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RESEARCH ARTICLE

Ecological Niche Overlap and Environmental Associations Among Species of the *Morchella* (Morchellaceae, Pezizomycotina) From P.R. China

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ABSTRACT

Morchella species, economically significant edible fungi, are affected by numerous environmental factors; however, details concerning their ecological niche are poorly understood. Consequently, this study aims to fill this deficiency by applying a modeling approach to the fundamental niche of the *Morchella* genus, incorporating species from the *elata* and *esculenta* clades. In this work, we examined the distribution patterns of *Morchella* species in relation to significant environmental factors. The MaxEnt algorithm was utilized to conclude habitat validity. The environmental variables incorporated into the final models comprised isothermality, temperature seasonality, maximum temperature of the warmest month, mean temperature of the warmest quarter, precipitation of the wettest month, precipitation seasonality, slope, and aspect. The PCA-env analysis revealed that the first two axes accounted for 69.55% of the overall variation in climatic conditions across the ranges of the two clades (PC1 = 41.36% and PC2 = 28.19%). An analysis and comparison of the climatic space engaged by the two primary clades, along with their overlap, were conducted. These findings emphasized the utility of ecological niche modeling for understanding how climatic conditions can influence the dispersal of *Morchella* clades. These results aid in formulating enhanced conservation strategies and in informed decision-making across different ecosystems. It is essential to adopt a holistic approach to ecological modeling to foster sustainable conservation, evaluate diversity, and manage the valuable *Morchella* resources.

1 | Introduction

1.1 | Morels as Valuable Fungi

True morels (*Morchella* spp., Morchellaceae, Pezizomycotina, Pezizales, Ascomycota) are highly valued edible fungi prized for their distinctive flavor and aroma (Du et al. 2019). They are rich in carbohydrates, proteins, vitamins, and minerals, making them nutritionally important as well (Hirzel and Le Lay 2008; Hu et al. 2016, 2020; Tietel and Masaphy 2018; Kuang et al. 2022; Li et al. 2023; Liu and Dong 2023). Beyond their culinary appeal, morels are recognized for bioactive properties, including antitumor, immunomodulatory, antioxidant, anti-inflammatory, neuroprotective, and hepatoprotective activities, suggesting potential roles in human health (Nitha et al. 2007, 2013; Fu et al. 2013; Liu et al. 2016; Li et al. 2017; Xiong et al. 2016; Li et al. 2024).

1.2 | Taxonomy and Diversity of Morchella

Molecular phylogenetics has revealed extensive cryptic speciation and strong geographic structuring within *Morchella* (Taşkın et al. 2010, 2012; O'Donnell et al. 2011; Richard et al. 2015). Phylogenetic analysis suggested that the species in the genus *Morchella* could have been divided into two large genetic clades, the *elata* clade and *esculenta* clade lineages (Sa et al. 2022). Two major clades are widely recognized: the *esculenta* clade (yellow morels) and the *elata* clade (black morels). Screening of Chinese specimens has shown exceptional phylogenetic diversity, confirming that China

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represents a primary center of *Morchella* diversification (Gilbert 1960; Liu 1988; Tsun-Shen 2001; Du et al. 2012). Unexplored regions in northwestern and central China are thought to harbor additional undiscovered lineages, underlining the need for comprehensive research and conservation strategies (Vandermeer 1972; Colwell and Rangel 2009; Xu et al. 2022; Urban 2024).

1.3 | Economic and Ecological Importance

The economic importance of morels is substantial. Global demand is high, and harvesting occurs across North America, Turkey, China, India, and Pakistan (Pilz 2007). In Western North America alone, trade is valued at $5–10 million annually (Pilz 2007). In China, annual trade volumes rose from 181,000 to 900,000 kg within a decade (Zhao et al. 2009; Du et al. 2015; Guillory and Brown 2021). Recently, cultivation techniques, particularly the use of exogenous nutrient bags, have enabled large-scale production and consistent yields of several species (Du and Yang 2021; Liu et al. 2018; Bosch et al. 2019; Zhang et al. 2023). As a result, the morel agroindustry has expanded rapidly and become a distinctive livelihood resource for local farmers (Figure 1).

Despite these advances, *Morchella* diversity faces threats from overexploitation and habitat degradation (Du et al. 2016; Prieto-Torres et al. 2016; Prieto-Zwiener et al. 2017; Srivastava et al. 2020; Thammanu et al. 2021). Conservation planning is hindered by a limited understanding of the ecological and environmental conditions governing morel distributions (Hussain and Sher 2021; Hending 2021; Hending et al. 2023). Compared to plants and animals, fungal biogeography and species–environment relationships remain underexplored (Taheri et al. 2021; Cailleau et al. 2023).

FIGURE 1 | Cultivation of morels at greenhouse farm.

1.4 | Ecological Niche Modeling in Fungal Research

The geographic ranges of species are shaped by both abiotic and biotic factors (Stohlgren and Schnase 2006; Seo et al. 2009; Warren and Seifert 2011; Godoy et al. 2018; Srivastava et al. 2020). The fundamental niche (abiotically suitable environment) is often narrower in practice due to biotic interactions and dispersal limitations, which together define the *realized niche* (Espindola et al. 2019; Clark et al. 2016; Cavalcante et al. 2020; Jiménez and Soberón 2022).

Ecological niche modeling (ENMs) is a quantitative approach that integrates species occurrence records with environmental variables to estimate species' ecological requirements and project their potential geographic distributions (Peterson et al. 2011; Ferrer-Sánchez and Rodriguez-Estrella 2016; Cordier et al. 2020; de Souza and Prevedello 2020). Presence-only methods, such as MaxEnt, are especially common in ENMs because they perform well with limited or biased datasets and identify areas with environmental conditions similar to those of observed occurrences (Phillips et al. 2006; Elith et al. 2011; Peterson and Soberón 2012; Scales et al. 2016; Urcádiz-Cázares et al. 2021).

ENMs are widely applied in conservation biology and ecology to identify priority habitats, evaluate the effects of climate change, detect invasive species' spread, assess niche overlap among taxa, and guide protected-area planning (Rissler and Apodaca 2007; West et al. 2015; Ahmadi et al. 2018; Chalghaf et al. 2018; Adhikari et al. 2019; Gilani et al. 2020; Malekian and Sadeghi 2020; López-Tirado et al. 2021; Quiroga and Souto 2022; Rubenstein et al. 2023). However, applications to fungi remain relatively rare (Andrew et al. 2019), and they face challenges including sample bias (Pilz 2007; Lakhanpal et al. 2010; Kulhanek et al. 2011; Pili et al. 2020; Nzei et al. 2022), taxonomic uncertainty, and the need to account for fine-scale spatiotemporal patterns and biotic interactions (Hao et al. 2020).

Given China's role as a center of *Morchella* diversity, this study applies ENMs to (a) map the potential geographic distributions of *Morchella* clades across China, (b) identify environmental factors influencing habitat suitability, and (c) quantify ecological niche overlap among clades. These analyses provide a scientific basis for conservation and sustainable utilization of *Morchella* resources, supporting biodiversity protection, germplasm management, and the development of the morel agroindustry.

2 | Materials and Methods

2.1 | Study Area

The study area includes the huge and ecologically diverse regions of China, where species of both the *elata* and *esculenta* clades of *Morchella* are known to occur. These species are distributed primarily in temperate forest ecosystems across China, with species in the *Elata* clade typically found at higher altitudes, often associated with mountainous regions, and preferring areas with higher moisture and well-drained soils, and are commonly found in coniferous and broadleaf forests. While species of the *esculenta* clade occupy a broader range of elevations, they are more adaptable to a variety of habitats, from disturbed forests to grasslands, and occur at lower altitudes. The distribution of *Morchella* species (*elata* and *esculenta* clades) in China, based on available occurrence data (Figures 2 and 3).

Sources: Esri, HERE, Garmin, USGS, Intermap, INCREMENT P, NRCan, Esri Japan, METI, Esri China (Hong Kong), Esri Korea, Esri (Thailand), NGCC, © OpenStreetMap contributors, and the GIS User Community

FIGURE 2 | Study area showing the presence points of *Morchella* species of *elata* (red) and *esculenta* (green) clade lineages.

2.2 | Occurrence Data

The occurrence data for *Morchella* species from both clades were obtained from published articles in China (Du et al. 2012; Du et al. 2016; Du et al. 2019; Sa et al. 2022; Yu et al. 2024). To minimize geographic sampling bias and improve the precision of niche overlap analysis, a spatial thinning procedure was applied to the occurrence data using the spThin package in R (Aiello-Lammens et al. 2015). Initially, there were 111 occurrence records for *elata* and 83 occurrence records for *esculenta* clade lineages. To account for spatial autocorrelation and ensure that occurrence points were sufficiently independent, the data were thinned to a 1 km spatial resolution. After applying the thinning procedure, the number of records was reduced to 43 for the *Elata* clade and 32 for the *esculenta* clade (Figure 3), helping minimize sampling bias and providing a more robust dataset for niche overlap analysis. This reduction in the number of records ensures that the niche overlap analysis reflects the true ecological relationships between the two clade lineages without the influence of spatial bias (Figure 6).

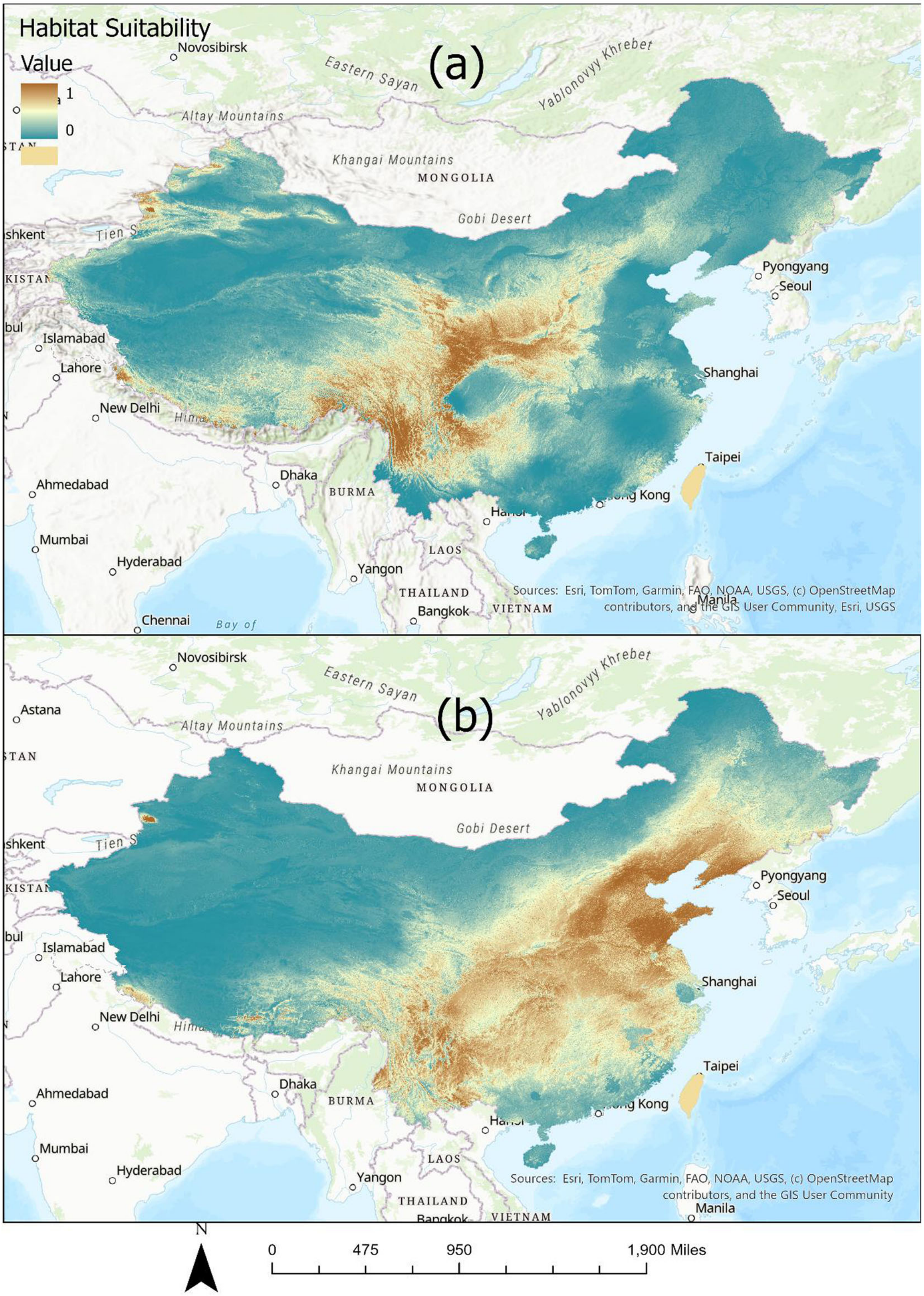
2.3 | Environmental Data

Environmental data consisted of 19 bioclimatic variables sourced from WorldClim (version 2.1, climate data for 1970–2000) at a spatial resolution of 30 arc-seconds (approximately 1 km^2). These variables included 19 temperature- and precipitation-related factors known to significantly influence species distribution (Table 1). In addition to the bioclimatic variables, topographic data—specifically altitude, slope, and aspect—were included, all derived from a digital elevation model (DEM) and resampled to the same 30 arc-second resolution to maintain consistency across the dataset. Prior to use in the models, all environmental variables underwent standard preprocessing steps to ensure they were comparable and suitable for analysis. The variables were resampled to the same spatial resolution of 30 arc-seconds, and each layer was masked to align with the study area. Furthermore, all variables were normalized to prevent discrepancies arising from using variables with different units or scales.

To mitigate multicollinearity and ensure that the predictor variables represented unique ecological information, a correlation threshold of 0.7 was applied. Variables exhibiting high pairwise correlations (greater than 0.7) were excluded from the analysis, leaving only the most ecologically relevant variables for inclusion in the species distribution models. The final set of environmental layers, used for modeling habitat suitability, consisted of eight variables, as shown in Table 1. These variables were used to evaluate habitat suitability for species of the *elata* and *esculenta* clades through the MaxEnt model.

2.4 | ENMs: Construction and Evaluation

We used MAXENT, a machine-learning algorithm based on maximum entropy (presence/pseudoabsence), to model the distribution of *Morchella* clades across mainland China. MAXENT



Sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, (c) OpenStreetMap contributors, and the GIS User Community, Esri, USGS

Sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, (c) OpenStreetMap contributors, and the GIS User Community

FIGURE 3 | Habitat suitability maps of *Morchella* species of *elata* (a) and *esculenta* (b) clade lineages from Mainland China.

estimates the probability distribution of a species using a specified set of predictor variables along with presence-only occurrence data. We chose MAXENT for several reasons: (a) It does not necessitate absence data, (b) it adeptly manages complex interactions between predictor and response variables, (c) as a generative model, it outperforms discriminative models when working with presence-only records, (d) it accommodates both categorical and continuous data variables, and (e) it effectively transfers model projections to different geographical regions. For model construction, presence-only data for each species were combined with 10,000 random background (pseudoabsence) points generated within the study area. The presence data were then split, with 80% used for model exercise and the remaining 20% for model testing.

The performance of the models was assessed using two main metrics: the area under the curve (AUC) and the true skill statistic (TSS). AUC was used to assess the model's discrimination,

TABLE 1 | List of climatic variables used for ecological modeling of the *Morchella elata* and *esculenta* clade lineages (the font represents the climate variables used for ENMs).

Climatic variables	Abbreviation
Annual mean temperature	bio_1
Mean diurnal range	bio_2
Isothermality	bio_3
Temperature seasonality	bio_4
Max temperature of warmest month	bio_5
Min temperature of coldest month	bio_6
Temperature annual range	bio_7
Mean temperature of wettest quarter	bio_8
Mean temperature of driest quarter	bio_9
Mean temperature of warmest quarter	bio_10
Mean temperature of coldest quarter	bio_11
Annual precipitation	bio_12
Precipitation of the wettest month	bio_13
Precipitation of driest month	bio_14
Precipitation seasonality	bio_15
Precipitation of wettest quarter	bio_16
Precipitation of driest quarter	bio_17
Precipitation of warmest quarter	bio_18
Precipitation of coldest quarter	bio_19
Digital elevation model	DEM
Percentage of slope	Slope
Aspect of slope	Aspect
Distance to water	Dist to water
Distance to Road	Dist to road
Distance to village	Dist to Vil
Soil type	Soil type

with values above 0.9 considered excellent and those between 0.8 and 0.9 indicating suitable performance. TSS (0–1) was calculated to assess agreement between model predictions and observed data; values above 0.85 were considered excellent. Following model evaluation, we categorized habitat suitability scores into four distinct levels: unsuitable (0–0.25), poor suitability (0.25–0.5), moderate suitability (0.5–0.75), and high suitability (0.75–1). The final suitability maps were then used to calculate the area of each suitability category, expressed in square kilometers. This classification was based on continuous habitat-suitability scores assigned to each grid cell, with higher scores indicating greater suitability for each species.

2.5 | Niche Overlap

To compare climatic conditions across the ranges of *Morchella* species (*elata* and *esculenta* clades), occurrence-density models were constructed, adjusting for the environmental conditions available to the species. In this analysis, principal component analysis (PCA) was used to examine shifts in climatic niches between the two species (Broennimann et al. 2012; Bates et al. 2020). The first two principal components were employed to evaluate the ecological circumstances at each species observed occurrence sites and to assess the existing environmental capacity for both *Morchella* clades (Figure 5). To define the calibration area for the models, we have created background areas by establishing buffers around occurrence points. The buffer distances were calculated based on the maximum distance between occurrence points and the average distance from all occurrences to their centroid (Poo-Muñoz et al. 2014). We set the buffer distance to 20 km for both species, representing the average distance between occurrence points. We applied 19 bioclimatic variables at a 30 arcsecond resolution, which were extracted from the WorldClim database (current conditions) (Fick and Hijmans 2017). PCA was used to reduce these variables to two principal components for each species' environmental niche (Silva et al. 2016). The data for each species were subsequently obtained from the occurrence locations and background regions utilizing ArcGIS (version 10.8).

The species within the ecological niche was created by applying PCA scores resulting from both occurrence locations and the surrounding area. The two-dimensional spatial grid's resolution was set in compliance with previous studies. We assessed species density within this environmental grid by considering incidence density alongside the convenience of environmental conditions in the background (Broennimann et al. 2014). To assess niche overlap, Schoener's *D* and Hellinger's *I* metrics were estimated. Both metrics range from 0 to 1, with higher values indicating greater overlap between the species' niches (Warren et al. 2008). The occurrence points were randomized to establish a null distribution of intersection values, which were then associated with the detected values to evaluate niche similarity. Furthermore, we assessed niche expansion, stability, and unfilling (Guisan et al. 2014). All the necessary designs and modeling for niche overlap analysis were directed using the ecospat package in R (v4.1.3) (Aiello-Lammens et al. 2015; Di Cola et al. 2017).

3 | Results

3.1 | ENM for *Morchella elata* and *esculenta* Clades

To assess the habitat suitability of *Morchella elata* and *esculenta* clades in China, the MaxEnt algorithm was applied (Figure 4), which was chosen due to its reliability in presence-only species distribution modeling. The environmental variables included in the final models were bio_3 (isothermality), bio_4 (temperature seasonality), bio_5 (max temperature of the warmest month), bio_9 (mean temperature of the warmest quarter), bio_13 (precipitation of the wettest month), bio_15 (precipitation seasonality), slope, and aspect. For the *elata* clade, the model achieved an AUC of 0.89 and a TSS of 0.82, indicating high model performance. Similarly, the *esculenta* clade model showed an AUC of 0.91 and a TSS of 0.81, both considered excellent thresholds for MaxEnt models. These values reflect the strong predictive power of the models in identifying suitable habitats for fungal species in both clades. The variable importance analysis revealed that species of the *elata* and *esculenta* clades shared several important environmental drivers with precipitation variables, such as bio_13 (precipitation of the wettest month) and

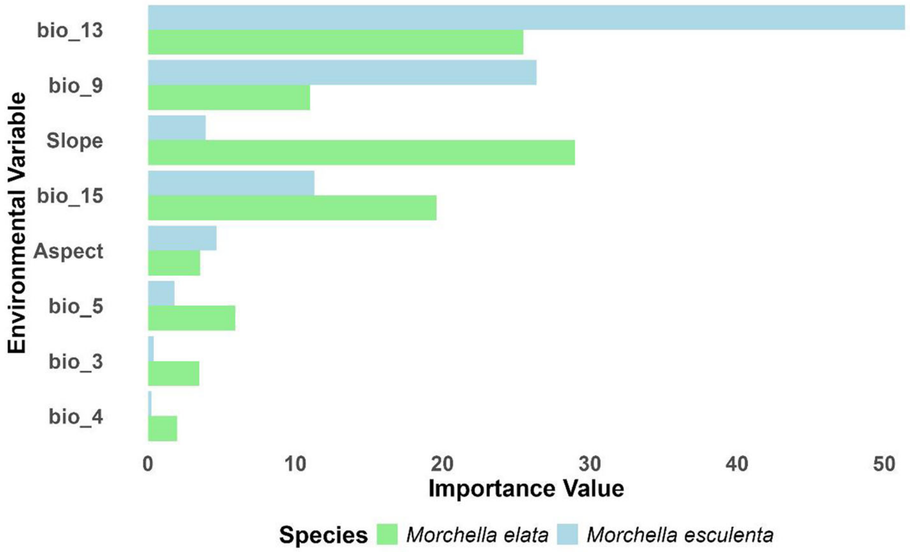


FIGURE 4 | Variable importance for the MaxEnt models of *Morchella elata* and *esculenta* clade lineages based on contribution (percentage of model contribution to the prediction) and permutation importance (change in model performance when the variable is permuted).

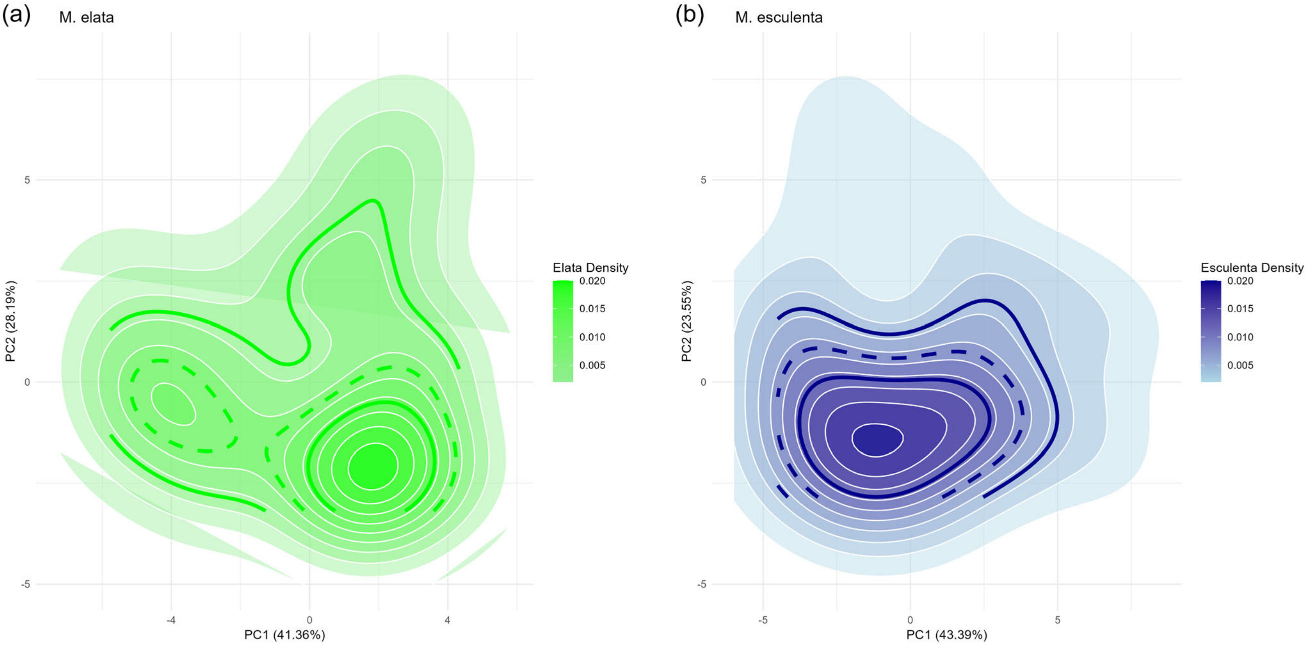


FIGURE 5 | Principal component analysis of environmental niches for *Morchella elata* and *esculenta* clade lineages. (a) *Morchella elata* environmental niche shown in the PCA space. The green shading represents the occurrence density, with solid and dashed contours representing 100% and 50% of the available environment, respectively. (b) *Morchella esculenta* environmental niche depicted similarly. The blue shading indicates the occurrence density, with contours showing the 100% and 50% available environments. The axes represent the first and second principal components (PC1 and PC2), with the percentage of variation explained by each component indicated.

bio_15 (precipitation seasonality), which contributed significantly to the models. Slope and aspect were also among the most significant variables in determining habitat suitability for both species, with higher precipitation and certain slopes corresponding to increased habitat suitability. The significance and permutation importance of each variable for both clades are illustrated (Figure 4). The results suggested that, for the *elata* clade, 67.9% of China's area is unsuitable, 18.14% is poorly suitable, 8.8% is moderately suitable, and 5.16% is highly suitable. Furthermore, for species of the *esculenta* clade, 55.4% of China's geographic area is unsuitable, 18.2% is poorly suitable, 17.7% is moderately suitable, and 8.7% is highly suitable.

3.2 | Niche Overlap

The PCA analysis indicated that the first two axes accounted for 69.55% of the variation in climatic conditions across the habitats of the two species (PC1 = 41.36% and PC2 = 28.19%). An analysis and comparison of the climatic space occupied by both species, as

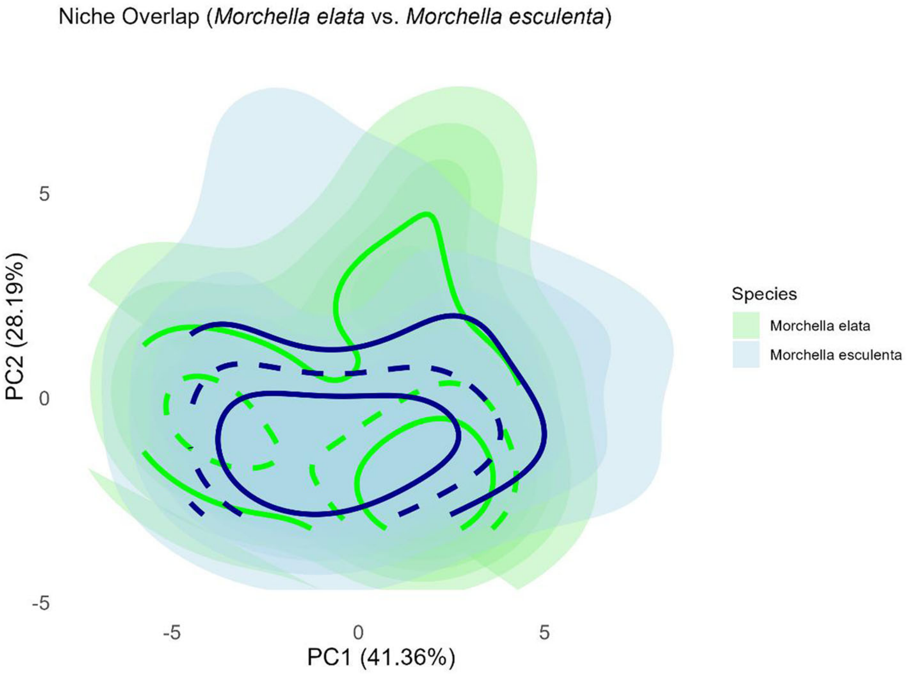


FIGURE 6 | Niche overlap between *Morchella elata* (green) and *esculenta* clade lineages (dark blue) in Mainland China, based on the principal component analysis of climate variables. The solid lines represent the 100% environmental envelope, while the dashed lines represent the 50% environmental envelope for each species. The overlapping regions indicate the areas of climatic niche stability shared by both species.

well as their overlap, was conducted (Figure 6). The niche overlap between the *elata* and *esculenta* clades was assessed using Schoener's *D* index and Hellinger's *I* index, yielding values of 0.84 for both, which signifies a substantial degree of niche overlap. Both indices were significantly different from random overlap (p values < 0.001). This suggests that the environmental niches of the two clade lineages shared a considerable portion of their climatic ranges (Figure 5).

The PCA-based analysis of the climatic niches of the *elata* and *esculenta* clades (Figure 5) revealed that both species occupy overlapping regions in environmental space, with the overlap representing niche stability. The environmental envelope of each species was characterized by solid (100% envelope) and dashed (50% envelope) lines. The overlap between these envelopes indicates the climatic conditions where both species are stable in their distributions. Niche stability was prominent, while niche expansion and unfilling were not observed (Table 2), suggesting that the two species are adapted to similar environmental conditions and may compete for the same ecological niches within the study area.

4 | Discussion

True morels (*Morchella* spp.) are classified within the Pezizales order and the Morchellaceae family, possessing considerable economic and medicinal importance (Hibbett et al. 2007). They have been recognized as one of the most prized edible fungi in the world (Tietel and Masaphy 2018). Most true morels are distributed in temperate regions of the northern hemisphere, and East Asia or China is considered to be the diversity center of *Morchella* species (Du et al. 2012). Overharvesting of morels has raised concerns about how to effectively preserve their biological and genetic diversity. A better understanding of their geographical distribution and suitable niche areas is needed to facilitate the development of strategies to conserve and sustain wild morel populations. Understanding the appropriate habitats for these species in their natural environment is crucial to the effective use and preservation of this resource. This research models the potential geographic distribution of *Morchella* in China. Overall, the existing potential distribution aligns with documented occurrence records of *Morchella* species and provides insights into new suitable habitats. Consequently, upcoming field surveys for *Morchella* species should focus on the highly suitable habitats.

4.1 | ENMs Performance and Environmental Determinants

This research utilized ecological niche models (ENMs) and multivariate niche analyses to evaluate the environmental differences among *Morchella* species in China, as suggested (Kaky et al. 2020;

TABLE 2 | Comparison of niche dynamics between *Morchella elata* and *esculenta* clade lineages.

Niche 1	Niche 2	Schoener's *D*	Hellinger's *I*	Equivalency test *p* value	Similarity test *p* value	Niche unfilling	Niche stability	Niche expansion
elata clade	esculenta clade	0.840533265	0.842208335	0.000999001	0.000999001	0	1	0

Note: The Schoener's *D* and Hellinger's *I* values indicate the degree of niche overlap, where values closer to 1 represent complete overlap. The equivalency and similarity test *p* values assess the statistical significance of niche equivalency and similarity, respectively.

Valavi et al. 2022). The models, including Random Forest (RF), MaxEnt, and MAXnet, can be considered dependable due to their AUC and TSS scores, which align well with real-world observations. RF and MaxEnt, in particular, are among the most effective presence models and have been extensively utilized in ecological studies (Hendrix and Vos 2019; Kaky et al. 2020; Rochat et al. 2020; Valavi et al. 2022). When properly calibrated, these algorithms demonstrate strong explanatory power and effective generalization, with minimal overfitting (Cerasoli et al. 2022). The application of the ensemble modeling approach enhances the reliability of the outcomes and the precision of the ecological maps produced (Valavi et al. 2022). When selecting models for ensemble modeling, it is crucial to use a variety of evaluation indices and evaluate the resulting map against actual data (Lauzeral et al. 2015).

The ensemble method was employed to assess the importance of the environmental factors in the anticipated suitable habitat for each *Morchella* clade. The study reports that precipitation variables, such as bio_13 (precipitation of the wettest month) and bio_15 (precipitation seasonality), make significant contributions to the models. Slope and aspect were also among the most vital variables in shaping the habitat fitness for *Morchella* species from both clades. It is confirmed that, with higher precipitation levels, certain slopes are associated with increased habitat suitability, as shown in Figure 3. The present study suggests that, for species from the *elata* clade, 5.16% of China's area is highly suitable, and for *esculenta*, 8.7%. The niche overlap between species from the *elata* and *esculenta* clades was quantified, demonstrating a high degree of niche overlap. This suggested that the ecological niches of both clades shared a considerable portion of their environmental ranges. The niche conservatism hypothesis posits that closely related species occupy similar ecological environments to preserve their fundamental niche across time (Suárez-Mota and Villaseñor 2020). According to the niche theory, species exhibit preferences for specific habitats and inhabit environments that provide suitable conditions (Vandermeer 1972). This means that species have bell-shaped distributions along ecological conditions and prefer the most favorable conditions.

5 | Conclusions

Several programs targeting biodiversity have also been established in China, including the renewed protected areas system, which includes national parks. With advances in recent years, the status of numerous endangered species, such as the giant panda and the crested ibis, has improved significantly in China through protective management and scientific research (Huang et al. 2021). The Ecological Conservation Redline (ECR) policy in China represents a significant advancement aimed at restricting human-induced changes in regions vital to national ecological security. It also suggests implementing protective legislation to prevent overexploitation in these areas. This approach aligns with China's commitment to global biodiversity conservation efforts beyond 2020 (Wei 2021). It is anticipated that these ecosystem conservation policies will have positive effects on the protection and use of *Morchella* and related fungal species with medical and industrial importance. This study aims to enhance our understanding of the species diversity and geographic distribution of *Morchella* species and to formulate a strategic plan to identify valuable and beneficial germplasm resources from the most suitable regions in China, with the goal of improving commercial morel production.

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Conflicts of Interest

The authors declare no conflicts of interest.

References

Adhikari, D., R. Tiwary, P. P. Singh, et al. 2019. "Ecological Niche Modeling as a Cumulative Environmental Impact Assessment Tool for Biodiversity Assessment and Conservation Planning: A Case Study of Critically Endangered Plant Lagerstroemia Minuticarpa in the Indian Eastern Himalaya." *Journal of Environmental Management* 243: 299–307.

Ahmadi, M., M. Naderi, M. Kaboli, M. Nazarizadeh, M. Karami, and S. M. Beitollahi. 2018. "Evolutionary Applications of Phylogenetically-Informed Ecological Niche Modelling (ENM) to Explore Cryptic Diversification over Cryptic Refugia." *Molecular Phylogenetics and Evolution* 127: 712–722.

Aiello-Lammens, M. E., R. A. Boria, A. Radosavljevic, B. Vilela, and R. P. Anderson. 2015. "spThin: an R Package for Spatial Thinning of Species Occurrence Records for use in Ecological Niche Models." *Ecography* 38: 541–545.

Andrew, C., J. Diez, T. Y. James, and H. Kauserud. 2019. "Fungarium Specimens: A Largely Untapped Source in Global Change Biology and Beyond." *Philosophical Transactions of the Royal Society B* 374: 20170392.

Bates, O. K., S. Ollier, and C. Bertelsmeier. 2020. "Smaller Climatic Niche Shifts in Invasive than Non-Invasive Alien Ant Species." *Nature Communications* 11: 5213.

Bosch, M., S. Herrando-Moraira, A. del Hoyo, et al. 2019. "New Conservation Viewpoints when Plants Are Viewed at One Level Higher. Integration of Phylogeographic Structure, Niche Modeling and Genetic Diversity in Conservation Planning of W Mediterranean Larkspurs." *Global Ecology and Conservation* 18: e00580.

Broennimann, O., M. C. Fitzpatrick, P. B. Pearman, et al. 2012. "Measuring Ecological Niche Overlap from Occurrence and Spatial Environmental Data." *Global Ecology and Biogeography* 21: 481–497.

Broennimann, O., P. Mráz, B. Petitpierre, A. Guisan, and H. Müller-Schärer. 2014. "Contrasting Spatio-Temporal Climatic Niche Dynamics during the Eastern and Western Invasions of Spotted Knapweed in North America." *Journal of Biogeography* 41: 1126–1136.

Cailleau, G., B. T. Hanson, M. Cravero, et al. 2023. "Associated Bacterial Communities, Confrontation Studies, and Comparative Genomics Reveal Important Interactions Between Morchella with Pseudomonas Spp." *Frontiers in Fungal Biology* 4: 1285531.

Cavalcante, T., A. de Souza Jesus, R. M. Rabelo, et al. 2020. "Niche Overlap between Two Sympatric Frugivorous Neotropical Primates:

Improving Ecological Niche Models Using Closely-Related Taxa." *Biodiversity and Conservation* 29: 2749–2763.

Cerasoli, F., P. D'Alessandro, and M. Biondi. 2022. "Fine-Tuned Ecological Niche Models Unveil Climatic Suitability and Association with Vegetation Groups for Selected Chaetocnema Species in South Africa (Coleoptera: Chrysomelidae)." *Diversity* 14: 100.

Chalghaf, B., J. Chemkhi, B. Mayala, et al. 2018. "Ecological Niche Modeling Predicting the Potential Distribution of Leishmania Vectors in the Mediterranean Basin: Impact of Climate Change." *Parasites & Vectors* 11: 1–9.

Clark, J. S., L. Iverson, C. W. Woodall, et al. 2016. "The Impacts of Increasing Drought on Forest Dynamics, Structure, and Biodiversity in the United States." *Global Change Biology* 22: 2329–2352.

Colwell, R. K., and T. F. Rangel. 2009. "Hutchinson's Duality: The once and Future Niche." *Proceedings of the National Academy of Sciences* 106: 19651–19658.

Cordier, J. M., R. Loyola, O. Rojas-Soto, and J. Nori. 2020. "Modeling Invasive Species Risk from Established Populations: Insights for Management and Conservation." *Perspectives in Ecology and Conservation* 18: 132–138.

Correa Nogueira, T. A., W. E. Ayala, J. S. Dayrell, R. de Fraga, and I. L. Kaefer. 2019. "Scale-Dependent Estimates of Niche Overlap and Environmental Effects on Two Sister Species of Neotropical Snakes." *Studies on Neotropical Fauna and Environment* 54: 121–132.

de Souza, A. C., and J. A. Prevedello. 2020. "The Importance of Protected Areas for Overexploited Plants: Evidence from a Biodiversity Hotspot." *Biological Conservation* 243: 108482.

Di Cola, V., O. Broennimann, B. Petitpierre, et al. 2017. "ecospat: An R Package to Support Spatial Analyses and Modeling of Species Niches and Distributions." *Ecography* 40: 774–787.

Du, X. H., D. M. Wu, G. Q. He, W. Wei, N. Xu, and T. L. Li. 2019. "Six New Species and Two New Records of Morchella in China Using Phylogenetic and Morphological Analyses." *Mycologia* 111: 857–870.

Du, X. H., and Z. L. Yang. 2021. "Mating Systems in True Morels (*Morchella*)." *Microbiology and Molecular Biology Reviews* 85.

Du, X. H., Q. Zhao, K. O'Donnell, A. P. Rooney, and Z. L. Yang. 2012. "Multigene Molecular Phylogenetics Reveals True Morels (*Morchella*) are Especially Species-Rich in China." *Fungal Genetics and Biology* 49: 455–469.

Du, X. H., Q. Zhao, J. Xu, and Z. L. Yang. 2016. "High Inbreeding, Limited Recombination and Divergent Evolutionary Patterns Between Two Sympatric Morel Species in China." *Scientific Reports* 6: 22434.

Du, X. H., Q. Zhao, and Z. L. Yang. 2015. "A Review on Research Advances, Issues, and Perspectives of Morels." *Mycology* 6: 78–85.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. "A Statistical Explanation of MaxEnt for Ecologists." *Diversity and Distributions* 17: 43–57.

Espindola, S., J. L. Parra, and E. Vázquez-Domínguez. 2019. "Fundamental Niche Unfilling and Potential Invasion Risk of the Slider Turtle Trachemys Scripta." *PeerJ* 7: e7923. https://doi.org/10.7717/peerj.7923.

Ferrer-Sánchez, Y., and R. Rodríguez-Estrella. 2016. "How Rare Species Conservation Management can be Strengthened with the Use of Ecological Niche Modelling: The Case for Endangered Endemic Gundlach's Hawk and Cuban Black-Hawk." *Global Ecology and Conservation* 5: 88–99.

Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: New 1-km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37: 4302–4315.

Fu, L., Y. Wang, J. Wang, Y. Yang, and L. Hao. 2013. "Evaluation of the Antioxidant Activity of Extracellular Polysaccharides from *Morchella esculenta*." *Food & Function* 4: 871–879.

Gilani, H., M. A. Goheer, H. Ahmad, and K. Hussain. 2020. "Under Predicted Climate Change: Distribution and Ecological Niche Modelling of Six Native Tree Species in Gilgit-Baltistan, Pakistan." *Ecological Indicators* 111: 106049.

Gilbert, F. A. 1960. "The Submerged Culture of *Morchella*." *Mycologia* 52: 201–209.

Godoy, B. S., L. M. Camargos, and S. Lodi. 2018. "When Phylogeny and Ecology Meet: Modeling the Occurrence of Trichoptera with Environmental and Phylogenetic Data." *Ecology and Evolution* 8: 5313–5322.

Guillory, W. X., and J. L. Brown. 2021. "A New Method for Integrating Ecological Niche Modeling with Phylogenetics to Estimate Ancestral Distributions." *Systematic Biology* 70: 1033–1045.

Guisan, A., B. Petitpierre, O. Broennimann, C. Daehler, and C. Kueffer. 2014. "Unifying Niche Shift Studies: Insights from Biological Invasions." *Trends in Ecology & Evolution* 29: 260–269.

Hao, T., G. Guillera-Arroita, T. W. May, J. J. Lahoz-Monfort, and J. Elith. 2020. "Using Species Distribution Models for Fungi." *Fungal Biology Reviews* 34: 74–88.

Hending, D. 2021. "Niche-Separation and Conservation Biogeography of Madagascar's Fork-Marked Lemurs (Cheirogaleidae: Phaner): Evidence of a New Cryptic Species?." *Global Ecology and Conservation* 29: e01738.

Hending, D., G. McCabe, S. Cotton, and M. Holderied. 2023. "Conservation Biogeography of the Dwarf Lemurs (Cheirogaleus) of Madagascar, Investigated via Ecological Niche Modelling." *International Journal of Primatology* 44: 960–983.

Hendrix, E., and R. Vos. 2019. "Differentiation Between Wild and Domesticated Ungulates Based on Ecological Niches." *BioRxiv* 629188.

Hibbett, D. S., M. Binder, J. F. Bischoff, et al. 2007. "A Higher-Level Phylogenetic Classification of the Fungi." *Mycological Research* 111: 509–547.

Hirzel, A. H., and G. Le Lay. 2008. "Habitat Suitability Modelling and Niche Theory." *Journal of Applied Ecology* 45: 1372–1381.

Hu, J., O. Broennimann, A. Guisan, B. Wang, Y. Huang, and J. Jiang. 2016. "Niche Conservatism in Gynandropaa Frogs on the Southeastern Qinghai-Tibetan Plateau." *Scientific Reports* 6: 32624.

Hu, W., Y. Wang, P. Dong, et al. 2020. "Predicting Potential Mangrove Distributions at the Global Northern Distribution Margin Using an Ecological Niche Model: Determining Conservation and Reforestation Involvement." *Forest Ecology and Management* 478: 118517.

Huang, G., X. Ping, W. Xu, et al. 2021. "Wildlife Conservation and Management in China: Achievements, Challenges and Perspectives." *National Science Review* 8: nwab042.

Hussain, S., and H. Sher. 2021. "Ecological Characterization of Morel (*Morchella* spp.) Habitats: A Multivariate Comparison from Three Forest Types of District Swat, Pakistan." *Acta Ecologica Sinica* 41: 1–9.

Jiménez, L., and J. Soberón. 2022. "Estimating the Fundamental Niche: Accounting for the Uneven Availability of Existing Climates in the Calibration Area." *Ecological Modelling* 464: 109823.

Kaky, E., V. Nolan, A. Alatawi, and F. Gilbert. 2020. "A Comparison Between Ensemble and MaxEnt Species Distribution Modelling Approaches for Conservation: A Case Study with Egyptian Medicinal Plants." *Ecological Informatics* 60: 101150.

Kuang, M. T., J. Y. Xu, J. Y. Li, et al. 2022. "Purification, Structural Characterization and Immunomodulatory Activities of a Polysaccharide from the Fruiting Body of *Morchella sextelata*." *International Journal of Biological Macromolecules* 213: 394–403.

Kulhanek, S. A., B. Leung, and A. Ricciardi. 2011. "Using Ecological Niche Models to Predict the Abundance and Impact of Invasive

Species: Application to the Common Carp." *Ecological Applications* 21: 203–213.

Lakhanpal, T. N., O. Shad, and M. Rana. 2010. Biology of Indian Morels. IK International Pvt Ltd.

Lauzeral, C., G. Grenouillet, and S. Brosse. 2015. "The Iterative Ensemble Modelling Approach Increases the Accuracy of Fish Distribution Models." *Ecography* 38: 213–220.

Li, D. X., X. Cheng, F. P. Ma, et al. 2023. "Identification of Metabolites from Edible Mushroom *Morchella Sextelata* and Their Biological Evaluation." *Natural Product Research* 37: 1774–1781.

Li, S., A. Gao, S. Dong, et al. 2017. "Purification, Antitumor and Immunomodulatory Activity of Polysaccharides from Soybean Residue Fermented with *Morchella esculenta*." *International Journal of Biological Macromolecules* 96: 26–34.

Li, Y., T. Yang, J. Qiao, et al. 2024. "Whole-Genome Sequencing and Evolutionary Analysis of the Wild Edible Mushroom, *Morchella eohespera*." *Frontiers in Microbiology* 14: 1309703.

Liu, C., Y. Sun, Q. Mao, et al. 2016. "Characteristics and Antitumor Activity of *Morchella esculenta* Polysaccharide Extracted by Pulsed Electric Field." *International Journal of Molecular Sciences* 17: 986.

Liu, K. B. 1988. "Quaternary History of the Temperate Forests of China." *Quaternary Science Reviews* 7: 1–20.

Liu, Q., H. Ma, Y. Zhang, and C. Dong. 2018. "Artificial Cultivation of True Morels: Current State, Issues and Perspectives." *Critical Reviews in Biotechnology* 38: 259–271.

Liu, Q. Z., and C. H. Dong. 2023. "Science and Technology Breakthroughs to Advance Artificial Cultivation of True Morels." *Frontiers in Microbiology* 14: 1259144.

López-Tirado, J., F. Vessella, J. Stephan, S. Ayan, B. Schirone, and P. J. Hidalgo. 2021. "Effect of Climate Change on Potential Distribution of Cedrus Libani A. Rich in the Twenty-First Century: An Ecological Niche Modeling Assessment." *New Forests* 52: 363–376.

Malekian, M., and M. Sadeghi. 2020. "Predicting Impacts of Climate Change on the Potential Distribution of Two Interacting Species in the Forests of Western Iran." *Meteorological Applications* 27: e1800.

Nitha, B., P. Fijesh, and K. Janardhanan, 2013. "Hepatoprotective Activity of Cultured Mycelium of Morel Mushroom, *Morchella esculenta*, *Experimental and Toxicologic Pathology* 65: 105–112.

Nitha, B., C. Meera, and K. Janardhanan. 2007. "Anti-Inflammatory and Antitumour Activities of Cultured Mycelium of Morel Mushroom, *Morchella Esculenta*." *Current Science* 92, no. 2: 235–239.

Nzei, J. M., V. M. Mwanzia, B. K. Ngarega, et al. 2022. "Ecological Niche Modeling of Water Lily (Nymphaea L.) Species in Australia under Climate Change to Ascertain Habitat Suitability for Conservation Measures." *Plants* 11: 1874.

O'Donnell, K., A. P. Rooney, G. L. Mills, M. Kuo, N. S. Weber, and S. A. Rehner. 2011. "Phylogeny and Historical Biogeography of True Morels (*Morchella*) Reveals an Early Cretaceous Origin and High Continental Endemism and Provincialism in the Holarctic." *Fungal Genetics and Biology* 48: 252–265.

Peterson, A. T., and J. Soberón. 2012. "Species Distribution Modeling and Ecological Niche Modeling: Getting the Concepts Right." *Natureza & Conservação* 10: 102–107.

Peterson, A. T., J. Soberón, R. G. Pearson, et al. 2011. *Ecological Niches and Geographic Distributions (MPB-49).* Princeton University Press.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. "Maximum Entropy Modeling of Species Geographic Distributions." *Ecological Modelling* 190: 231–259.

Pili, A. N., R. Tingley, E. Y. Sy, M. L. L. Diesmos, and A. C. Diesmos. 2020. "Niche Shifts and Environmental Non-Equilibrium Undermine the Usefulness of Ecological Niche Models for Invasion Risk Assessments." *Scientific Reports* 10: 7972.

Pilz, D. 2007. *Ecology and Management of Morels Harvested from the Forests of Western North America.*

Poo-Muñoz, D. A., L. E. Escobar, A. T. Peterson, F. Astorga, J. F. Organ, and G. Medina-Vogel. 2014. "Galictis Cuja (Mammalia): An Update of Current Knowledge and Geographic Distribution." *Iheringia Série Zoologia* 104: 341–346.

Prieto-Torres, D. A., A. G. Navarro-Sigüenza, D. Santiago-Alarcon, and O. R. Rojas-Soto. 2016. "Response of the Endangered Tropical Dry Forests to Climate Change and the Role of Mexican Protected Areas for their Conservation." *Global Change Biology* 22: 364–379.

Quiroga, M. P., and C. P. Souto. 2022. "Ecological Niche Modeling, Niche Overlap, and Good Old Rabinowitz's Rarities Applied to the Conservation of Gymnosperms in a Global Biodiversity Hotspot." *Landscape Ecology* 37: 2571–2588.

Richard, F., J.-M. Bellanger, P. Clowez, et al. 2015. "True Morels (*Morchella*, Pezizales) of Europe and North America: Evolutionary Relationships Inferred from Multilocus Data and a Unified Taxonomy." *Mycologia* 107: 359–382.

Rissler, L. J., and J. J. Apodaca. 2007. "Adding More Ecology into Species Delimitation: Ecological Niche Models and Phylogeography Help Define Cryptic Species in the Black Salamander (Aneides Flavipunctatus)." *Systematic Biology* 56: 924–942.

Rochat, E., S. Vuilleumier, S. Aeby, et al. 2020. "Nested Species Distribution Models of *Chlamydiales* in Ixodes Ricinus (Tick) Hosts in Switzerland." *Applied and Environmental Microbiology* 87: e01237–01220.

Rubenstein, M. A., S. R. Weiskopf, R. Bertrand, et al. 2023. "Climate Change and the Global Redistribution of Biodiversity: Substantial Variation in Empirical Support for Expected Range Shifts." *Environmental Evidence* 12: 1–21.

Sa, W., J. Qiao, Q. Gao, Z. Li, and Q. Shang. 2022. "DNA Barcoding and Species Classification of *Morchella*." *Genes* 13: 1806.

Scales, K. L., P. I. Miller, S. N. Ingram, E. L. Hazen, S. J. Bograd, and R. A. Phillips. 2016. "Identifying Predictable Foraging Habitats for a Wide-Ranging Marine Predator Using Ensemble Ecological Niche Models." *Diversity and Distributions* 22: 212–224.

Seo, C., J. H. Thorne, L. Hannah, and W. Thuiller. 2009. "Scale Effects in Species Distribution Models: Implications for Conservation Planning Under Climate Change." *Biology Letters* 5: 39–43.

Silva, C. A., C. Klauberg, A. T. Hudak, et al. 2016. "A Principal Component Approach for Predicting the Stem Volume in Eucalyptus Plantations in Brazil Using Airborne LiDAR Data." *Forestry: An International Journal of Forest Research* 89: 422–433.

Srivastava, V., W. Liang, M. A. Keena, A. D. Roe, R. C. Hamelin, and V. C. Griess. 2020. "Assessing Niche Shifts and Conservatism by Comparing the Native and Post-Invasion Niches of Major Forest Invasive Species." *Insects* 11, no. 8: 479.

Stohlgren, T. J., and J. L. Schnase. 2006. "Risk Analysis for Biological Hazards: What we Need to Know About Invasive Species." *Risk Analysis* 26: 163–173. https://doi.org/10.1111/j.1539-6924.2006.00707.x.

Suárez-Mota, M. E., and J. L. Villaseñor. 2020. "Ecological Niche Overlap Among Species of the Genus Zaluzania (Asteraceae) from the Dry Regions of Mexico." *Plant Ecology and Evolution* 153: 337–347.

Taheri, S., B. Naimi, C. Rahbek, and M. B. Araújo. 2021. "Improvements in Reports of Species Redistribution Under Climate Change are Required." *Science Advances* 7: eabe1110.

Taşkın, H., S. Büyükalaca, H. H. Doğan, S. A. Rehner, and K. O'Donnell. 2010. "A Multigene Molecular Phylogenetic Assessment of True Morels (*Morchella*) in Turkey." *Fungal Genetics and Biology* 47: 672–682.

Taşkın, H., S. Büyükalaca, K. Hansen, and K. O'Donnell. 2012. "Multilocus Phylogenetic Analysis of True Morels (*Morchella*) Reveals High Levels of Endemics in Turkey Relative to Other Regions of Europe." *Mycologia* 104: 446–461.

Thammanu, S., D. Marod, H. Han, et al. 2021. "The Influence of Environmental Factors on Species Composition and Distribution in a Community Forest in Northern Thailand." *Journal of Forestry Research* 32: 649–662.

Tietel, Z., and S. Masaphy. 2018. "True Morels (*Morchella*)—Nutritional and Phytochemical Composition, Health Benefits and Flavor: A Review." *Critical Reviews in Food Science and Nutrition* 58: 1888–1901.

Tsun-Shen, Y. 2001. "Species Diversity and Distribution Pattern of Seed Plants in China." *Biodiversity Science* 9: 393–398.

Urban, D. L. 2024. "Species Distribution Modeling." In *Landscape Ecology: A Task-Oriented Perspective*, 29–79. Springer Nature Switzerland. https://doi.org/10.1007/978-3-031-72251-6_2.

Urcádiz-Cázares, F. J., V. H. Cruz-Escalona, M. S. Peterson, et al. 2021. "Ecological Niche Modelling of Endemic Fish Within La Paz Bay: Implications for Conservation." *Journal for Nature Conservation* 60: 125981.

Valavi, R., G. Guillera-Arroita, J. J. Lahoz-Monfort, and J. Elith. 2022. "Predictive Performance of Presence-Only Species Distribution Models: A Benchmark Study with Reproducible Code." *Ecological Monographs* 92: e01486.

Vandermeer, J. H. 1972. "Niche Theory." *Annual Review of Ecology and Systematics* 3: 107–132.

Warren, D. L., R. E. Glor, and M. Turelli. 2008. "Environmental Niche Equivalency versus Conservatism: Quantitative Approaches to Niche Evolution." *Evolution* 62: 2868–2883.

Warren, D. L., and S. N. Seifert. 2011. "Ecological Niche Modeling in Maxent: The Importance of Model Complexity and the Performance of Model Selection Criteria." *Ecological Applications* 21: 335–342.

Wei, F. 2021. "Toward Post-2020 Global Biodiversity Conservation: Footprint and Direction in China." *Innovation* 2: 100175.

West, A. M., S. Kumar, T. Wakie, et al. 2015. "Using High-Resolution Future Climate Scenarios to Forecast Bromus Tectorum Invasion in Rocky Mountain National Park." *PLoS One* 10: e0117893.

Xiong, C., Q. Li, C. Chen, Z. Chen, and W. Huang. 2016. "Neuroprotective Effect of Crude Polysaccharide Isolated from the Fruiting Bodies of *Morchella importuna* Against H_2O_2-Induced PC12 Cell Cytotoxicity by Reducing Oxidative Stress." *Biomedicine & Pharmacotherapy* 83: 569–576.

Xu, Y., J. Tang, Y. Wang, et al. 2022. "Large-Scale Commercial Cultivation of Morels: Current State and Perspectives." *Applied Microbiology and Biotechnology* 106: 4401–4412.

Yu, F. M., R. S. Jayawardena, T. Luangharn, et al. 2024. "Species Diversity of Fungal Pathogens on Cultivated Mushrooms: A Case Study on Morels (*Morchella*, Pezizales." *Fungal Diversity* 125: 157–220.

Zhang, C., X. Shi, J. Zhang, Y. Zhang, and W. Wang. 2023. "Dynamics of Soil Microbiome Throughout the Cultivation Life Cycle of Morel (*Morchella sextelata*)." *Frontiers in Microbiology* 14: 979835.

Zhao, Q., Z. Z. Xu, Y. H. Cheng, et al. 2009. "Bionic Cultivation of *Morchella* Conica." *Southwest China Journal of Agricultural Sciences* 22: 1690–1693.

Zwiener, V. P., A. A. Padial, M. C. Marques, F. V. Faleiro, R. Loyola, and A. T. Peterson. 2017. "Planning for Conservation and Restoration under Climate and Land use Change in the Brazilian Atlantic Forest." *Diversity and Distributions* 23: 955–966.