

Article

Climate-Driven Variation in Habitat Suitability and Phytochemical Composition of *Dendrobium officinale* in China

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Abstract

Dendrobium Officinale is an endangered medicinal orchid with high therapeutic value. Understanding where it can grow well and where its medicinal compounds accumulate most is important for both conservation and cultivation. In this study, we used species distribution modeling (MaxEnt) to predict suitable habitats for *D. officinale* in China, and combined this with field sampling and UV-Vis spectrophotometry to analyze the content of bioactive compounds in plants from four producing areas in Guizhou Province. Our results show that the potential distribution of *D. officinale* is primarily constrained by moisture-related variables, especially precipitation of the driest quarter, annual precipitation, and vapor pressure, as well as vegetation activity (NDVI). The total suitable area was estimated at approximately 21.4×10^4 km². Phytochemical analysis of samples from four sites in Guizhou Province suggested that the accumulation of polysaccharides, alkaloids, and total phenols may respond differently to environmental factors. Alkaloids and total phenols showed strong negative correlations with precipitation-related variables (bio12, bio17), while polysaccharides exhibited positive correlations with these same variables. However, these correlations are based on a small sample ($n = 4$) and should be interpreted as exploratory hypotheses specific to Guizhou, rather than as established relationships. They point to the possibility that water availability during the dry season may exert opposing effects on different classes of secondary metabolites, but this conjecture requires verification with expanded sampling. Overall, this study provides a spatial framework that can inform site selection for cultivation and conservation, rather than a fully validated precision agriculture tool.

Keywords: potential suitable area; MaxEnt model; environmental variable; under-forest economy; active ingredient



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1. Introduction

Dendrobium officinale is a perennial epiphytic herb belonging to the Orchidaceae family. Its stems are erect or climbing, with oblong-lanceolate leaves and elegantly shaped flowers, giving it considerable ornamental value. In traditional Chinese medicine, it has long been regarded as a precious medicinal herb. In recent years, it has also been widely used in functional foods and health products because of its rich nutritional content and diverse pharmacological effects. The species is currently listed as Endangered (EN) on the IUCN

Red List of Threatened Species [1]. In China, it typically grows as an epiphyte on tree trunks and rocks in humid evergreen broad-leaved forests (detailed distribution in Section 2.1).

The ecological and cultural significance of *D. officinale* deserves attention. Ecologically, as an endangered species with high medicinal value, research on its habitat suitability and quality formation can support the conservation of wild germplasm resources, the maintenance of biodiversity, and the development of sustainable forest-medicine composite ecosystems. Such studies also help us understand how plants regulate secondary metabolite biosynthesis in response to environmental stress. Culturally, *D. officinale* embodies the long tradition of Dao-di herbs (geo-authentic medicinal materials) in Chinese medicine. Applying modern scientific approaches to clarify how ecological factors affect its quality not only helps preserve the cultural meaning of “geo-authenticity” but also promotes bionic cultivation models that mimic natural conditions. This integration of traditional knowledge with modern science can strengthen confidence in the quality of Chinese medicinal materials, while also supporting rural economic development through the medicinal plant industry [2].

Pharmacological studies have shown that *D. officinale* possesses multiple biological activities, including anti-inflammatory, antioxidant, immunomodulatory, and cardiovascular protective effects [3]. Guo et al. [4] demonstrated that polysaccharides and flavonoids are the main active components, and they exert their effects through various mechanisms. Xu et al. [5] found that *D. officinale* polysaccharides can enhance immune function by activating immune cells and increasing cytokine secretion. Its antioxidant effects are achieved by scavenging free radicals and reducing oxidative damage to cells [6]. In clinical settings, its anti-inflammatory and immunomodulatory properties show promise for treating chronic inflammatory diseases. In addition, research on its polysaccharides for antiviral and antitumor applications has made notable progress [7].

D. officinale uses Crassulacean Acid Metabolism (CAM) for photosynthesis, which allows it to tolerate dry or variable conditions by reducing water loss. As a CAM plant, it opens its stomata at night to take up CO₂ (stored as malic acid) and closes them during the day to prevent dehydration—an adaptation that suits its rocky or epiphytic habitats. The plant grows best at 15–28 °C; temperatures above 35 °C or below 5 °C can impair growth. Cooler nights (10–20 °C) improve CAM efficiency by promoting CO₂ uptake. High humidity (60–80%) supports nocturnal stomatal opening for CO₂ absorption, whereas low humidity triggers stomatal closure to save water, though prolonged dryness may hinder growth [7].

In China, its natural distribution is mainly restricted to subtropical regions, including Yunnan, Guizhou, Sichuan, Fujian, Zhejiang, Guangxi, Jiangxi, and parts of Anhui, where it typically grows as an epiphyte on tree trunks and rocks in humid evergreen broad-leaved forests [8]. In recent years, market demand for *D. officinale* has grown steadily, and artificial cultivation bases have been established across the country. Currently, most cultivation is carried out outdoors, either in ground beds under shade nets or through epiphytic planting on tree trunks. Greenhouse cultivation is used mainly for seedling propagation. Because our study focuses on natural climatic and topographical variables, our findings are most directly relevant to these open-field cultivation systems. However, the quality of *D. officinale* varies considerably among production areas. Problems such as declining habitat suitability, low yield, and insufficient active ingredient content have become common. These issues are largely due to a lack of scientific site selection and standardized management when cultivation bases are established. However, a critical knowledge gap remains: how do environmental variables jointly regulate both the large-scale habitat suitability and the local-scale phytochemical quality of *D. officinale*? To address this question, we used an optimized MaxEnt model to map suitable growth regions and examined the climatic correlates of

active components (polysaccharides, alkaloids, and total phenols). This study aimed at identifying areas where both growth suitability and compound accumulation are favorable. This work contributes to research on the authenticity and regional suitability of *D. officinale* as a medicinal herb.

Species distribution models (SDMs) are widely used to characterize species–environment relationships and predict geographic ranges by linking occurrence data with environmental variables [9]. Among these, the maximum entropy (MaxEnt) model is particularly useful for presence-only data. Its popularity in ecological research stems from the complexity of natural systems, where multiple interacting factors make it difficult to isolate key drivers. MaxEnt does not require prior variable selection and has been shown to produce accurate macroecological predictions while also helping to reveal underlying ecological mechanisms [10]. The model estimates a probability distribution with maximum entropy, constrained by environmental conditions, and remains relatively stable with small sample sizes [11]. These advantages have made MaxEnt a common tool for predicting species distributions in recent years [12,13]. More than 40 SDMs are available globally, but MaxEnt has become particularly widely used since its introduction in 2006. Its mathematical algorithm can infer unknown distributions from limited data, and its continuous output allows fine-scale mapping of habitat suitability, improving the adaptability and precision of ecological models [14]. Previous studies have used MaxEnt to project climate change impacts on species distributions, support conservation planning for threatened species [15,16], assess invasion risks, test evolutionary hypotheses, and model disease spread [17–19]. However, complex species–environment relationships can lead to models that fit one dataset well but generalize poorly to others [20–22]. For example, MaxEnt performance can decline when model settings and optimization are not carefully configured [23,24]. Studies have confirmed that an optimized MaxEnt framework can substantially improve predictive accuracy and produce more reliable and ecologically meaningful distribution maps [16,25].

Predicting the potentially suitable habitats of *D. officinale* in China contributes to understanding how environmental changes may affect the species' distribution, and provides a scientific basis for conservation and management decisions [26,27]. In this study, we aimed to: (1) predict the suitable habitat distribution and the accumulation patterns of key bioactive compounds for *D. officinale* using an optimized MaxEnt model; (2) identify the key environmental variables and limiting factors that shape its ecological niche; and explore their relationships with bioactive compound accumulation patterns; and (3) explore how environmental factors influence both the plant's distribution and its bioactive compound accumulation, thereby clarifying the ecological basis of its genuine production areas. By establishing a spatially explicit baseline of current habitat suitability, this work is intended to support the long-term management, conservation, and sustainable use of this medicinal plant.

2. Materials and Methods

2.1. Data Sources for *D. officinale* Distribution

Species occurrence records were compiled from multiple sources, including published literature and online databases: the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>, accessed on 6 March 2024), the Chinese Virtual Herbarium (CVH, <https://www.cvh.ac.cn/>, accessed on 6 March 2024), the Specimen Resources Sharing Platform for Education (SRSP, <https://mnh.scu.edu.cn/>, accessed on 6 March 2024), and the National Specimen Information Infrastructure (NSII, <https://www.nsii.org.cn/2017/home.php>, accessed on 6 March 2024). The records spanned the period from 1980 to 2020. We included only records that met the following criteria: (1) geographic coordinates with a precision of ≤ 1 km; (2) records from natural, wild populations—records from cultivation bases,

botanical gardens, or herbarium specimens without clear wild provenance were excluded; and (3) records were cross-verified and subsequently subjected to spatial thinning to reduce sampling bias. For records with detailed longitude and latitude information, we used them directly. For records with detailed location descriptions but without coordinates, we used Google Earth (Google LLC, Mountain View, CA, USA, <https://www.google.com/earth/>) to obtain accurate longitude and latitude. Records with unclear location descriptions were discarded. To minimize spatial autocorrelation and align with the 30-arcsecond resolution of the climate and environmental data, we retained only one occurrence point within a 1 km radius. After processing, 128 distinct geographic coordinates were retained for MaxEnt modeling (Figure 1). A Supplementary table (Table S1) listing all occurrence records, their geographic coordinates, data sources, and retention/exclusion status is provided to improve transparency and reproducibility. All 128 occurrence records used in this study, along with their geographic coordinates and original data sources (GBIF, CVH, NSII, or published literature), are provided in Supplementary Table S1. The online databases were accessed on 6 March 2024.

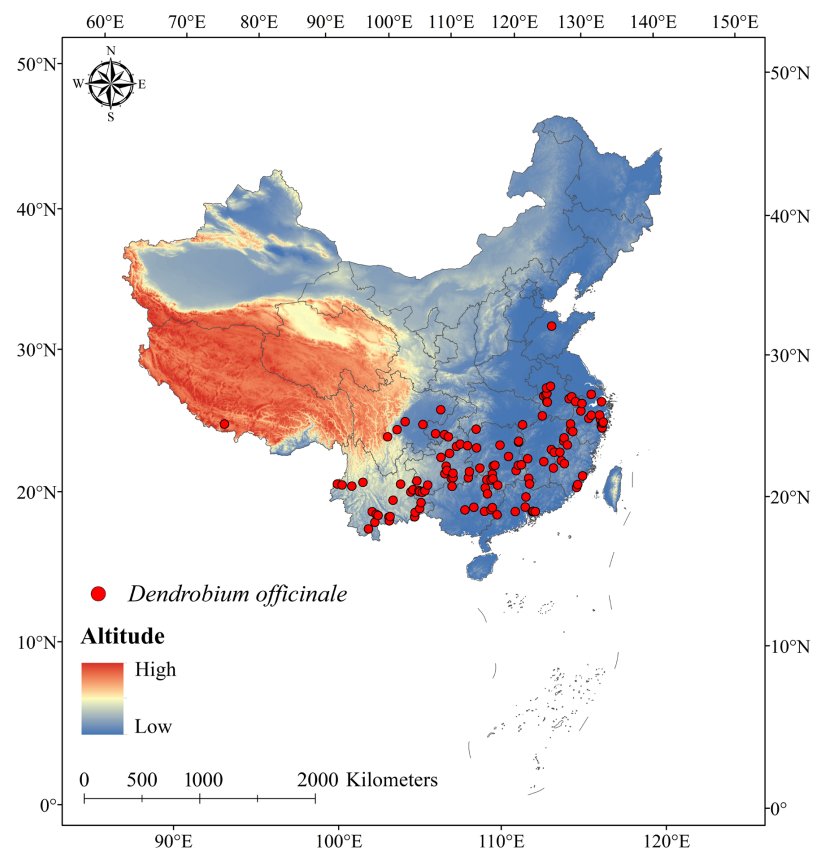


Figure 1. Georeferenced occurrences of *D. officinale* used for modeling. The 128 spatially rarefied points (red circles) were selected to minimize sampling bias and spatial autocorrelation.

2.2. Environmental Data Sources and Screening

We used 26 environmental variables, recognized as key determinants of species distributions [28], to model the ecological niche of *D. officinale*. Nineteen bioclimatic variables and altitude (ALT) for the baseline period 1970–2000 were obtained from WorldClim (<https://www.worldclim.org>, accessed on 6 March 2024). Slope (SLO) and aspect (ASP) were derived from ALT data using ArcGIS 10.4 (ESRI, Redlands, CA, USA). Surface solar radiation (SRAD) data were obtained from the National Tibetan Plateau Data Center (<https://data.tpdc.ac.cn>). Water vapor pressure (VAPR) data for the same baseline period were also obtained from WorldClim version 2.1 (<https://www.worldclim.org>), at approxi-

mately 1 km² spatial resolution. The normalized difference vegetation index (NDVI) data were sourced from NASA EARTHDATA (<https://www.earthdata.nasa.gov/>). To align with the 1 km resolution of the other environmental variables, the NDVI data were resampled using the nearest neighbor method in ArcGIS 10.4 (ESRI, Redlands, CA, USA). The Human Footprint dataset (HF), obtained from the Center for International Earth Science Information Network (CIESIN, <https://www.geodata.cn/main/>), was used to represent human activity intensity. The 19 bioclimatic factors—temperature and precipitation variables—are generally considered the most important elements influencing species distribution, particularly for medicinal plants. SRAD reflects potential evapotranspiration [29]. VAPR represents the actual water vapor content in the atmosphere, and different plants show varying sensitivity to VAPR [30]. ALT, SLO, and ASP are also important factors that affect plant distribution patterns, as they influence the redistribution of water, heat, light, and soil [31]. NDVI reflects vegetation photosynthetic activity and physiological status, serving as a proxy for habitat quality [32]. HF reflects the extent of human disturbance [33]. It should be noted that the occurrence records span a broader time range (1980–2020) than the standard WorldClim baseline (1970–2000). Ideally, SDM calibration should use climate data that exactly match the temporal window of the occurrence records. However, high-resolution, spatially continuous climate layers covering the full 1980–2020 period are not available for China at the 1 km resolution used in this study. As a pragmatic compromise, we used the 1970–2000 baseline as a proxy for long-term average conditions. This implicitly assumes that the relative ranking of climatic suitability among locations has remained broadly consistent over the study period—an assumption we cannot directly test with the available data. If significant climate trends (e.g., regional drying or warming) occurred during this period, our model may overestimate suitability in areas that have become less favorable or underestimate it in areas that have improved. We therefore interpret our results as reflecting long-term average conditions of the late 20th century, rather than a precise snapshot of any specific year. All environmental variables were clipped to the extent of China, and their geographic coordinate systems were adjusted to WGS_1984 to match the requirements of the MaxEnt model. The resolution of all environmental layers was resampled to 1 km to match our occurrence data. Detailed information on the environmental variables is provided in Table 1.

To reduce multicollinearity and prevent model overfitting, we systematically filtered the 19 bioclimatic variables using Pearson correlation analysis. First, we used ArcGIS 10.4 to extract the values of the 19 bioclimatic variables at each occurrence point of *D. officinale*. We then performed a correlation analysis in R and generated a correlation heatmap (Figure 2). We adopted a threshold of $|r| \geq 0.85$ for the initial screening. This threshold has been widely used in MaxEnt-based species distribution modeling and provides an effective balance between reducing collinearity and preserving environmental heterogeneity [33,34]. While thresholds of 0.70 or 0.75 are also commonly applied, we chose the more liberal 0.85 cutoff to retain a broader range of climatic information for a species whose distribution is influenced by multiple interacting factors. Importantly, this initial screening was complemented by a VIF analysis to confirm that multicollinearity remained within acceptable limits (see below). When the correlation coefficient between two variables was ≥ 0.85 , we retained the one considered more ecologically relevant to *D. officinale* according to previous studies on its habitat ecology, which consistently identify moisture-related factors as primary determinants of its distribution [8]. When $|r|$ was < 0.85 , both variables were retained [34,35]. Through this process, we identified 11 key bioclimatic variables (bio2, bio3, bio4, bio8, bio10, bio11, bio12, bio15, bio16, bio17, bio18) for further modeling. For the remaining environmental variables (SRAD, VAPR, ALT, SLO, ASP, NDVI, and HF), which are fewer in number and represent distinct environmental dimensions, we did not

apply the same correlation filter. Instead, we selected them based on ecological relevance. These 7 variables were then combined with the 11 bioclimatic variables, yielding a final set of 18 environmental predictors for MaxEnt modeling. We performed a Variance Inflation Factor (VIF) analysis on this final set to ensure that multicollinearity was within acceptable limits (all VIF < 10; Supplementary Table S2).

Table 1. Environmental determinants of *D. officinale* distribution.

No.	Environment Variable	Interpretation	Source Resolution	Unit	Date
1	bio_1	Annual mean temperature	1 km	°C	1970–2000
2	bio_2	Mean diurnal temperature range	1 km	°C	1970–2000
3	bio_3	Isothermality (bio_2/bio_7)	1 km	/	1970–2000
4	bio_4	Temperature seasonality	1 km	/	1970–2000
5	bio_5	Maxtemperature of warmest month	1 km	°C	1970–2000
6	bio_6	Mintemperature of coldest month	1 km	°C	1970–2000
7	bio_7	Temperature annual range	1 km	°C	1970–2000
8	bio_8	Mean temperature of wettest quarter	1 km	°C	1970–2000
9	bio_9	Mean temperature of driest quarter	1 km	°C	1970–2000
10	bio_10	Mean temperature of warmest quarter	1 km	°C	1970–2000
11	bio_11	Mean temperature of coldest quarter	1 km	°C	1970–2000
12	bio_12	Annual precipitation	1 km	mm	1970–2000
13	bio_13	Precipitation of wettest month	1 km	mm	1970–2000
14	bio_14	Precipitation of driest month	1 km	mm	1970–2000
15	bio_15	Precipitation seasonality (Coefficient of variation)	1 km	mm	1970–2000
16	bio_16	Precipitation of wettest quarter	1 km	mm	1970–2000
17	bio_17	Precipitation of driest quarter	1 km	mm	1970–2000
18	bio_18	Precipitation of warmest quarter	1 km	mm	1970–2000
19	bio_19	Precipitation of coldest quarter	1 km	mm	1970–2000
20	SRAD	Solar radiation	1 km	J/m ² ·d	1970–2000
21	VAPR	Vapor pressure	1 km	Pa	1970–2000
22	ALT	Altitude	1 km	m	1970–2000
23	SLO	Slope	1 km	°	1970–2000
24	ASP	Aspect	1 km	°	1970–2000
25	NDVI	Normalized Difference Vegetation Index	30 m	/	2020
26	HF	Human Footprint	1 km	/	2009

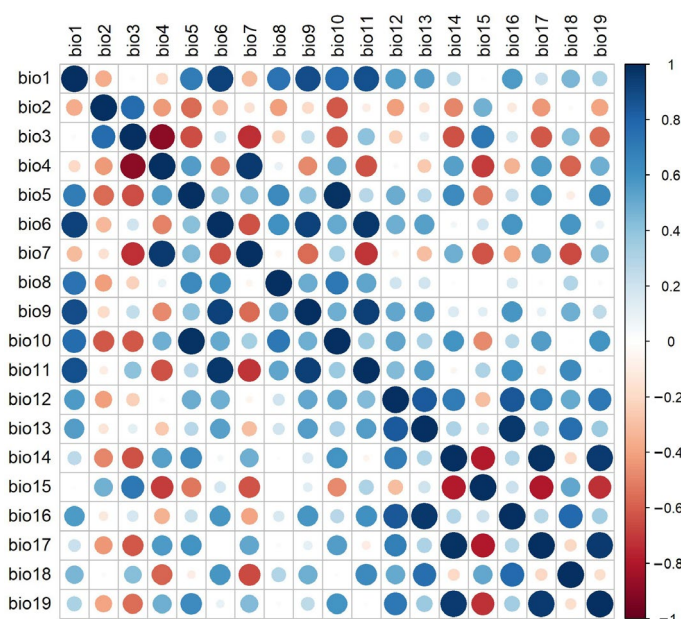


Figure 2. Correlation matrix of key environmental variables. Variable codes are detailed in Table 1.

2.3. A Maxent Modeling Framework: Establishment, Optimization, and Evaluation

We performed model parameter optimization using the kuenm package (version 1.1.9, <https://github.com/marlonecobos/kuenm>, accessed on 12 July 2026) in R 3.6.3. We tested regularization multipliers (RM) from 0.5 to 4 (in increments of 0.5) across 29 feature class (FC) combinations (L, Q, H, P, T, where L = Linear, Q = Quadratic, H = Hinge, P = Product, T = Threshold) [36]. To select the optimal combination of model parameters, we evaluated models using partial ROC, omission rates at the 5% threshold, and the Akaike Information Criterion corrected for small sample sizes (AICc). A model was considered to have predictive ability significantly better than random when the partial ROC ratio (AUC_ratio) was >1 with a corresponding p -value < 0.05. The model with the lowest delta AICc was selected as the best-fitting model [15].

For model calibration, we generated 10,000 background points randomly across the study area (China). To account for spatial autocorrelation, we employed a spatial blocking approach for cross-validation rather than random k -fold partitioning. Specifically, we used the ‘block’ method in the ‘kuenm’ package, which partitions the study area into four geographic blocks (latitudinal and longitudinal bands) to ensure that training and testing data are spatially independent, thereby providing a more realistic evaluation of model transferability. In each of the 10 replicates, three blocks were used for training and the remaining block for testing. The final ensemble model was averaged over the 10 replicate runs.

The optimized MaxEnt model was then run with the selected parameters, the *D. officinale* occurrence data, and the final set of environmental variables. Model performance was evaluated using the AUC value, with values interpreted as: <0.6 (fail), 0.6–0.7 (poor), 0.7–0.8 (fair), 0.8–0.9 (good), and >0.9 (excellent). In addition to AUC, we calculated the True Skill Statistic (TSS) to further assess the model’s discriminatory power; a TSS > 0.7 is generally considered good. The relative contribution of each environmental variable was assessed using the Jackknife method. The continuous model output was imported into ArcGIS 10.8 and reclassified into a binary (suitable/unsuitable) map using the threshold of maximum training sensitivity plus specificity, which is recognized as a robust method for species distribution classification [37]. We then classified the potential habitats into four suitability grades: not suitable (0–0.2), low suitability (0.2–0.4), medium suitability (0.4–0.6), and high suitability (0.6–1) [38–41] (Figure 3).

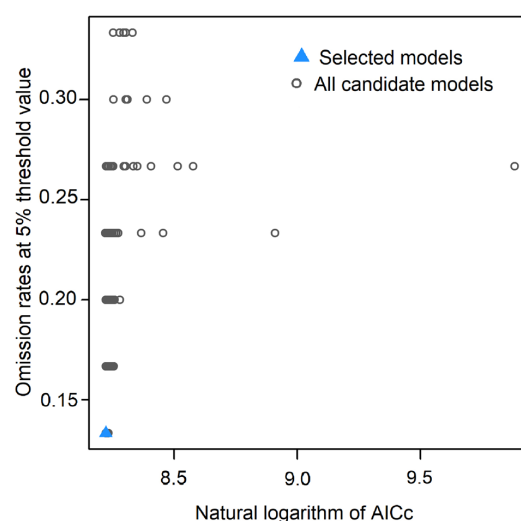


Figure 3. Candidate model screening and optimization. The x -axis represents the difference in AICc (Δ AICc) between each candidate model and the best-fit model. The y -axis represents the omission rate at the 5% training threshold. Filled circles indicate candidate models, and the triangle marks the selected optimal model.

2.4. Determination of Chemical Components

Sampling was conducted in November 2020 at four artificial cultivation bases in Guizhou Province: Anlong, Songtao, Pingtang, and Dejiang. All samples were collected from cultivated populations, as wild *D. officinale* is an endangered species protected under Chinese law and destructive sampling is not permitted. It is important to note that these cultivated samples were used only for phytochemical analysis; the MaxEnt habitat suitability model was built using independent occurrence records from wild populations (Section 2.1). Thus, the environmental correlates of compound accumulation identified here reflect conditions under cultivation, and their relevance to wild populations requires further investigation. At each site, three 10 m × 10 m plots were randomly established, and five individuals were randomly harvested from each plot. Initially, we identified nine potential sites for field sampling, but due to logistical constraints and the need to ensure sample integrity for chemical analysis, we obtained usable samples from only these four locations. The remaining five sites were either inaccessible or had insufficient material for robust analysis. A map showing the sampling locations is provided in Supplementary Figure S1.

The stems were cleaned, cut into 2–3 cm segments, and dried at 60 °C to constant weight. Dried samples were ground into fine powder (60-mesh) and stored at −20 °C prior to analysis. For extraction, 2.0 g of dried powder was extracted with 50 mL of 80% ethanol (*v/v*) (Sinopharm Chemical Reagent Co., Ltd., Shanghai, China) in a water bath at 60 °C for 2 h with occasional shaking. The extract was filtered through qualitative filter paper (equivalent to Whatman No. 1, OCOME or Hawach, China), and the residue was re-extracted once under the same conditions. The combined filtrates were evaporated to dryness under reduced pressure using a rotary evaporator (IKA® RV 10, IKA-Werke GmbH & Co. KG, Staufen, Germany) and re-dissolved in 10 mL of distilled water for subsequent analysis. The contents of polysaccharides, alkaloids, and total phenols were determined using a TU-1901 ultraviolet-visible (UV-Vis) spectrophotometer (Beijing Purkinje General Instrument Co., Ltd., Beijing, China) according to the 2020 edition of the Pharmacopoeia of the People's Republic of China (Part I). Each sample was analyzed in three technical replicates ($n = 3$), and the mean values were used for statistical analysis. The standard curves were: polysaccharides: $y = 38.407x + 0.0704$ ($R^2 = 0.9994$); total alkaloids: $y = 3.0209x - 0.0117$ ($R^2 = 0.9990$); and total phenols: $y = 2.808x + 0.0012$ ($R^2 = 0.9994$) [42].

We want to emphasize that our phytochemical data were collected from only four sites within a single province. Therefore, the correlations we observed between chemical constituents and climatic variables are exploratory and statistically fragile ($n = 4$). Our MaxEnt model provides a national-scale view of habitat suitability based on 128 occurrence records with spatial cross-validation, but the phytochemical–climate relationships should be interpreted as preliminary hypotheses that require independent validation with expanded sampling across multiple provinces. These correlations are not suitable for predictive mapping at the national scale, and any spatial extrapolation must be viewed as purely illustrative and hypothesis-generating.

2.5. Data Analysis

Statistical analyses were performed using R software (version 4.2.1, R Foundation for Statistical Computing, Vienna, Austria, <https://www.r-project.org/>) and its associated packages. Prior to one-way ANOVA, normality of the data was assessed using the Shapiro–Wilk test ($p > 0.05$), and homogeneity of variances was verified using Levene's test ($p > 0.05$). Both assumptions were satisfied for all compound content datasets across the four sampling regions. To compare bioactive compound contents among the four sampling regions, we used one-way analysis of variance (ANOVA) followed by Fisher's Least Significant

Difference (LSD) post hoc test. For the correlation analysis between environmental variables and compound contents, we used Pearson's correlation. For this analysis, we specifically focused on the environmental variables that were identified as the primary drivers of habitat suitability in the MaxEnt model (bio12, bio17, NDVI, and HF, as shown in Table 2), rather than using variables that had been discarded during the variable-selection phase. Graphs were generated using the 'ggplot2' (version 3.3.6, <https://ggplot2.tidyverse.org/>) and 'corrplot' (version 0.92, <https://github.com/taiyun/corrplot>, accessed on 12 July 2026) packages in R. Given the small sample size ($n = 4$) in the phytochemical analysis, we performed a Cook's distance analysis using the built-in 'cooks.distance()' function to assess whether any single data point had an excessive influence on the correlation results [29].

Table 2. Assessment of environmental variable contributions and importance to the potential habitat distribution of *D. officinale*.

Variable	Percent Contribution (%)	Permutation Importance (%)
bio17	83.3	30.5
bio12	10.6	7.8
NDVI	1.6	8.5
VAPR	1.4	13.3
bio3	0.8	14.5
bio15	0.7	13.6
SRAD	0.5	7.8
ASPECT	0.3	0
bio4	0.2	0.2
bio11	0.1	0.4
ALT	0.1	0
bio2	0.1	0
SLOPE	0.1	0.5
BIO16	0	0
HF	0	1.4
BIO18	0	1.4
BIO8	0	0
BIO10	0	0

No experimental treatments (e.g., fertilization, irrigation, shading) were applied in this study. The comparisons were made among different geographic sampling regions (Anlong, Songtao, Pingtang, and Dejiang) that represent distinct environmental conditions.

3. Results and Analysis

3.1. Model Optimization and Performance Validation

Using the 128 species occurrence records and the selected environmental variables, we simulated the potential suitable habitats of *D. officinale* using the MaxEnt model. The optimal parameter combination was RM = 4 and FC = LH, which satisfied all selection criteria (partial ROC, omission rates, and AICc). The final ensemble model, averaged over 10 replicate runs, achieved an AUC value of 0.899, indicating good predictive accuracy [43] and a TSS value of 0.78, further confirming the model's discriminatory power (Figure 4).

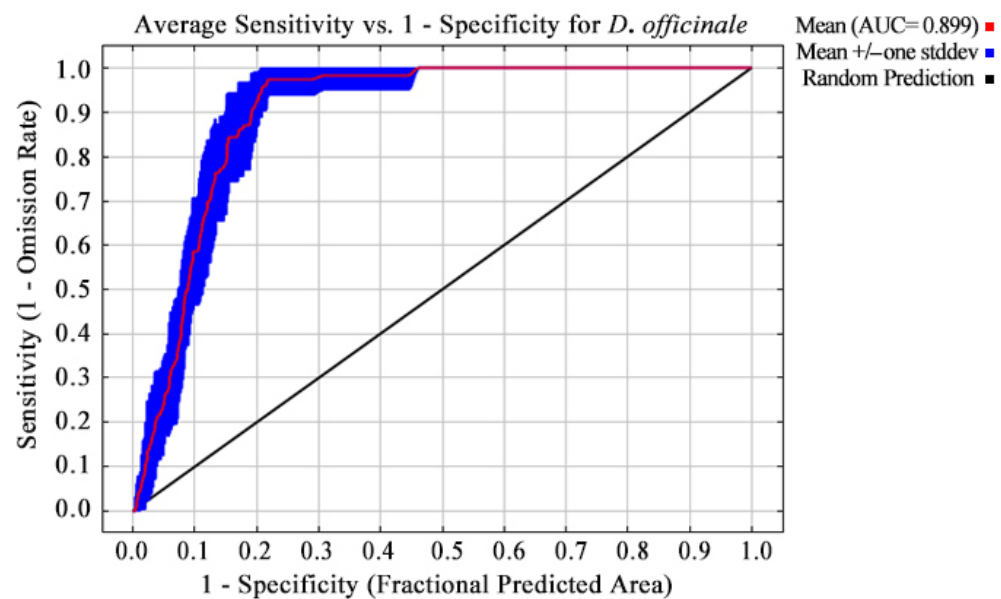


Figure 4. Receiver Operating Characteristic (ROC) curve for the final model prediction.

3.2. Currently Suitable *D. officinale* Habitat Distribution

The model predicted that suitable habitats for *D. officinale* are mainly concentrated in southern and southeastern China, including Taiwan Province. The areas with the highest suitability are found in Hunan, Guangdong, Guangxi, Fujian, and Zhejiang. The total suitable habitat was estimated at approximately 214,000 km² (21.4×10^4 km²), which was further classified into high (34,100 km², 15.94%), medium (132,100 km², 61.76%), and low (47,700 km², 22.30%) suitability categories (Figure 5). It is important to note that our model was calibrated using occurrence data from China only, so the predicted suitability map represents relative suitability within this national extent and does not reflect the species' full environmental niche at a global scale.

3.3. Major Environmental Factors Affecting *D. officinale* Resource Distribution

We assessed the relative importance of environmental variables using the Jackknife method in MaxEnt (Figure 6). The variable contribution analysis showed that bio17 (Precipitation of the Driest Quarter) was the dominant predictor, accounting for 83.3% of the model's contribution, far exceeding all other variables. Three other variables—bio12 (Annual Precipitation, 10.6%), NDVI (1.6%), and VAPR (1.4%)—together contributed an additional 13.6%, suggesting that they play a secondary but potentially important modulating role, although their relative contributions were distinctly different from that of bio17. The permutation importance analysis confirmed the importance of a similar set of variables, with bio17, bio12, NDVI, and VAPR again ranking among the most influential (Table 2). The noticeable difference between percent contribution and permutation importance for some variables (e.g., bio3, bio15) may reflect collinearity or complex interactions with other variables in the model. We therefore interpret the key environmental drivers by considering both metrics together. The response curves for the key variables (Figure 7) showed the optimal ranges and thresholds for *D. officinale* suitability: bio17 (threshold ≥ 38.86 mm, peak at 726.16 mm), bio12 (threshold ≥ 885.13 mm, peak at 1214.24 mm), NDVI (threshold ≥ 129 , peak at 226.36), and VAPR (threshold ≥ 1.13 kPa, peak at 1.78 kPa). Overall, precipitation regimes (bio17, bio12), vegetation cover (NDVI), and atmospheric moisture (VAPR) were the primary determinants of the species' potential distribution.

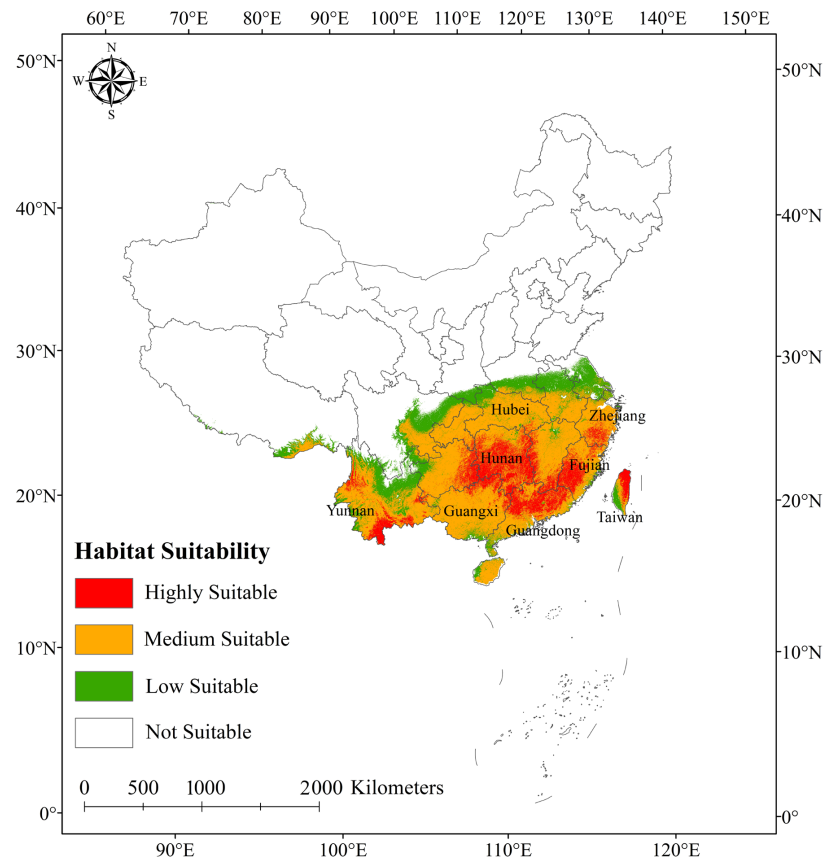


Figure 5. Spatial distribution of modeled suitable habitat for *D. officinale* in China. Areas are classified into high, medium, and low suitability.

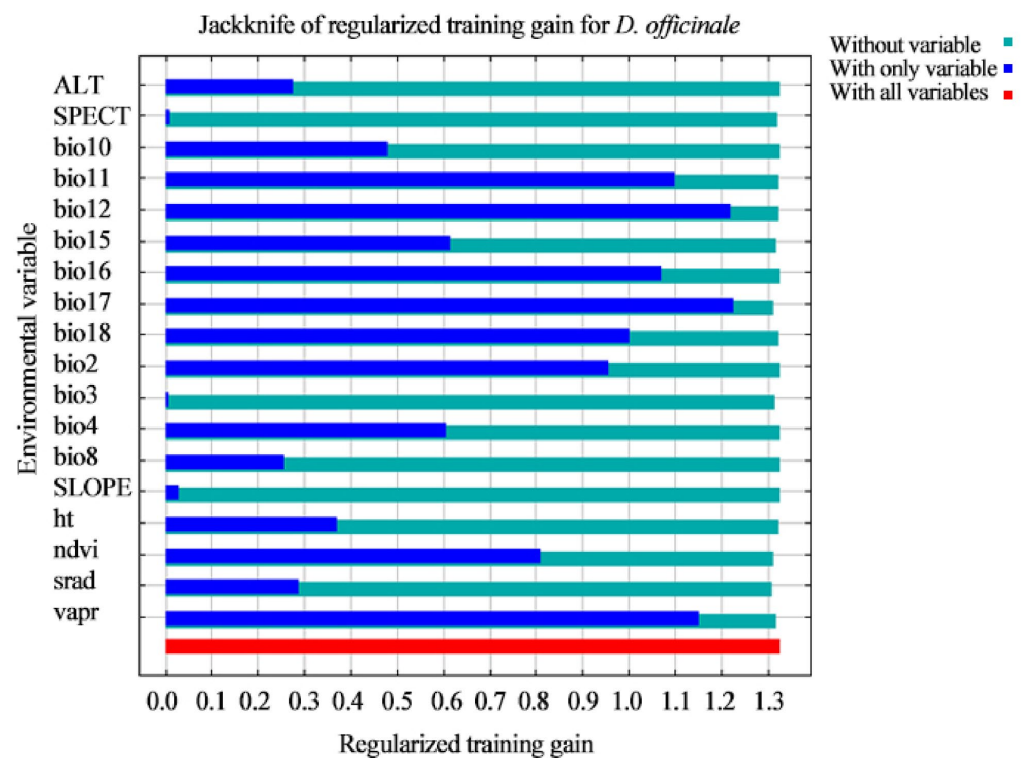


Figure 6. Jackknife test of major environmental variables.

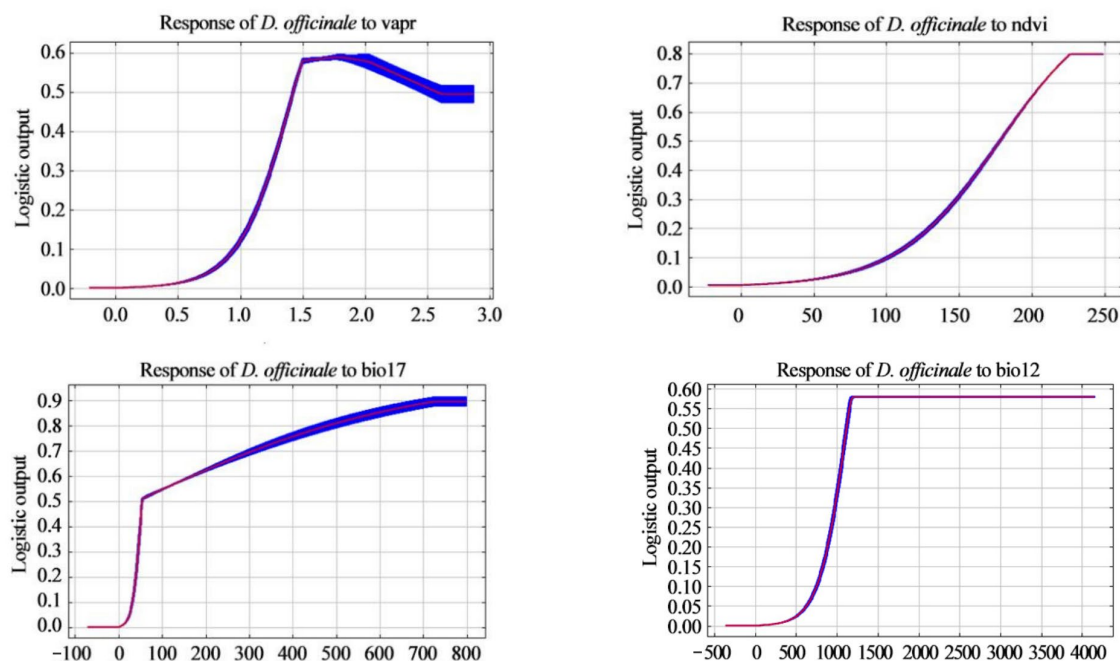


Figure 7. Response curves of key environmental variables for *D. officinale* habitat suitability. The red line represents the mean response across 10 model runs, with the blue shaded area indicating the standard deviation.

3.4. Regional Variation in Bioactive Compound Profiles of *D. officinale* Across Guizhou Province

We analyzed the bioactive compound contents of *D. officinale* from four regions in Guizhou Province. Significant regional differences were found for all measured parameters ($p < 0.05$) (one-way ANOVA with LSD post hoc test). Anlong samples had the highest values for water content ($9.04 \pm 0.15\%$), alcohol extracts ($25.27 \pm 0.20\%$), flavonoids (8.49 ± 0.03 mg/g), phenols (4.62 ± 0.32 mg/g), and alkaloids (1.76 ± 0.11 mg/g). Songtao samples had the lowest alcohol extract content ($12.33 \pm 0.08\%$) and alkaloid levels (0.22 ± 0.06 mg/g), but the highest polysaccharide content (305.06 ± 2.81 mg/g). Pingtang samples showed moderate values across most parameters, including polysaccharides (263.58 ± 1.60 mg/g). Dejiang samples showed moderate values for most parameters, except for polysaccharides, which were the lowest among the four regions (68.25 ± 1.08 mg/g) (Figure 8). These results suggest that geographic origin has a significant influence on the phytochemical profile of *D. officinale*, with the Anlong region showing particularly favorable accumulation of multiple bioactive compounds. The observed differences may be related to local microclimates, soil conditions, or cultivation practices.

3.5. Differential Responses of Bioactive Compounds to Seasonal Precipitation Patterns in *D. officinale*

Pearson correlation analysis based on the measured data revealed distinct response patterns of bioactive compounds to seasonal precipitation variables in *D. officinale* (Figure 9). Alkaloids exhibited consistently strong negative correlations with annual precipitation (bio12, $r = -0.89$, $p = 0.11$), precipitation of the driest quarter (bio17, $r = -0.99$, $p = 0.001$), and the Human Footprint index (HF, $r = -0.99$, $p = 0.001$). Similarly, total phenols showed pronounced negative correlations with these variables ($r = -0.88$, $p = 0.12$; $r = -0.97$, $p = 0.017$; and $r = -0.96$, $p = 0.04$, respectively), while total flavonoids also displayed negative associations ($r = -0.83$, $p = 0.17$; $r = -0.93$, $p = 0.07$; and $r = -0.83$, $p = 0.17$). Alcohol extract followed a comparable but weaker trend, with correlation coefficients of -0.74 ($p = 0.26$), -0.95 ($p = 0.05$), and -0.36 ($p = 0.64$) against bio12, bio17, and HF, respectively. In marked contrast, polysaccharides showed strong positive correlations with

annual precipitation ($r = 0.77$, $p = 0.23$), driest quarter precipitation ($r = 0.90$, $p = 0.10$), and HF ($r = 0.99$, $p = 0.001$), indicating an opposing accumulation tendency. Notably, NDVI exhibited relatively weak correlations with all bioactive compounds ($|r| < 0.45$, all $p > 0.05$), suggesting limited direct influence of vegetation cover on metabolite accumulation. It is important to note that while alkaloids and phenols showed significant correlations with bio17 ($p < 0.05$), the polysaccharide correlations with bio12 and bio17 did not reach statistical significance ($p = 0.23$ and $p = 0.10$, respectively), though the correlation with HF was significant ($p = 0.001$). Given the small sample size ($n = 4$), we performed a Cook's distance analysis; all values were below the critical threshold of 1, suggesting that the observed correlations were not driven by a single outlier. Nevertheless, with only four sites, these correlations cannot be considered robust; they should be viewed as tentative patterns that warrant testing with a much larger sample. The observed differential signs—negative for alkaloids and phenols versus positive for polysaccharides—are suggestive of possible opposing regulatory effects of water availability on different metabolic pathways, but this interpretation remains speculative until confirmed by broader sampling and experimental studies.

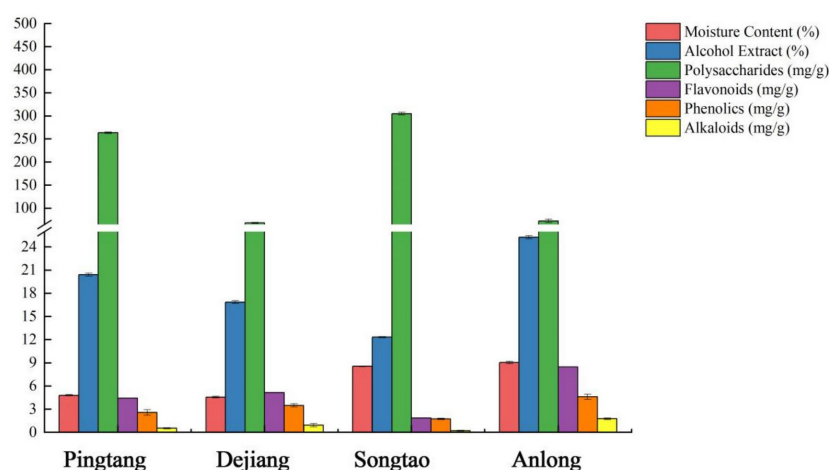


Figure 8. Chemical composition of *D. officinale* from four regions. Error bars represent $\pm$ SE. Different letters above bars indicate significant differences between regions (one-way ANOVA with LSD post hoc test, $p < 0.05$). Note the break on the y-axis to accommodate the different magnitudes of measured components (moisture and polysaccharides vs. alkaloids and phenols).

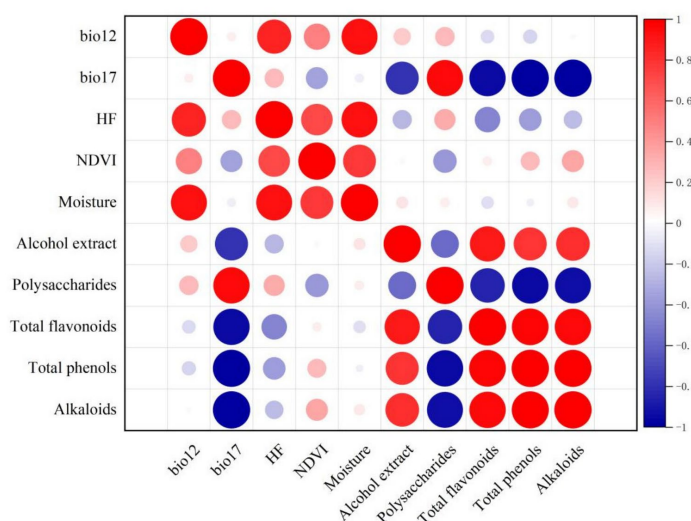


Figure 9. Correlation analysis between chemical components of *D. officinale* and environmental factors.

4. Discussion

4.1. Model Predictive Performance

Our MaxEnt model provided a robust assessment of the national-scale distribution of potential *D. officinale* habitats under current climatic conditions. The model's strong predictive performance, indicated by AUC (0.899) and TSS (0.78), suggests that it reliably captures the species' relationship with regional climate variables. The key environmental determinants identified—precipitation of the driest quarter, annual precipitation, NDVI, and VAPR—offer useful guidance for identifying suitable cultivation areas. However, the reliability of any SDM depends on multiple factors, including the quality of occurrence data, the spatial scale of the study, and the environmental predictors selected [44]. Although we focused on bioclimatic variables, other factors such as biotic interactions, soil properties, evolutionary history, and dispersal limitations may also influence species distributions [45]. Ecological data for *D. officinale* remain limited, as is the case for many plant species. Despite the inherent uncertainties in SDM projections, these models remain valuable tools for investigating broad-scale ecological patterns and species-climate relationships [46–49]. Our study provides a baseline of current habitat suitability. Future work that incorporates climate change scenarios will be needed to project how suitable areas might shift under global change.

4.2. Potential Distribution Area and Ecological Characteristics of *D. officinale*

Consistent with previous studies, our model identified Hunan, Guangxi, Guangdong, Fujian, Yunnan, and Zhejiang as core areas of high habitat suitability for *D. officinale*. However, we also observed that the predicted optimal zones were concentrated in southwestern Yunnan, southwestern Guizhou, and Taiwan, while some traditionally recognized suitable regions in Fujian and Zhejiang showed lower relative suitability. This discrepancy may be explained by several factors. First, the occurrence data used in this study ($n = 128$) were more comprehensive, integrating field surveys, herbarium specimens, and GBIF records, whereas previous work may have relied on a more limited dataset [50]. Second, our model incorporated additional environmental predictors—NDVI and VAPR—that were not included in earlier analyses, which could influence the predicted suitability patterns. Third, differences in MaxEnt parameter configurations, spatial resolution, and the specific climate datasets employed may also contribute to the observed variation. This discrepancy suggests that the environmental factors shaping the current distribution may differ from those that influenced historical cultivation patterns. The total potential suitable area under current climatic conditions was estimated at $21.4 \times 10^4 \text{ km}^2$. The key environmental drivers—precipitation of the driest quarter, annual precipitation, NDVI, and VAPR—are broadly consistent with prior work, which estimated a suitable range of approximately $229.08 \times 10^4 \text{ km}^2$ and also highlighted annual precipitation as a dominant factor, with concentrations in the middle and lower Yangtze River basin [50]. A direct comparison between our predicted high-suitability zones and documented occurrence records (including those from traditional Dao-di regions) showed only partial overlap with known points in Fujian and Zhejiang. This mismatch could reflect the influence of recent climate change on habitat suitability, or it could indicate that the phytochemical criteria for “Dao-di” quality are shaped by additional, unmeasured factors such as long-term cultivation practices or specific soil microbiomes. This opens up interesting questions for future research that integrates ecological niche modeling with traditional ethnobotanical knowledge. The important role we identified for vapor pressure is also noteworthy, as its specific effects on plant performance remain understudied and deserve further experimental investigation.

4.3. The Relationship Between the Chemical Components of *D. officinale* and Environmental Factors

Our correlation analysis, which focused on the key climatic drivers identified by the MaxEnt model (bio12, bio17, NDVI, and HF), revealed that alkaloids, total phenols, and total flavonoids were negatively correlated with annual precipitation and precipitation of the driest quarter, whereas polysaccharides showed positive correlations with these same variables. This finding suggests that water availability during the dry season may exert opposing regulatory effects on different classes of secondary metabolites. The negative correlations observed for alkaloids and phenolics indicate that reduced rainfall may promote the accumulation of these defense-related compounds. In southern China, the driest quarter coincides with winter, so water scarcity during this period may act as an environmental stress that triggers the upregulation of secondary metabolic pathways involved in alkaloid and phenolic production. A possible mechanism is that drought stress shifts resource allocation from growth toward the production of defense compounds. Conversely, the positive correlations between polysaccharides and precipitation variables suggest that higher moisture availability favors polysaccharide accumulation. This opposing pattern between polysaccharides and phenolic/alkaloid compounds is ecologically interesting—it implies that a trade-off between primary and secondary metabolism in *D. officinale* may be modulated by water availability [51–53]. It should also be noted that our phytochemical data came from cultivated populations growing under managed conditions, whereas the climatic correlations we examined were derived from broad-scale environmental layers. Management interventions may buffer or amplify the effects of climate on secondary metabolism, potentially weakening or obscuring the relationships that might exist in wild populations. This distinction should be kept in mind when interpreting the observed correlations. Notably, HF (Human Footprint) showed correlation patterns similar to precipitation variables, which may reflect the fact that human-disturbed areas in Guizhou are often located in valleys and low-elevation zones where water availability is higher, rather than indicating a direct causal effect of human activity on secondary metabolism [54]. However, the mechanisms underlying these differential responses remain unclear and require further investigation at the physiological and molecular levels.

It should be noted that our MaxEnt results identified precipitation-related variables (bio17 and bio12) as the dominant drivers of habitat suitability, together accounting for 93.9% of the model's contribution, while temperature-related variables (bio1–bio11) showed negligible contributions (<0.3% each) to the model. This is consistent with the ecological characteristics of *D. officinale*, which is primarily limited by moisture availability in its subtropical distribution range. Therefore, our discussion focuses on the climatic factors that actually drive the species' distribution—namely, precipitation regimes, vegetation cover (NDVI), and atmospheric moisture (VAPR)—rather than temperature or shade, which were not identified as important predictors in our model. The mention of temperature and shade in earlier versions of this section was inadvertently retained from a broader review of the literature on medicinal plant cultivation, and we have now removed these references to ensure that our discussion is strictly aligned with the actual results of this study [50].

It is important to acknowledge that other factors not measured in this study—such as soil total nitrogen, soil pH, maximum relative humidity, and sunshine duration—have been reported in previous studies as important determinants of secondary metabolite accumulation in medicinal plants. However, these variables were not included in our analytical framework. Our analysis, which is based solely on climatic variables and HF, suggests that the relationships between environment and phytochemicals are complex and possibly site-specific. The relatively weak correlations observed for NDVI with all compounds ($|r| < 0.45$) further indicate that vegetation cover, at least at the scale measured here,

may not be a primary driver of metabolite accumulation in this system. Future research that integrates detailed soil and microclimate measurements with larger phytochemical sampling datasets will be needed to disentangle these effects.

4.4. Regional Gradation of Chemical Content Production

The significant correlations observed between alkaloids/total phenols and bio17 ($r = -0.99$ and -0.97 , respectively), though based on a very limited sample ($n = 4$), prompt us to ask whether water availability during the driest quarter might influence secondary metabolite accumulation in *D. officinale*. To visually illustrate this tentative hypothesis across China's landscape, we generated a schematic map (Figure 10) by projecting the spatial pattern of bio17, the dominant predictor in our MaxEnt model, across the study area. We emphasize that Figure 10 is not a validated predictive map. It is a hypothesis-generating visualization that should be interpreted with extreme caution. The underlying statistical relationship is based on only four sampling sites within Guizhou Province, and extrapolating this relationship to the national scale involves substantial uncertainty. This map does not constitute a prediction of compound contents; rather, it serves to highlight regions where future, more intensive sampling might usefully test whether the patterns observed in Guizhou hold more broadly. Ground-truthing with field samples from multiple provinces is essential before any spatially explicit claims about compound accumulation can be made [50,51]. The resulting map (Figure 10) is intended only to illustrate where future sampling efforts might be prioritized to test whether the bio17–compound relationships observed in Guizhou are generalizable to other regions [55]. We emphasize, however, that this mapping exercise is preliminary. Because our phytochemical sampling was limited to four sites within Guizhou Province, the bio17-based chemical zoning map (Figure 10) should be viewed as a hypothesis-generating tool rather than a validated predictive map. Furthermore, the phytochemical data were obtained from cultivated plants, whereas the MaxEnt model was calibrated on wild occurrence records. Cultivation practices—including irrigation, shading, and fertilization—may substantially modify the environmental signals that drive secondary metabolite accumulation. Therefore, the bio17-based spatial visualization shown in Figure 10 should be interpreted as a hypothesis about potential climatic influences on compound accumulation under semi-natural cultivation conditions, not as a direct prediction for either wild populations or intensively managed plantations. Future studies with broader, multi-province sampling will be needed to test these spatial predictions.

The two maps presented in Figure 10a,b can be overlaid to identify areas that simultaneously satisfy conditions for both moisture availability (higher bio12, associated with higher moisture content) and potential alkaloid/phenolic accumulation (lower bio17, associated with higher compound content). An overlay of these two gradients would highlight regions where both climatic conditions converge—areas with high annual precipitation and low precipitation during the driest quarter. However, given the preliminary nature of the phytochemical correlations ($n = 4$, Guizhou-only sampling), this overlay exercise would be hypothesis-generating only and is not presented here as a validated predictive map. We explicitly caution against interpreting any such overlay as a confirmed prediction of compound yields [2].

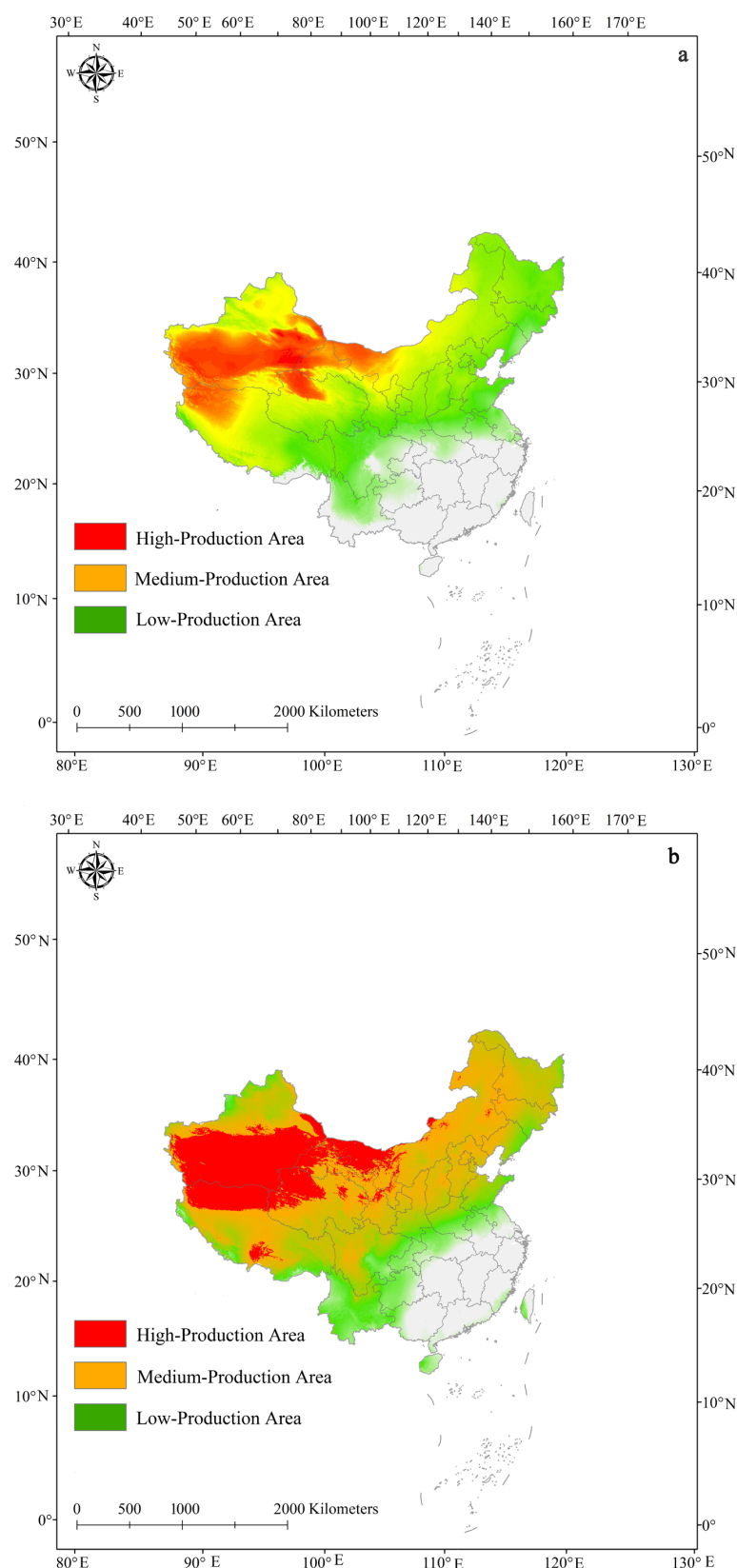


Figure 10. Illustrative spatial visualization of annual precipitation (bio12; (a)) and precipitation of the driest quarter (bio17; (b)) across China. This figure is for visualization purposes only and does not represent a validated prediction of compound contents. The relationships between bio17 and alkaloid/phenolic contents shown in Figure 9 are based on only four sampling sites (all in Guizhou Province) and should not be extrapolated to the national scale without independent validation. Areas with lower bio17 values may merit prioritized sampling in future studies to test whether the Guizhou-

based correlations hold more broadly. This is a hypothesis-generating map, not a predictive one. The two maps in (a,b) may be overlaid to identify areas with both high annual precipitation (favorable for moisture) and low dry-season precipitation (potentially favorable for alkaloid/phenolic accumulation). However, because the underlying phytochemical correlations are based on only four sites in Guizhou, any such overlay would be hypothesis-generating, not predictive, and is not included as a formal map here.

It is important to note that we did not measure soil pH in this study, nor did we include soil variables in our analytical framework. The correlations we report are based exclusively on climatic variables (bio12, bio17, NDVI, and HF). While previous studies have suggested that soil properties such as pH and nutrient availability may influence secondary metabolite accumulation in medicinal plants, these factors were beyond the scope of the present investigation. Future research integrating detailed soil measurements with expanded phytochemical sampling will be needed to evaluate the relative contributions of soil versus climatic factors to compound accumulation in *D. officinale* [51].

We also note that several specific quantitative claims that appeared in our original submission—such as specific R^2 values, percentage reductions in suitable area by 2050, and yield improvement percentages—were not supported by our data and have been removed. While our findings provide a spatial framework for identifying priority areas for cultivation, developing specific management practices and certification systems would require much more research and field testing beyond the scope of this study. Our work represents an initial ecological modeling step in what should be a longer research process. Future research should focus on developing dynamic models that integrate real-time environmental data and expanded phytochemical sampling to improve production forecasts under changing conditions [56]. In particular, the molecular mechanisms underlying environmental stress responses in *Dendrobium* species warrant further investigation [57].

5. Conclusions

In this study, we explored how environmental factors influence both the habitat suitability and the medicinal quality of *D. officinale*. Our results show that the species' potential distribution in China is mainly determined by a few key bioclimatic variables, especially precipitation of the driest quarter and annual precipitation. We also found that alkaloid, total phenol, and total flavonoid contents were significantly and negatively correlated with precipitation-related variables, while polysaccharides showed positive correlations with these same variables. This opposing pattern suggests that water availability during the dry season may exert differential regulatory effects on primary versus secondary metabolism in *D. officinale*. However, because our phytochemical sampling was geographically limited to four sites in Guizhou Province, these climate-compound relationships should be interpreted as preliminary hypotheses for this region, rather than as definitive conclusions for the whole country. One interesting finding was the possible role of drought stress during the cold-dry season in promoting alkaloid and phenolic accumulation, which points to a complex interplay between environmental stress and secondary metabolism. By combining a validated national-scale habitat suitability model (based on 128 occurrence records with spatial cross-validation) with exploratory phytochemical data (from four sites in Guizhou), we identified testable hypotheses about the possible co-occurrence of high habitat suitability and high bioactive compound accumulation. This is not yet a validated framework for precision cultivation, but rather a proof-of-concept that demonstrates how SDM outputs can be used to generate hypotheses for targeted phytochemical sampling. Future studies with expanded spatial coverage are needed to validate whether these preliminary correlations hold across a wider geographic range. However, this 'dual-criteria' idea remains conjectural at this stage, as the phytochemical component of our study lacks the spatial

coverage and statistical power needed for predictive mapping. We offer this framework not as a validated tool, but as a starting point for future hypothesis-driven sampling and field validation. This dual-criteria framework provides a starting point for future research on precision cultivation, but it requires further validation with expanded sampling. Moreover, because our chemical data came from cultivated populations while the MaxEnt model was based on wild occurrence records, the integrative mapping we present (Figure 10) should be viewed as a conceptual illustration rather than a direct predictive tool. The relationships between climate and compound accumulation may differ between cultivated and wild settings due to management interventions.

Looking ahead, several directions are worth pursuing: (1) expanding phytochemical sampling across a wider geographical range and larger environmental gradient to test the generality of the climate-compound relationships we observed; (2) investigating the physiological and molecular mechanisms that link specific environmental signals, particularly water stress, to secondary metabolite production; (3) developing more comprehensive models that include soil properties, biotic interactions, and other factors beyond climate; and (4) ground-truthing our spatial predictions with field cultivation trials. In short, the sustainable conservation and use of this endangered medicinal plant will depend on moving from traditional, experience-based cultivation toward a more data-driven, climate-informed, and quality-oriented approach. Such an integrated strategy could help preserve the valued “Dao-di” quality of *D. officinale* in a changing world.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/agronomy16141353/s1>, Table S1. List of all *D. officinale* occurrence records used in this study, including geographic coordinates, data source, and retention/exclusion status. Table S2. Variance Inflation Factor (VIF) values for all 18 environmental variables used in the MaxEnt model. Figure S1. Map showing the four phytochemical sampling locations (Anlong, Songtao, Pingtang, Dejiang) in Guizhou Province, China. Supplementary Figure S2. Spatial blocks for cross-validation based on latitudinal and longitudinal bands following the block method in the ‘kuenm’ package.

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