Characteristics of Potential Suitable Habitats and Environmental Driving Factors for the Genus Petrocodon Postprint

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Abstract

Petrocodon Hance is a renowned ornamental plant genus; however, due to climate fluctuations and intense anthropogenic disturbances, the majority of its species have been assessed as Critically Endangered (CR), or at least Vulnerable (VU) or higher. This study reconstructs the spatiotemporal dynamics of potential suitable habitats for Petrocodon since the Last Interglacial period and explores the response relationships between suitable habitats and environmental changes, providing theoretical guidance for research on the origin and geographical differentiation of Petrocodon, as well as for the conservation of Chinese endemic germplasm resources and horticultural development and utilization. By integrating 120 distribution records and 17 environmental variables, this research employs an optimized MaxEnt model and Geographic Information Technology (ArcGIS) to simulate the suitable habitats and distribution patterns of Petrocodon in China and the Indochinese Peninsula; dominant factors influencing the current geographical distribution of Petrocodon are evaluated through stepwise multiple linear regression analysis, redundancy analysis, and Monte Carlo tests. The results demonstrate: (1) The optimized MaxEnt model exhibits high predictive accuracy, with AUC values exceeding 0.96; the current suitable habitats of Petrocodon are continuously distributed from southwestern China to northern Vietnam, scattered across central and southern China, and patchily distributed in northern Myanmar, with the southern Yunnan-Guizhou Plateau representing the most optimal suitable region. (2) The dominant environmental variables constraining the current geographical distribution of Petrocodon include precipitation of the driest month (bio14), mean precipitation of the warmest quarter (bio18), precipitation of the wettest season (bio16), temperature variability (bio4), minimum temperature of the coldest month (bio6), and altitude (alt). (3) Under climate change scenarios, the expansion and contraction zones of suitable habitats for Petrocodon are located in the northern and northeastern portions of the current potential distribution area, representing sensitive regions vulnerable to climate change impacts. During the Last Interglacial period, suitable habitats of Petrocodon expanded substantially, whereas almost no suitable distribution areas existed during the Last Glacial Maximum under dry and cold conditions. Subsequently, suitable habitats of Petrocodon increased rapidly toward higher latitudes while decreasing at lower latitudes. (4) The centroid of suitable habitats for Petrocodon migrated northward from Yongfu County, Guangxi (110.10° E, 24.69° N) to Chengbu County, Hunan (110.29° E, 26.05° N). In summary, global warming exerts certain positive effects on the potential distribution areas of Petrocodon; however, extreme warming will lead to habitat reduction and ecological niche narrowing for Petrocodon, while the region from southwestern China to northern Vietnam, characterized by mature karst landform advantages, may serve as its primary refuge.

Full Text

Preamble

Characteristics of Potential Suitable Areas of *Petrocodon* Hance and Its Environmental Driving Factors

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Abstract: *Petrocodon* Hance is a renowned ornamental plant genus, yet most of its species have been assessed as Critically Endangered (CR) or at least Vulnerable (VU) due to climate fluctuations and intensive human disturbance. This study reconstructs the spatiotemporal dynamics of *Petrocodon*' s potential suitable areas since the Last Interglacial period and explores how these areas respond to environmental changes, providing theoretical guidance for research on the genus' s origin and geographic differentiation, as well as for the conservation and horticultural development of endemic Chinese germplasm resources. Using 120 distribution records and 17 environmental variables, we simulated the suitable areas and distribution patterns of *Petrocodon* across China and the Indo-China Peninsula with an optimized MaxEnt model and geographic information technology (ArcGIS). Stepwise multiple linear regression, redundancy analysis (RDA), and Monte Carlo tests were employed to evaluate the dominant factors influencing the genus's current geographic distribution. The results show: (1) The optimized MaxEnt model demonstrated high predictive accuracy with AUC values exceeding 0.96. Current suitable areas extend continuously from southwestern China to northern Vietnam, with scattered distributions in central and southern China and patchy distributions in northern Myanmar, with the southern Yunnan-Guizhou Plateau representing the most optimal habitat. (2) The primary environmental variables constraining *Petrocodon*' s distribution are precipitation of the driest month (bio14), precipitation of the warmest quarter (bio18), precipitation of the wettest quarter (bio16), temperature seasonality (bio4), minimum temperature of the coldest month (bio6), and altitude (alt). (3) Under climate change scenarios, expansion and contraction of suitable habitats occur primarily in the northern and northeastern portions of the current potential distribution range, representing climate-sensitive zones. During the Last Interglacial, suitable areas expanded substantially, but nearly disappeared during the cold, dry Last Glacial Maximum. Subsequently, suitable habitats increased rapidly toward higher latitudes while decreasing at lower latitudes. (4) The centroid of suitable areas migrated northward from Yongfu County, Guangxi (110.10°E, 24.69°N) to Chengbu County, Hunan (110.29°E, 26.05°N). Overall, global warming has a positive effect on *Petrocodon*' s potential distribution, yet extreme warming may shrink suitable habitats and narrow its ecological niche. The mature karst landscapes from southwestern China to northern Vietnam likely serve as major refugia for the genus.

Keywords: potential suitable areas, climate change, environmental variables, MaxEnt model, distribution centroid

Introduction

Global climate change continuously affects species' life habits, geographic distributions, community composition, and ecosystem structure (Doxford & Freckleton, 2012; Zhao et al., 2016; Matías et al., 2017), driving habitat-specialist plants toward extinction by eliminating migration pathways while also disrupting phenological rhythms and causing ecological disarray (Sandel et al., 2011; Li & Chen, 2014). Climate change alters the redistribution of surface temperature and precipitation, which fundamentally determines vegetation formation and evolution (Lambert et al., 2010; Wang et al., 2014), thereby significantly impacting richness patterns of rare species with limited dispersal capabilities and narrow distributions (Walther et al., 2002; Hewitt, 2004; Svenning & Skov, 2007). Energy constitutes the foundation and source for plant life activities, while water is essential for physiological processes (Fang, 1991). Consequently, examining species' responses to past and future climate change not only illuminates historical drivers of speciation and geographic distribution shifts but also informs scientific germplasm resource management strategies.

According to current literature, *Petrocodon* Hance primarily inhabits karst regions across China and the Indo-China Peninsula (Lu et al., 2017), comprising 47 species (including one variety), with 44 species reported from China (GRC, 2022; Wen et al., 2022b). This genus exhibits remarkable floral variation encompassing nearly all corolla characteristics of the Gesneriaceae family (Ge, 2012; Lu et al., 2017), with diverse growth forms, vibrant colors, and corollas often featuring different-colored halos, stripes, spots, or reticulations, demonstrating excellent prospects for industrial development (Lu et al., 2017). These plants grow in shaded, moist karst landforms (with a few species found in Danxia landforms) such as canyons, rock crevices, cliff faces, or dimly lit cave entrances, showing substrate specificity for calcareous soils and restricted distribution to the most ecologically favorable locations within broad regions (Wen, 2021). Most species have small populations, narrow ranges, strict environmental requirements, and fragile adaptability, making them important indicator taxa for evaluating local environmental quality (Wei, 2018; Xin et al., 2019). Changes in their ecological niches often signal species or population extirpation (Ge, 2012; Wen, 2021). Notably, due to climate turbulence and intensive human disturbance, all recently described taxa except *P. luteoflorus* Lei Cai & F.Wen (Fan et al., 2020) are at least Vulnerable (VU), with most assessed as Critically Endangered (CR) (Li et al., 2019; Su et al., 2019; Zhang et al., 2019; Fan et al., 2020; Li et al., 2020; Xin et al., 2021; Nong et al., 2021).

Current research on *Petrocodon* has focused primarily on new taxon description, phylogeny, and re-evaluation of endangered status (Ge, 2012; Wen et al., 2022a). Systematic and in-depth studies on the characteristics of potential suitable areas and their environmental drivers remain lacking, with much of the genus' s value unexplored while species face critical endangerment. Although extensive field surveys and endangered status re-evaluations have been conducted, field data and threat categories inadequately reflect the genus' s overall distribution pattern. Liu et al. (2017) suggested that *Petrocodon* species distribution directly correlates with geographic environments and is constrained by numerous environmental variables. As species formed in specific regions or specialized microhabitats, they possess distinct spatial information characteristics (Wen et al., 2022b). Therefore, reconstructing distribution patterns across different climate conditions and analyzing ecological suitability are essential.

The ecological niche represents the sum of all conditions enabling species survival and reproduction in specific areas or microhabitats (Qiao et al., 2013). Niche studies can be achieved through ecological modeling (Zhu et al., 2013; Ahmed et al., 2015), which employs known distribution data and environmental variables with statistical methods to infer species' ecological requirements and project results across spatiotemporal dimensions to predict potential geographic distributions (Zhu et al., 2013). Currently, applying the Maximum Entropy model (MaxEnt) to simulate plant potential distributions has become a research trend yielding robust results (Higgins et al., 2012; Cory et al., 2013; Higgins et al., 2020; Zhao et al., 2021). Particularly when combining MaxEnt, ArcGIS, R, and ENMTools, results more closely approximate realized niches compared to other species distribution models (Higgins et al., 2012), while offering analytical convenience (Ahmed et al., 2015) and relatively high accuracy (Phillips & Dudík, 2008; Elith et al., 2011), especially for species with widespread distributions and uncertain location data (Farashi et al., 2013). Consequently, MaxEnt is the most widely used ecological niche model (Ahmed et al., 2015; Barbosa & Schneck, 2015; Vaz et al., 2015). While MaxEnt helps infer potential distributions within known ranges, its extrapolation capacity may be limited by biotic interactions, dispersal constraints, and persistence in unsuitable environments (Higgins et al., 2020), restricting predictions beyond known distributions (Sillero, 2011). Therefore, this study selected MaxEnt to simulate *Petrocodon*'s potential distribution across China and the Indo-China Peninsula under different climate conditions.

Current research on *Petrocodon*' s suitable areas and climate change relationships remains weak, hindering value assessment and resource management. This study addresses this gap by: (1) predicting spatiotemporal distribution patterns of suitable areas; (2) identifying key environmental variables limiting current distribution and comprehensively analyzing their relationships with geographic distribution; and (3) providing scientific foundations for conservation and development.

1.1 Study Area

Petrocodon is concentrated in China and the Indo-China Peninsula, ranging from 98.8°-117.2°E and 10.7°-33.3°N, at altitudes of 120-1,700 m. Topographically, the study area shows a north-high, south-low pattern (Qian, 2021), representing the northern margin of Asian tropics under combined influences of South Asian, East Asian, and Northwest Pacific monsoons. This region encompasses southwestern China and the Indo-China Peninsula where large rivers, mountains, and karst landforms are concentrated (Jiang et al., 2017). Under the influence of complex topography and diverse climate conditions, numerous localized microclimates and zonal vegetation types have formed (Zhu, 2013; Ren, 2015), creating a hotspot for tropical plant adaptation, differentiation, and regional endemism (Myers et al., 2000).

1.2.1 Species Distribution Data Collection and Processing

Distribution records were obtained from: (1) field surveys by our research team; (2) herbarium specimens and databases including the Chinese Virtual Herbarium (CVH, https://www.cvh.ac.cn/), Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), and Plants of the World Online (POWO, https://powo.science.kew.org/); and (3) literature records. To avoid overfitting from closely spaced records, we first compiled distribution data by species name with longitude (X) and latitude (Y) coordinates, saving them as *.csv files (180 total records). Species with fewer than 3 records were retained for modeling, while those with >3 records underwent further screening. Using ENMTools, we removed redundant occurrences within 10 km × 10 km grids, retaining only one point per 10 km radius (Bian & Shi, 2019). This yielded 120 final distribution records for* Petrocodon*.

1.2.2 Environmental Variables and Screening

Thirty-five environmental variables were initially considered . Nineteen bioclimatic variables were sourced from WorldClim (https://www.worldclim.org/) using the CCSM4 climate system model, which offers advantages for climate simulation (Xiao et al., 2021). Climate data spanned six periods: Last Interglacial (LIG, ~120,000–140,000 years BP), Last Glacial Maximum (LGM, ~22,000 years BP), Mid-Holocene (MH, ~6,000 years BP), current period (1950–2000), 2050 (2041–2060 average), and 2070 (2061–2080 average). Thirteen soil variables came from the FAO' s Harmonized World Soil Database (HWSD, https://www.fao.org/land-water/databases-and-software/hwsd/en/). Altitude was obtained from WorldClim, while slope and aspect were derived in ArcGIS using surface analysis tools. Vector map data were sourced from the Ministry of Natural Resources (http://bzdt.ch.mnr.gov.cn/).

All environmental variables were clipped to uniform administrative boundaries with consistent grid cell size (0.0083°, 0.0083°), geographic coordinate system (WGS 1984), and projection coordinate system (WGS 1984 EASE Grid Global). To avoid multicollinearity-induced overfitting, we first ran MaxEnt with Jackknife tests to assess variable importance, removing variables with zero contribution (Zhu & Qiao, 2016). Distribution data and environmental variables were then imported into ArcGIS for sampling using the Sample tool, exported to Excel, and analyzed in SPSS for correlations. Variables with correlation coefficients >0.95 were retained. Pearson correlation analysis was performed in ENMTools, with correlation heatmaps generated in R [Figure 1: see original paper]. When correlation coefficients exceeded 0.8, variables with lower predictive contributions were removed. The final dataset comprised 9 climate variables (bio2, bio3, bio4, bio6, bio14, bio15, bio16, bio18, bio19), 5 soil variables (t_{texture}, t_{caco3}, t_{oc}, t_{sand}, s_{gravel}), and 3 topographic variables (alt, aspect, slope).

1.3 Model Parameter Optimization

MaxEnt model complexity affects transferability (Merow et al., 2013; Qiao et al., 2015), with low transferability yielding unreliable or uninterpretable predictions (Zhu & Qiao, 2016). Complexity is closely related to regularization multiplier

(RM) and feature combination (FC) parameters (Muscarella et al., 2015; Zhu & Qiao, 2016). The Kuenm package can regulate RM and FC to analyze parameter complexity and select models with low complexity but high transferability (Zhu & Qiao, 2016). MaxEnt' s default parameters include five features: linear (L), quadratic (Q), hinge (H), product (P), and threshold (T), with RM=1.

Using the Kuenm package in R (Cobos et al., 2019), we tested RM values from 0.1 to 4 (40 increments) with six FC settings: L, LQ, H, LQH, LQHP, and LQHPT (Zhu & Qiao, 2016). This generated 31$×$40 parameter combinations. Optimal models were selected based on: pROC significance (pval_{pROC} significant), omission rate <5%, W_{AICc} <2, and delta_{AICc} = 0 (Phillips et al., 2017; Cobos et al., 2019; Zhuo et al., 2020).

1.4 Model Simulation

The 17 selected environmental variables and 120 distribution records were imported into MaxEnt 3.4.1 with the following settings: random test proportion = 25%; environmental response curves and prediction maps enabled; Jackknife assessment of variable importance; logistic output format; RM and FC set according to optimization results; 10 replicate runs with average output. All other parameters remained default. ArcGIS 10.4 was used to edit output raster maps, where each cell value represents presence probability (0-1). Using Jenks natural breaks, we reclassified potential distributions into four levels: unsuitable (0-0.1), low suitability (0.1-0.3), high suitability (0.3-0.5), and optimal suitability (0.5-1). High and optimal suitability zones were defined as total suitable habitat.

1.5 Response Relationships Between Environmental Variables and Natural Distribution

SPSS 20.0 was used for descriptive statistics of climate characteristics in suitable areas, with coefficient of variation (CV) measuring variable dispersion (Fang & Yoda, 1991). Stepwise multiple linear regression analyzed relationships between the 17 environmental variables and *Petrocodon* presence probability. Redundancy analysis (RDA) in CANOCO 5.0, combined with Monte Carlo tests, quantified each climate variable' s contribution to geographic distribution to identify dominant factors.

1.6 Spatial Patterns of Suitable Distribution Areas

Grid cells with species presence probability $ $0.30 were defined as suitable, while those <0.30 were unsuitable. Presence/absence (0/1) matrices were constructed for current, past, and future climate scenarios. Suitable habitats were assigned 1 (present) and unsuitable habitats 0 (absent). Based on these matrices , we analyzed spatial pattern changes under historical and future climates, defining four change categories: newly suitable, contracted, retained, and unsuitable areas. Area changes were calculated relative to current suitable area.

1.7 Centroid Shift Analysis

Centroid position changes reflect migration direction and distance of suitable habitats (Zhao et al., 2021). Using the Kuenm package in R, we calculated spatial changes and geometric centroids of suitable areas for LIG, LGM, MH, current, and future periods (Bateman et al., 2016; Laurent et al., 2018). SDMs tools tracked centroid latitudes/longitudes to examine temporal shifts, calculate coordinates, and determine migration distances (Cong et al., 2020).

2.1 Model Optimization and Accuracy Assessment

Based on 120 distribution points and 17 environmental variables, MaxEnt simulated potential suitable distributions. Optimization results showed: pval_{pROC} = 0 (statistically significant), omission rate = 0.0333% (<5% and below MaxEnt default), W_{AICc} = 1 (<2), corresponding to RM = 0.1 and FC = L.

The Receiver Operating Characteristic (ROC) curve area ranges from 0.5–1.0. AUC values of 0.5–0.7 indicate low reliability, 0.7–0.9 moderate reliability, and >0.9 high reliability (Hosmer & Lemeshow, 2000). Our results showed AUC >0.9 for all periods [Figure 2: see original paper], confirming high model credibility.

2.2 Environmental Variables Limiting Current Potential Distribution

Stepwise linear regression between *Petrocodon* presence probability and environmental variables revealed significant water variables: precipitation of driest month (bio14), precipitation of coldest quarter (bio19), precipitation of warmest quarter (bio18), and precipitation of wettest quarter (bio16). Energy variables included: mean diurnal range (bio2), isothermality (bio3), temperature seasonality (bio4), and max temperature of warmest month (bio5). Topographic variables comprised altitude (alt) and aspect. Soil variables included topsoil calcium carbonate (t_{caco3}), subsoil gravel content (s_{gravel}), topsoil sand content (t_{sand}), and topsoil texture (t_{texture}). These dominant variables explained 98.1% of variance (P<0.01). Slope, topsoil organic carbon (t_{oc}), and precipitation seasonality (bio15) were excluded as they showed minimal influence.

To further explain spatial variation, we constructed a matrix of 14 selected environmental variables and 120 distribution records for RDA in CANOCO 5.0. After forward selection, Monte Carlo tests ranked variable explanatory power . Variables with $P<0.005$ were considered dominant. Six variables reached this significance threshold: precipitation of driest month (bio14), precipitation of warmest quarter (bio18), precipitation of wettest quarter (bio16), temperature seasonality (bio4), minimum temperature of coldest month (bio6), and altitude (alt). Energy variables bio4 and bio6 showed the highest cumulative explanation (75.5%) and contribution (79.4%). Water variables bio14, bio18, and bio16 explained 7.4% with 8% contribution. Topographic variables explained 10.7% with 11.7% contribution. Soil variables were non-significant ($P>0.05$). Thus, dominant environmental variables are bio4, alt, bio14, bio16, bio18, and bio6, with influence ranking: energy > topography > water.

RDA ordination of these six significant climate variables [Figure 3: see original paper] showed the first two axes explained 73.32% and 90.27% of variance. Longitude (X) positively correlated with bio14 and bio4, negatively correlated with alt, bio6, and bio18, and showed no correlation with bio16. Latitude (Y) positively correlated with bio4 and bio14, negatively correlated with bio16 and bio6, and showed no correlation with alt or bio18.

Response curves for the six dominant variables [Figure 4: see original paper] revealed suitable ranges: temperature seasonality (bio4) 98–920, precipitation of warmest quarter (bio18) 185–1,207 mm, altitude (alt) 70–2,084 m, precipitation of driest month (bio14) 1–54 mm, precipitation of wettest quarter (bio16) 406–1,207 mm, and minimum temperature of coldest month (bio6) -6.17 to 3°C. Coefficients of variation ranged 17.20%–79.37%, with bio6 showing highest variability and bio16 the lowest. Overall, suitable areas exhibit warm-humid climate characteristics .

2.3 Current Potential Geographic Distribution Characteristics

ArcGIS mapping of 120 geographic records showed actual distributions concentrated continuously from southwestern China to northern Indo-China Peninsula, with scattered occurrences in coastal South China and Central China. Prediction maps [FIGURE:5, FIGURE:6] indicated 103 of 120 records fell within predicted suitable areas, demonstrating strong agreement. Under current climate, total suitable habitat covers 1.87×10^{7} km^2 (11.66% of total land area in China and Indo-China Peninsula), with high-suitability habitat at 9.98×10^{6} km^2 (6.21%) and optimal habitat at 8.76×10^{6} km^2 (5.45%). The current suitable range spans 104°–112°E and 18°–32°N, extending continuously from southwestern China to northern Vietnam, with scattered distributions in South and Central China and patchy distribution in northern Myanmar.

2.4 Spatiotemporal Changes in Distribution Patterns and Area Under Climate Change

Based on current distribution and environmental data, we generated potential distribution predictions [FIGURE:5, FIGURE:6]. During the Last Interglacial, suitable habitat comprised 10.73% of total area, with a 2.26% gain and 3.96% loss relative to current, resulting in net contraction. Current suitable area (11.66%) exceeds the Last Interglacial, though distribution centers shifted toward higher-latitude mountainous regions with increased fragmentation. The Last Glacial Maximum showed virtually no suitable habitat (11.71% loss rate » gain rate), indicating cold, dry conditions were unsuitable. The Mid-Holocene showed similar distribution contours to present, with 10.33% suitable area (0.86% gain, 3.26% loss), suggesting still-unfavorable conditions. Historically, highly suitable areas from the Yunnan-Guizhou Plateau to northern Vietnam have significantly contracted and fragmented since the Last Interglacial.

Under future climate scenarios [Figure 7: see original paper], suitable habitat peaks at 14.66% in 2050 (2.61% gain, 0.04% loss), with expansion in eastern and northern portions of current distribution. By 2070, suitable habitat comprises 14.17% (2.72% gain, 0.24% loss). Both future periods show expansion in northern and eastern areas—climate-sensitive zones requiring prioritized conservation. The results indicate that moderate warming through 2050 concentrates highly suitable habitats and benefits *Petrocodon* distribution, but by 2070, further warming reduces suitable area.

2.5 Migration Routes of Potential Distribution Centers Under Climate Change

The Last Interglacial centroid [Figure 8: see original paper] was located in Yongfu County, Guangxi (110.10°E, 24.69°N), migrating northwest to Danzhai County, Guizhou (107.94°E, 26.16°N) by the Last Glacial Maximum, then southeast to southern Sanjiang County, Guangxi (109.60°E, 25.54°N), northeast to eastern Tongdao County, Hunan (109.95°E, 26.24°N) in the Mid-Holocene, east to northwestern Chengbu County, Hunan (110.29°E, 26.05°N) in the current period, and southeast to southern Chengbu County (110.19°E, 26.30°N) by 2070. The centroid shifted 179 km southward from the Last Interglacial to present, 194 km westward from the Last Glacial Maximum to present, and 87 km southwest from the Mid-Holocene to present. Future shifts include 25 km northeast by 2050 and 40 km southeast by 2070. Overall, suitable habitats have migrated toward higher latitudes since the Last Interglacial, reaching the southern Hunan region as the northernmost boundary, with varying migration distances across periods.

3.1 Model Precision Analysis

MaxEnt' s default parameters were developed from testing 226 species across six regions (Phillips & Dudík, 2008), with ROC curve evaluation. However, species-specific parameter settings are more effective than defaults for particular taxa (Anderson & Gonzalez, 2011), preventing overfitting (Zhu & Qiao, 2016). Our optimized MaxEnt produced smooth response curves with AUC $ $0.96, indicating that fine-tuning reasonably reflects the genus' s distribution responses to climate variables (Zhu & Qiao, 2016) and accurately predicts potential distributions, demonstrating high credibility for *Petrocodon*.

3.2 Analysis of Current Potential Suitable Areas

MaxEnt predictions represent maximum likelihood distributions rather than actual ranges—i.e., potential rather than realized distributions. Our results show that from the Last Interglacial through 2070 (six periods), *Petrocodon*' s potential range extends continuously from southwestern China to northern Vietnam, with scattered distributions in South and Central China and patchy distribution in northern Myanmar. The topographic advantages of southwestern China to northern Vietnam likely serve as major refugia. These suitable areas represent hotspots for *Petrocodon* germplasm resources and should be prioritized for conservation.

As previously noted, monsoons are prerequisites for *Petrocodon*' s dispersal from typical tropical regions to the tropical northern margins of southwestern China (Ren, 2015), with mountain-river valleys and karst landforms being primary distribution areas. The study region lies at the northern edge of Asian tropics, under combined monsoon influences, and features concentrated karst landscapes (Jiang et al., 2017). Highly heterogeneous local topography creates diverse habitats favorable for *Petrocodon* growth and reproduction, enabling adaptation to seasonal dry-wet climates and high-calcium limestone soils. Seasonally, South Asian monsoons peak in May–July, East Asian monsoons in June–August, and Northwest Pacific monsoons in May–September—coinciding with the genus' s growth and reproductive period. Therefore, monsoon conditions should be prioritized when selecting introduction and cultivation sites.

3.3 Relationships Between Environmental Variables and Potential Geographic Distribution

Due to *Petrocodon*' s physiological characteristics and specialized habitats, distribution is restricted to specific regions or microhabitats. While soil and topographic variables remain relatively stable across periods, climate fluctuations and human disturbance drive distribution changes. Dominant environmental constraints are precipitation of driest month (bio14), precipitation of warmest quarter (bio18), precipitation of wettest quarter (bio16), temperature seasonality (bio4), minimum temperature of coldest month (bio6), and altitude (alt). Temperature and precipitation significantly affect physiological traits, distribution ranges, diversity, and richness, while altitude influences distribution by redistributing precipitation and temperature (Lambert et al., 2010; Wang et al., 2014).

Petrocodon flowers from May–September and produces mature capsules from October–December, coinciding with the warmest quarter. Dry and cold periods may thus prevent reproduction. The dominance of temperature seasonality (bio4) and coldest month minimum temperature (bio6) is reasonable because temperature variation and minimum temperature are crucial regulators of plant growth, development, and flowering (Khodorova et al., 2014). However, extreme cold below -6.17°C is detrimental, likely because *Petrocodon* evolved in tropical/humid regions without cold tolerance mechanisms (Li, 1996). For cultivation, priority should be given to areas with coldest month temperatures of -6.17 to 3°C and temperature seasonality of 98–920.

Contrary to Liu et al. (2017), who found precipitation and altitude did not significantly affect Gesneriaceae distribution patterns, our study shows bio14, bio18, bio16, and alt significantly influence *Petrocodon*. This may reflect the genus' s growth on karst cliffs, where warm quarter precipitation (185–1,207 mm) accelerates limestone mineralization, providing nutrients (Xu et al., 2018). Presence probability decreases with altitude, peaking at mid-low elevations (0–1,500 m). While this broader than the actual range (120–1,700 m), elevations >1,500 m are unsuitable for most species. As the water-energy hypothesis suggests, combined water and energy effects shape species distribution patterns (Allen, 2002; Hawkins et al., 2003; Bradford et al., 2003; Wang et al., 2004a). We hypothesize that low probability at high elevations results from reduced mineralization rates in cold environments and karst geology' s rapid water loss, creating dry, cold, water-deficient conditions unsuitable for *Petrocodon* (Hawkins et al., 2003; Wang et al., 2004b). Therefore, future production should prioritize areas with warm quarter precipitation of 185–1,207 mm, driest month precipitation of 1–54 mm, and wettest quarter precipitation of 406–1,207 mm.

In summary, environmental variables control *Petrocodon*' s growth and development, thereby affecting distribution patterns. Energy, altitude, and water variables play primary roles in shaping ecological adaptation, while soil variables have minimal impact, likely because *Petrocodon* primarily grows epiphytically on rock surfaces in karst regions. At large scales, soil physicochemical properties inadequately represent the genus' s soil mechanisms. Additionally, all distribution records (except *P. asterocalyx* from Danxia landforms at the Guangxi-Hunan border) come from karst landforms, so soil variables reflecting karst background cannot differentiate interspecific geographic distributions.

3.4 Response of Suitable Area Spatial Patterns to Climate Change

From the Last Interglacial to 2070 (six scenarios), suitable habitat area for *Petrocodon* in China and the Indo-China Peninsula dropped sharply during the LGM, increased exponentially in the Mid-Holocene, slowly increased thereafter, peaked in 2050, then slightly declined by 2070, with overall northward migration. According to climate stability hypothesis, climate fluctuations endanger species while stable climates increase regional richness (Stevens, 1989). During the Last Interglacial, enhanced East Asian monsoons and increased precipitation created warmth comparable to current conditions, with distribution patterns similar to present but smaller area, possibly due to weaker vegetation feedback effects on precipitation (Zhang & Chen, 2020). The cold, dry, highly variable LGM climate was unsuitable, causing 11.71% habitat loss. Post-LGM warming during deglaciation led to the relatively stable Holocene warm period (Kuang et al., 2021), with rapid northern and northeastern expansion reaching 10.33% suitable area. From current to 2050, gradual warming facilitated expansion to a maximum of 14.29% suitable area, indicating moderate warming benefits dispersal. However, 2070 showed slight decline, suggesting extreme warming may narrow the realized niche, as *Petrocodon*' s specialization for limestone soils limits tracking of suitable climate northward.

Overall, relatively stable high-suitability areas are concentrated in southwestern China (Guangxi, Guizhou, southeastern Yunnan) and northern Vietnam. Enhanced protection and legal enforcement against overharvesting are needed in these regions. The northward migration pattern aligns with previous studies (Sekercioglu et al., 2008; Fang et al., 2018). Contraction and expansion in northern and northeastern suitable areas represent climate-sensitive zones (Thuiller et al., 2005; Diamond et al., 2011) requiring intensified monitoring and targeted conservation strategies.

Given *Petrocodon*' s critical endangerment and high ornamental value, we recommend systematic surveys of natural populations in highly suitable areas to clarify endangerment mechanisms, and introduction/development research based on potential suitable distributions to prepare for horticultural applications.

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Note: Figure translations are in progress. See original paper for figures.