woody plant coverage of less than 40% should be classified as grassland [86]. However, the grassland area calculated based on the area of herbaceous vegetation here is underestimated.

Topography (elevation, slope, and aspect) has a significant impact on the spatial distribution of plants by influencing habitat temperature and humidity [87,88]. *Meconopsis* species richness revealed a unimodal distribution pattern along the elevational gradients in mountainous regions (Figure 5), similar to prior studies [89–91]. This may be attributed to the appropriate mild habitats for plant growth in mid-elevation [92], and this mid-domain effect was highly pronounced in the Himalaya [91], which brings in more rainfall than higher elevations in monsoon and decreases from the southernmost to the northernmost slopes [93]. The optimum temperature decreases along with the elevation increase, and only a few species can adapt to harsh environments [91,94]. Lower *Meconopsis* species richness beyond mid-elevations can be attributed to the decrease of soil cover with more rocks and slow biogeochemical cycle in contrast with favorable mid-elevation providing higher atmospheric moisture and cooler summer temperature [95]. Some species have specific requirements for slope and aspect [96], which directly or indirectly influence the solar radiation, temperature, and soil conditions [97,98] In concordance with other studies, we found that species richness of *Meconopsis* was higher on the sunlit southern slope as compared to the northern slope [99]. Meanwhile, the steeper slope triggers soil erosion [97] which stunts seed settling and plant growth [100]. Therefore, gentle slopes have higher species richness and plant growth as compared to steeper slopes. [97]. All the aforementioned topographical variables play essential and unique roles in the distribution of *Meconopsis*.

4.3. Linkage and Relations between Landscape Heterogeneity and Species Richness

The complex spatial heterogeneity of mountain areas provides advantageous conditions for biodiversity with a variety of patch types [101]. However, our study did not find a relatively clear relationship between landscape fragmentation and species richness, which might be relevant to inconsistent scale and metastability [29,30,102]. At the landscape scale, the degree of landscape fragmentation seems to have little impact on the species richness of *Meconopsis*. Given that spatial heterogeneity such as topography can significantly affect the richness [103], the effects of landscape fragmentation are probably more pronounced at comparatively smaller scales.

A larger habitat can harbor more species and support richer plant communities with more available resources [104]. Therefore, it is easy to understand why the species richness is higher on the plateau platform than in other parts, whose higher species richness is mainly concentrated in the southeastern part. Blocked by the Himalaya and Gangdise mountains, warm moist air from the Indian Ocean flows into China along the Hengduan Mountains, thus bringing abundant rain to the southeastern of the Qinghai-Tibetan Plateau. While the western Himalaya has the lowest species richness with a quite fragmented landscape, the region is inherently less suitable for *Meconopsis* because of poor hydrothermal conditions [105], and this is consistent with the current potential distribution modeling results. The lower latitudes of the central and eastern Himalaya on the southern slope of the Himalaya with abundant summer rainfall have a higher species richness. [105,106]. The Hengduan Mountains are climatically influenced by the westerly circulation and the Indian and Pacific monsoon circulation, with dry winters and rainy summers, which are ideal for the more abundant *Meconopsis*; despite their smaller area than the plateau platform, the species richness of *Meconopsis* is more abundant.

5. Conclusions

Our study discovered that the potential distribution regions with medium- and high-suitable habitats for *Meconopsis*, under the current climate scenario, were mainly located in the central and eastern Himalaya, Hengduan Mountains, and the southeast edge of the plateau platform. Precipitation of the warmest quarter had the greatest impact on the distribution of *Meconopsis* species. We also found species richness within the genus *Meconopsis* was distributed in a unimodal pattern along geospatial gradients except for the longitudinal gradient in pan-Himalaya. However, no obvious consistent relationships exist between landscape fragmentation and species richness for *Meconopsis*. Our findings not only promote an understanding of the distribution and diversity of *Meconopsis* species but also provide an indispensable foundation for future studies on *Meconopsis* plant functions and the sustainability of alpine ecosystems. This study also provides data and theoretical support for species diversity protection policies in pan-Himalaya and adjacent regions.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/d14080661/s1: Table S1: The number of presence locations of each species.

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