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RESEARCH ARTICLE

Ecological niche differentiation and future distribution dynamics of threatened *Lagochilus* (Lamiaceae) species in Central Asian mountain–desert ecosystems

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Abstract

Climatic gradients play a fundamental role in shaping plant distributions in arid mountain ecosystems, yet the comparative niche dynamics of threatened xerophytic taxa remain insufficiently studied in Central Asia. In this study, ecological niche modelling using the Maxent algorithm was applied to assess climatic determinants, niche differentiation, and potential future distribution shifts of four *Lagochilus* species in Central Uzbekistan. A total of 85 georeferenced occurrence records were compiled and analyzed together with bioclimatic variables from the WorldClim database. Future projections were generated under the SSP245 scenario using the BCC-CSM2-MR climate model for the years 2050 and 2070. All models demonstrated high predictive performance (AUC > 0.94), indicating robust model reliability. Species distributions were primarily influenced by precipitation of the driest month

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and temperature seasonality, suggesting strong climatic control over realized ecological niches. Niche overlap analyses revealed generally low to moderate similarity among species, indicating substantial ecological differentiation despite partial spatial overlap. Future climate projections suggest contraction and fragmentation of suitable habitats for narrowly distributed taxa, whereas more widespread species are expected to maintain relatively stable suitability patterns. Mountain systems, particularly the Nuratau Range, remained climatically suitable across all scenarios and may function as important refugia for threatened species. Overall, the results indicate that ongoing climate change is likely to reinforce ecological divergence rather than promote niche convergence among *Lagochilus* species. These findings provide spatially explicit insights into climate-driven niche dynamics and offer valuable guidance for biodiversity conservation in arid mountain ecosystems.

Keywords
Climate change, conservation biogeography, ecological niche modelling, *Lagochilus*, MaxEnt, mountain ecosystems

Introduction

The genus *Lagochilus* Bunge (Lamiaceae) represents a taxonomically and ecologically distinctive lineage of perennial herbs and subshrubs predominantly distributed across the arid and semi-arid regions of Central and Western Asia. Species of this genus are typically associated with xerophytic habitats, including rocky slopes, gravelly and stony substrates, desert uplands, and foothill zones. These environments are characterized by chronic water limitation, strong temperature seasonality, and pronounced interannual climatic variability. Consequently, *Lagochilus* species exhibit a wide range of morphological, physiological, and ecological adaptations to drought stress and thermal extremes, which strongly shape their realised ecological niches (Bunge 1873; Kamelin 1973; Tojibaev et al. 2021; Mamadalieva et al. 2021; 2026).

At a biogeographical scale, the primary center of diversity of *Lagochilus* lies within the Irano–Turanian floristic region (Lavrenko and Sochava 1954; Takhtajan 1986), one of the major global centers of xerophytic plant diversification. Central Asia – particularly Uzbekistan and adjacent mountain systems – represents a core area of diversification for the flora, driven by complex geological history, pronounced topographic heterogeneity, and strong climatic gradients (Akhmedov et al. 2021; Cai et al. 2023; Ma et al. 2024; Kurbaniyazova et al. 2026). These factors have facilitated long-term isolation, ecological differentiation, and high levels of endemism.

Recent studies have highlighted the increasing vulnerability of endemic plant species in Central Asia under ongoing climate change, particularly in arid ecosystems. For example, Akhmedov et al. (2021) demonstrated elevated extinction risk for several endemic *Lagochilus* species under projected drying trends.

Within Uzbekistan, *Lagochilus* species exhibit highly uneven and fragmented distributions across desert plains, remnant uplands of the Kyzylkum Desert, and

mountain systems such as the Nuratau Range and the western Pamir–Alay foothills. These regions combine heterogeneous substrates, steep elevational gradients, and contrasting moisture regimes over short spatial scales, creating a mosaic of microhabitats. While such environmental complexity promotes ecological divergence and niche specialization, it also increases the vulnerability of narrowly distributed taxa to environmental disturbance and climate change.

The four species selected for the present study represent ecologically and geographically distinct elements of the *Lagochilus* flora of Uzbekistan. *Lagochilus inebrians* is a semishrub occurring from desert plains to foothills, where it inhabits clay deserts, piedmont plains, stony slopes, and gravelly substrates; its distribution includes the Nuratau and Aktau ranges, the Nuratau relict mountains, and Malguzar (Tojibaev et al. 2014; Tojibaev et al. 2021). In contrast, *L. olgae* is a rare endemic of the Nuratau Range, distributed in the Jizzakh, Navoi, and Samarkand regions and occurring mainly on stony and gravelly slopes of the lower and middle mountain zones (The Red Data Book of the Republic of Uzbekistan 2019; Tojibaev et al. 2021). *Lagochilus proskorjakovii* has a still narrower ecological and geographical distribution: it is an extremely rare, narrow endemic of the Nuratau Range, known from the Jizzakh and Samarkand regions, where it occurs mainly on dry stony and gravelly slopes of the middle mountain zone (The Red Data Book of the Republic of Uzbekistan 2019; Tojibaev et al. 2021). *Lagochilus vvedenskyi* is a rare endemic of the Kyzylkum Desert, restricted to the relict low mountains of Kuljuktau, Kingirtau, Bukantau, and Aktau in the Bukhara and Navoi regions, where it inhabits eroded slopes (The Red Data Book of the Republic of Uzbekistan 2019). Thus, although all four species are adapted to arid environments, they differ substantially in geographic range, habitat breadth, and elevational distribution, providing an appropriate comparative system for evaluating species-specific responses to future climate change.

Several *Lagochilus* species are characterized by small, spatially isolated populations and are listed in the Red Data Book of the Republic of Uzbekistan. Understanding their ecological requirements and potential responses to climate change is therefore critical for effective conservation planning.

Ecological niche modeling (ENM) provides a robust quantitative framework for linking species occurrence data with environmental variables, identifying climatically suitable habitats, and predicting potential distributional changes under alternative climate scenarios (Elith et al. 2011; Peterson et al. 2011; Araújo and Peterson 2012). Among ENM approaches, the Maximum Entropy algorithm (MaxEnt) is particularly effective for rare species with limited occurrence data due to its strong predictive performance under presence-only conditions (Phillips et al. 2006; Merow et al. 2013). Recent studies have increasingly applied MaxEnt-based ecological niche modeling to evaluate the impacts of climate change on plant species distributions and habitat suitability (Ren et al. 2025). These approaches are particularly useful for predicting species responses to future environmental changes and identifying areas of potential range contraction or expansion.

Applying ENM to *Lagochilus* is especially informative given the genus' ecological specialization and sensitivity to climatic extremes. Comparative niche modeling across multiple species allows assessment of ecological differentiation, niche overlap, and potential divergence under future climate change scenarios. Despite recent advances in phylogenetic and floristic studies, the ecological niche structure, climatic sensitivity, and future distribution dynamics of *Lagochilus* species in Central Asia remain insufficiently resolved.

The present study aims to (1) identify the main climatic determinants of species distributions, (2) quantify ecological niche differentiation and overlap among four threatened *Lagochilus* species, and (3) predict potential shifts in habitat suitability under future climate scenarios. By integrating ecological niche modeling within a comparative, multi-species framework, this study provides new insights into climate-driven niche dynamics and contributes to evidence-based conservation of endemic flora in arid mountain ecosystems.

Materials and methods

Occurrence data

A total of 85 georeferenced occurrence records representing four *Lagochilus* species were compiled for ecological niche modeling (Fig. 1). Occurrence data were obtained from verified herbarium collections (TASH, LE, MW), international biodiversity databases (GBIF, IPNI, Plantarium), published literature, and field surveys conducted between 2023 and 2025. Only taxonomically confirmed and accurately georeferenced records were retained following standard data quality protocols (Chapman 2005; Peterson et al. 2011).

Species-specific sample sizes were as follows: *Lagochilus olgae* (16 records), *L. proskorjakovii* (12), *L. vvedenskyi* (14), and *L. inebrians* (43). Duplicate records falling within the same environmental grid cell were removed to avoid spatial redundancy and pseudo-replication. After filtering, narrowly distributed species retained relatively small sample sizes (e.g., *L. proskorjakovii*), reflecting their true restricted geographic ranges rather than sampling deficiency.

Environmental predictors

Nineteen bioclimatic variables (BIO1–BIO19) were obtained from the WorldClim v2.1 database (Fick & Hijmans 2017) at 10 arc-minute spatial resolution (~18–20 km) for the baseline period 1970–2000. Elevation was also included as an additional predictor.

The use of a coarser spatial resolution was justified by the limited number of occurrence records for several species. This approach helps reduce model complex-

ity, minimize overfitting, and improve model generalization under small-sample conditions (Wisz et al. 2008).

Future climate projections for the 2050s (2041–2060) and 2070s (2061–2080) were derived from the CMIP6 global climate model BCC-CSM2-MR under the SSP2-4.5 (SSP245) scenario. SSP2-4.5 represents an intermediate "middle-of-the-road" pathway, with radiative forcing reaching approximately 4.5 W m^{-2} by 2100 (IPCC 2021). For the arid and mountainous regions of Central Asia, CMIP6 projections indicate continued warming accompanied by changes in precipitation regimes and increasing hydroclimatic variability, while mountain regions are additionally expected to experience substantial changes in snow cover (Lalande et al. 2021; Cao et al. 2023). These changes are particularly relevant to arid and montane plant species because shifts in temperature and water availability may alter the spatial and elevational distribution of climatically suitable habitats. The BCC-CSM2-MR model was selected for the present study to generate future bioclimatic projections under SSP2-4.5.

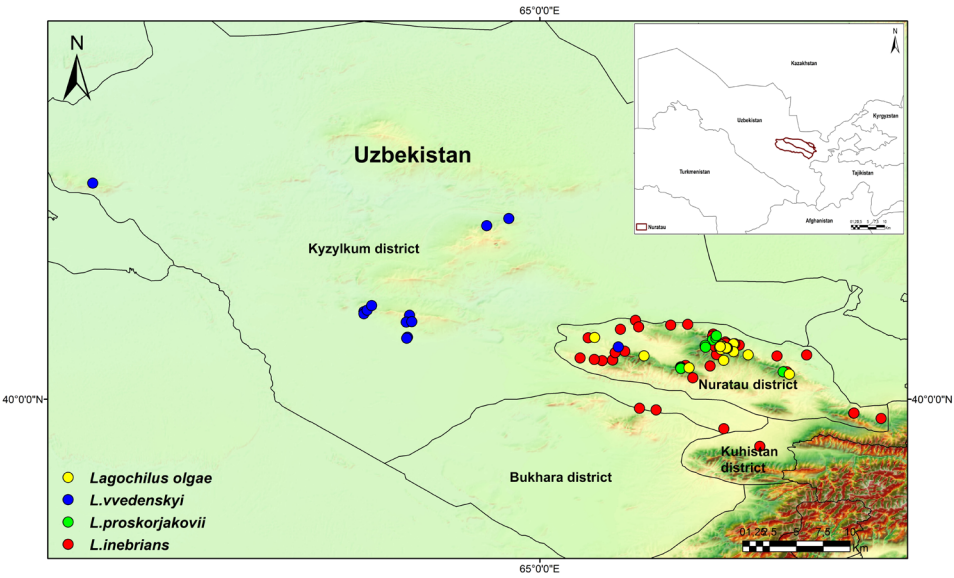


Figure 1. Geographic distribution of occurrence records of four *Lagochilus* species in Uzbekistan and adjacent areas: *L. olgae* (yellow), *L. vvedenskyi* (blue), *L. proskorjakovii* (green), and *L. inebrians* (red). Occurrence data were compiled from herbarium collections (TASH, LE), field surveys, and online biodiversity databases (GBIF and iNaturalist). Shaded relief is shown to illustrate the topographic heterogeneity of the study area. The boundaries and names of the Kyzylkum, Nuratau, Bukhara, and Kuhistan floristic districts follow the botanical-geographical regionalization of the Flora of Uzbekistan. The inset shows the location of the study area within Central Asia.

All environmental layers were clipped to the study region using ArcGIS 10.8.1 and converted to ASCII format for compatibility with MaxEnt.

To reduce multicollinearity among predictors, Pearson correlation analysis was conducted following Dormann et al. (2013). Highly correlated variables ($|r| \geq 0.8$) were examined, and ecologically less meaningful predictors were removed. This procedure ensured retention of independent climatic gradients associated with drought intensity, precipitation seasonality, and temperature extremes, which are key determinants of plant distributions in arid Central Asia.

The initial set of environmental predictors comprised the 19 standard bioclimatic variables (BIO1–BIO19) obtained from WorldClim. The full names and definitions of these variables are provided in Table 1.

Table 1. Bioclimatic variables used in the initial environmental dataset

Variable	Description
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range
BIO3	Isothermality
BIO4	Temperature Seasonality
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

MaxEnt modeling procedure

Species distribution models were developed using MaxEnt version 3.4.4 (Phillips et al. 2006; Phillips & Dudík 2008). Occurrence data and environmental layers were used to generate continuous habitat suitability maps under present (1970–2000) and future climate scenarios.

To minimize overfitting, particularly for species with limited occurrence records, models were run using the linear feature class (L) only. Restricting feature classes is recommended for small-sample datasets to reduce model complexity and prevent spurious response curves (Merow et al. 2013). The default regularization multiplier ($\beta = 1$) was retained.

Output format was set to logistic, and the maximum number of iterations was set to 500. The algorithm converged before reaching the maximum iteration limit.

For each species, 75% of occurrence records were used for model training and 25% for testing. Ten replicate runs were performed using random seed partitioning, and 10,000 background points were used to characterize environmental space.

Final habitat suitability maps were generated by averaging predictions across replicate runs to reduce model uncertainty and improve robustness. To convert continuous suitability outputs into binary presence–absence maps, the maximum training sensitivity plus specificity threshold was applied.

Model evaluation

Model performance was assessed using the Area Under the Receiver Operating Characteristic Curve (AUC). Training and test AUC values were averaged across replicates. Models with AUC > 0.9 were interpreted as having excellent discriminatory capacity.

For narrowly distributed species (e.g., *L. proskorjakovii*), small test sample sizes may result in unstable standard deviation estimates. Therefore, model reliability was evaluated not only based on AUC values but also by assessing ecological plausibility of response curves and jackknife tests of variable importance.

Although small sample sizes may potentially inflate AUC values, previous studies have shown that MaxEnt performs robustly under limited presence data when model complexity is appropriately constrained (Phillips et al. 2006; Merow et al. 2013).

Niche overlap analysis

Ecological niche overlap among species was quantified using Schoener's D and Hellinger's I indices (Warren et al. 2008). Habitat suitability rasters generated by MaxEnt were normalized and compared across shared geographic space.

Overlap calculations were implemented in Python using raster-based array operations (NumPy library). Suitability grids were converted to probability distributions, and overlap indices were computed following standard formulas. Schoener's D ranges from 0 (no overlap) to 1 (complete overlap), while Hellinger's I similarly quantifies environmental similarity in geographic space.

Niche overlap was evaluated under both present and future climate scenarios to assess temporal dynamics of ecological similarity.

Map classification and visualization

Continuous habitat suitability outputs were reclassified into four categories (unsuitable, low, moderate, and high suitability) using threshold-based methods following Liu et al. (2005). Raster processing and cartographic visualization were conducted in ArcGIS 10.8.1. Final figures were exported at 360 dpi resolution to ensure publication-quality output.

Results

Spatial distribution and modeled current suitability

After spatial filtering at a 10 arc-minute resolution, a total of 85 validated occurrence records were retained for modeling. The four *Lagochilus* species exhibited distinct spatial patterns across Central Uzbekistan, as reflected in the modeled suitability maps (Figs 2A–B, 3A–B).

Lagochilus olgae and *L. proskorjakovii* were largely confined to the Nuratau Mountains, forming compact and fragmented clusters of high suitability, indicative of strongly restricted montane distributions. In contrast, *L. vvedenskyi* and particularly *L. inebrians* exhibited broader spatial extents, extending toward the Kyzylkum Desert margins, the Bukhara region, and foothill zones of the Kuhistan area (Fig. 3A–B).

These spatial patterns indicate substantial differences in the geographic extent and configuration of modeled suitable habitats among the four species.

Model performance and predictive accuracy

All MaxEnt models demonstrated high predictive performance (Table 2), with mean training AUC values ranging from 0.94 to 0.985 and mean test AUC values ranging from 0.94 to 0.989. These results indicate strong discrimination between suitable and unsuitable habitats.

For *L. proskorjakovii*, training AUC reached 0.985 and test AUC 0.989. However, due to the limited number of occurrence points, standard deviation estimates were unstable. Therefore, model robustness was additionally assessed using response curves and jackknife tests (Suppl. material 1: Figs S1–S6), which provided additional information on variable responses and model behavior.

Contribution of environmental variables

The importance of environmental predictors varied among species (Table 3; Suppl. material 1: Figs S1–S2), indicating species-specific climatic constraints.

Table 2. Performance statistics of MaxEnt models for four *Lagochilus* species under current climatic conditions (1970–2000)

Species	Training AUC (mean ± SD)	Test AUC (mean ± SD)	No. of occurrence records
L. olgae	0.96 ± 0.02	0.95 ± 0.03	16
L. proskorjakovii	0.985 ± NA	0.989 ±NA	12
L. vvedenskyi	0.94 ± 0.04	0.94 ± 0.05	14
L. inebrians	0.97 ± 0.01	0.96 ± 0.02	43

Note: Standard deviation is unstable for *L. proskorjakovii* due to small test sample size.

Table 3. Relative contribution (%) of the most influential bioclimatic variables in MaxEnt models

Species	BIO14	BIO12	BIO4	BIO6	BIO1
L. olgae	12.3	9.1	48.7	8.2	6.5
L. proskorjakovii	21.4	17.2	9.8	15.1	7.4
L. vvedenskyi	35.6	10.2	7.3	6.4	5.1
L. inebrians	41.8	22.5	6.2	4.3	3.7

For *L. inebrians*, precipitation of the driest month (BIO14) and annual precipitation (BIO12) were dominant predictors, highlighting sensitivity to drought conditions. In *L. olgae*, temperature seasonality (BIO4) contributed substantially, indicating adaptation to environments with strong thermal variability.

L. vvedenskyi showed the strongest contribution from BIO14 (35.6%), whereas *L. proskorjakovii* showed a more distributed contribution among BIO14 (21.4%), BIO12 (17.2%), and BIO6 (15.1%).

Habitat suitability under future climate scenarios

Under the SSP245 scenario, projections revealed species-specific and temporally dynamic responses (Figs 2C–F, 3C–F).

In contrast, CD reveals a non-uniform sampling effort across the study area. Areas of high sampling intensity are primarily associated with accessible locations, while remote and less accessible zones remain comparatively under-sampled. Notably, spatial patterns of SR and CD do not fully coincide, indicating potential sampling bias and suggesting that some floristically rich areas may remain insufficiently documented.

By 2050, all four species showed increases in total modeled suitable habitat area, although the magnitude and spatial configuration of these changes differed substantially among species. *Lagochilus olgae* showed a progressive increase in suitable

area, whereas *L. proskorjakovii* and *L. vvedenskyi* exhibited particularly pronounced expansions. *Lagochilus inebrians* also showed a marked increase in suitable habitat by 2050.

By 2070, strongly divergent trajectories emerged. Suitable habitat for *L. olgae* continued to increase, whereas the pronounced mid-century expansions of *L. proskorjakovii* and *L. vvedenskyi* were followed by substantial contractions. *Lagochilus inebrians* also showed a reversal of its 2050 expansion, returning to approximately its current modeled suitable area by 2070.

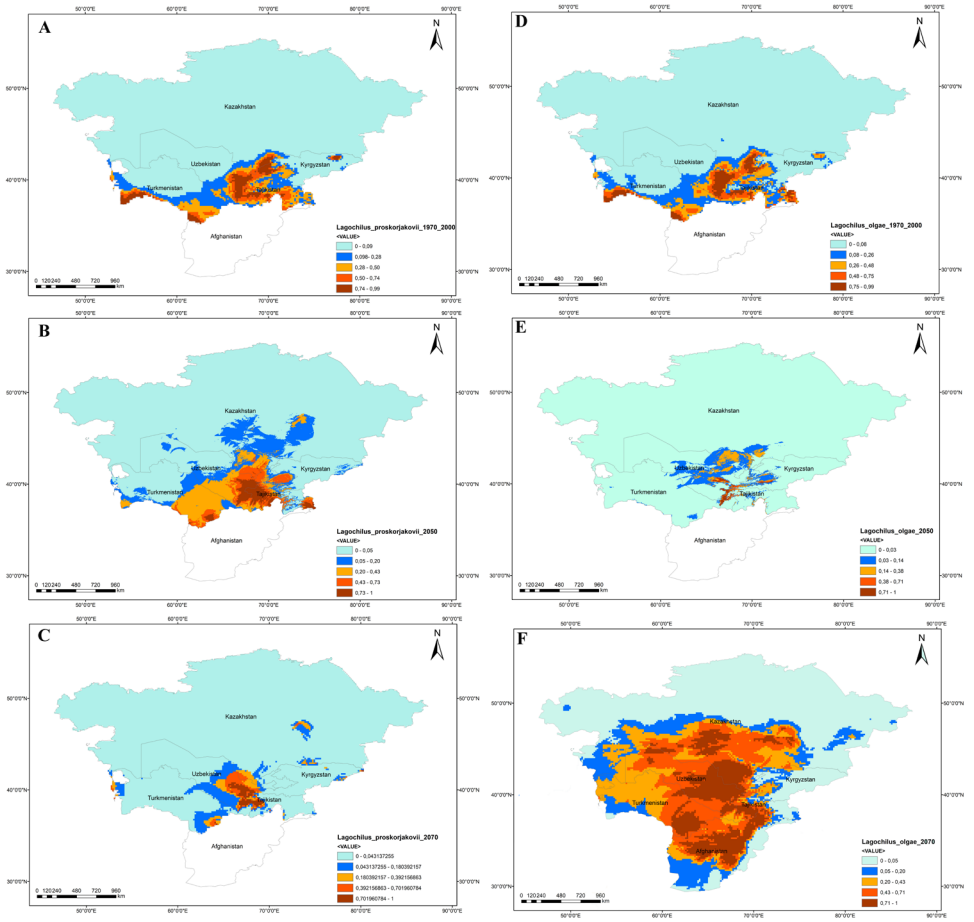


Figure 2. Modeled habitat suitability of two narrowly distributed endemic *Lagochilus* species under present and future climate scenarios (SSP245). (A–C) *L. proskorjakovii* under current climate (1970–2000), 2050 (2041–2060), and 2070 (2061–2080), respectively. (D–F) *L. olgae* under the same time periods. Habitat suitability is shown as a continuous gradient from low (blue) to high (red). Projections are based on the BCC-CSM2-MR global climate model.

Quantitative analysis of suitable habitat area (Suppl. material 1: Fig. S7) confirmed these contrasting temporal patterns. For *L. olgae*, modeled suitable area increased from 549,828 km² under current conditions to approximately 1.2 million km² in 2050 and 2.6 million km² in 2070. L*agochilus proskorjakovii* increased from 614,628 km² to approximately 9.9 million km² by 2050, followed by a decline to 187,272 km² by 2070. Similarly, *L. vvedenskyi* increased from 994,032 km² to approximately 17.5 million km² in 2050 before declining to 742,932 km² in 2070. *Lagochilus inebrians* increased from 93,960 km² to 918,864 km² in 2050 and subsequently returned to 94,932 km² by 2070.

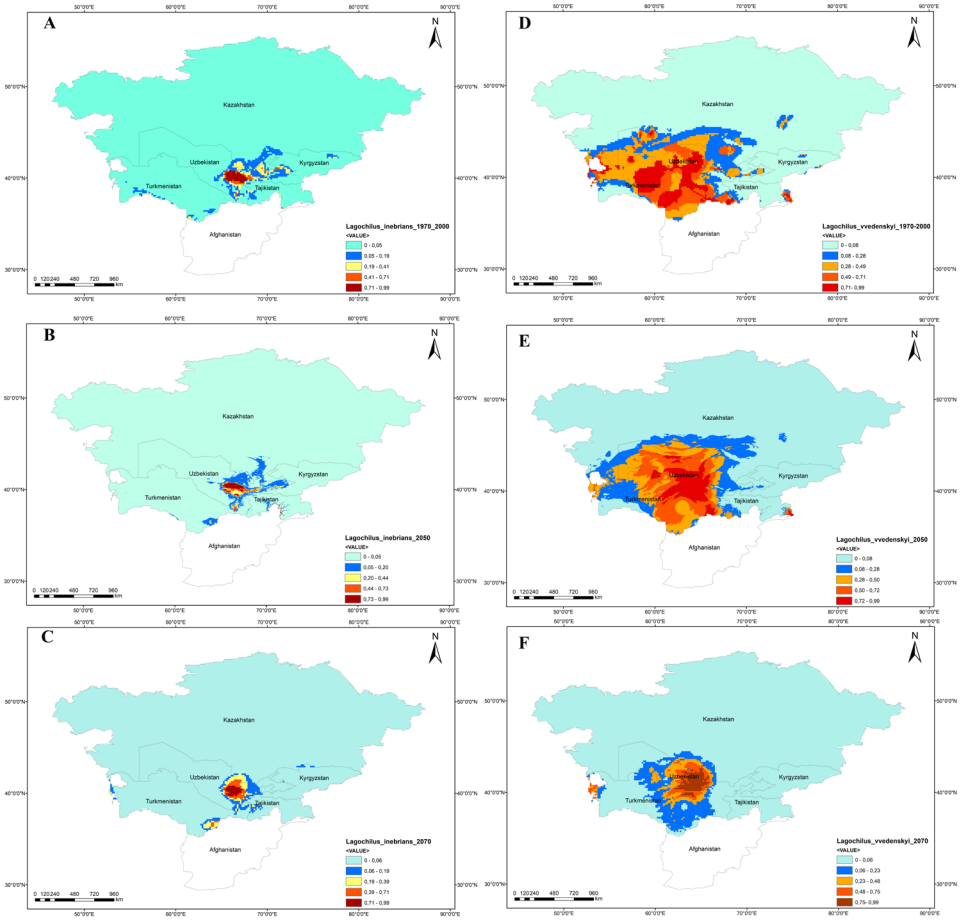


Figure 3. Modeled habitat suitability of widespread *Lagochilus* species under present and future climate scenarios (SSP245). (A–C) *L. inebrians* under current climate (1970–2000), 2050 (2041–2060), and 2070 (2061–2080), respectively. (D–F) *L. vvedenskyi* under the same time periods. Habitat suitability is shown as a continuous gradient from low (blue) to high (red). Projections are based on the BCC-CSM2-MR global climate model.

Ecological niche overlap and temporal dynamics

Niche overlap analysis revealed generally low to moderate similarity among species pairs (Table 4). The highest overlap occurred between *L. inebrians* and *L. olgae*, whereas *L. vvedenskyi* and *L. proskorjakovii* showed the lowest similarity, indicating strong ecological differentiation.

Temporal comparisons (Table 5) showed divergent responses under climate change. *L. vvedenskyi* exhibited the strongest decline in niche similarity by 2050, indicating substantial environmental shifts. Temporal niche-overlap comparisons (Table 5) revealed substantial differences between current and future suitability patterns. *L. vvedenskyi* showed the lowest current-to-future overlap in 2050 (D = 0.109), followed by *L. proskorjakovii* (D = 0.192) and L. olgae (D = 0.210), whereas L. inebrians retained comparatively higher overlap (D = 0.340). By 2070, overlap values increased to 0.355 for L. olgae, 0.310 for *L. proskorjakovii*, 0.180 for *L. vvedenskyi*, and 0.360 for *L. inebrians*.

Overall, the projections revealed strongly species-specific temporal changes in the extent and spatial configuration of climatically suitable habitats.

Table 4. Pairwise niche overlap (Schoener's D / Hellinger's I) under current climate

Species	*L. olgae*	*L. proskorjakovii*	*L. vvedenskyi*	*L. inebrians*
L. olgae	–	–	–	0.428 / 0.466
L. proskorjakovii	–	–	0.311 / 0.334	–
L. vvedenskyi	–	0.311 / 0.334	–	–
L. inebrians	0.428 / 0.466	–	–	–

Table 5. Temporal niche overlap (Schoener's D) between present and future projections under SSP245 scenario

Species	2050 D	2070 D
L. olgae	0.210	0.355
L. vvedenskyi	0.109	0.180
L. inebrians	0.340	0.360
L. proskorjakovii	0.192	0.310

Discussion

Climatic control of *Lagochilus* distributions in arid Central Asia

Our results demonstrate that the distribution of *Lagochilus* species in Central Uzbekistan is strongly determined by climatic gradients, particularly precipitation of the driest month (BIO14), annual precipitation (BIO12), and temperature seasonal-

ity (BIO4). These findings are consistent with previous studies indicating that water availability and temperature variability are primary determinants of plant distributions in arid and semi-arid ecosystems of Central Asia (Breckle 2002; Lioubimtseva and Henebry, 2009; Chen et al. 2008; Liu et al. 2019).

Species-specific responses revealed clear ecological differentiation. The dominance of BIO14 in *L. inebrians* and *L. vvedenskyi* underscores the importance of dry-season precipitation in shaping their modeled climatic niches. The importance of water availability for the distribution and vulnerability of *Lagochilus* species in arid Central Asia is also consistent with previous species-specific assessments under a drying climate (Akhmedov et al. 2021). In contrast, the high contribution of temperature seasonality (BIO4) in *L. olgae* indicates adaptation to environments characterized by strong thermal contrasts typical of mid-elevation mountain systems. *L. olgae* demonstrated temporary niche displacement followed by recovery, while *L. inebrians* showed moderate decline with partial stabilization.

For the narrowly distributed *L. proskorjakovii*, the combined importance of precipitation and minimum temperature variables suggests dependence on climatically buffered microrefugia. Mountain refugial dynamics have been widely recognized as key drivers of persistence and endemism in Central Asian floras (Manafzadeh et al. 2014; Nowak et al. 2016; Ma et al. 2024), as well as in the neighboring Irano-Anatolian region (Noroozi et al. 2018). Moreover, climatic stability in these regions has been linked to high concentrations of endemic plant species (Harrison and Noss 2017; Cai et al. 2023). On a global scale, the Irano-Turanian floristic region, including the mountains of Central Asia, is recognized as one of the major hotspots of seed-plant phylogenetic endemism among mainland regions (Cai et al. 2023). The accumulation of endemic species in mountainous areas can be explained by relatively low climate change velocity during the Quaternary period (Sandel et al. 2011).

Model reliability under limited occurrence data

Although small sample sizes may potentially inflate AUC values, particularly in presence-only modeling (Lobo et al. 2008), the close agreement between training and test AUC values across species indicates limited overfitting. Moreover, restricting feature classes to linear functions and using coarser-resolution predictors helped constrain model complexity, which is recommended for small-sample MaxEnt applications (Wisz et al. 2008; Merow et al. 2013).

The ecological plausibility of response curves and consistent jackknife patterns further support model robustness. Recent studies have demonstrated that MaxEnt can produce reliable predictions even with limited presence data when appropriate parameterization is applied (Shcheglovitova and Anderson 2013; Morales et al. 2017). Thus, our modeling framework provides a credible representation of climatic suitability patterns.

Ecological segregation and niche differentiation

Despite partial geographic overlap, niche overlap indices revealed generally low to moderate environmental similarity among species. The highest similarity between *L. inebrians* and *L. olgae* likely reflects shared montane climatic envelopes, whereas low overlap between *L. vvedenskyi* and *L. proskorjakovii* indicates pronounced ecological differentiation.

Such niche partitioning is common among closely related taxa in arid mountain systems and may reflect adaptive divergence along moisture and temperature gradients (Warren et al. 2008; Peterson et al. 2011). In drylands it can be connected with diverse water-use strategies and root plasticities (Li et al. 2025). Perennial herbaceous plants of the genus *Dysosma* growing in rather moist conditions also showed ecological niche differentiation caused by high heterogeneity in niche relationships (Chen et al. 2011). In our case increasing ecological divergence under future climate projections suggests that climatic shifts may reinforce environmental segregation rather than homogenize species niches. Detailed analyses including ecological niche modeling, multivariate analyses, hypervolume-based quantifications, and density overlap metrics for three mountainous *Dianthus* species from Khorassan–Kopet Dagh floristic region revealed significant ecological niche differentiation among the studied taxa (Behroozian 2026). At broader spatial and temporal scales, plant diversity and endemism patterns in drylands are strongly influenced by both contemporary environmental gradients and historical climate dynamics (Liu et al. 2019; Sandel et al. 2011). Regions characterized by long-term climatic stability often act as refugia, maintaining high levels of endemism and persistence of specialized taxa (Harrison and Noss 2017; Baumgartner et al. 2018; Sandel et al. 2017). Climate projections indicate increasing aridity and temperature variability across high mountains of Asia during the 21st century (Lalande et al. 2021), which may lead to habitat contraction, fragmentation, and shifts toward climatically stable refugial areas.

Future climate projections and refugial stability

Under the SSP245 scenario, narrowly distributed taxa exhibited contraction and fragmentation of highly suitable habitats by 2050. This pattern aligns with broader projections indicating heightened vulnerability of mountain endemics to warming and increasing aridity (Thuiller et al. 2005; Pauli et al. 2012; Chen et al. 2011).

However, the persistence of suitable habitats within the Nuratau Mountains across all scenarios highlights the potential role of this mountain system as a climatic refugium. Mountain regions in Central Asia have been identified as long-term stability zones that buffer climatic extremes and support endemic richness (Manafzadeh et al. 2014; Nowak et al. 2016).

Global-scale analyses indicate that regions with low historical climate change velocity tend to maintain long-term climatic stability and serve as refugia for endemic species (Sandel et al. 2017).

Projected suitable habitat areas revealed pronounced species-specific and temporally non-linear responses to future climate change. *Lagochilus olgae* showed the clearest sustained expansion, with suitable habitat increasing from approximately 549,828 km² under current conditions to about 1.2 million km² by 2050 and 2.6 million km² by 2070, representing a nearly fivefold increase relative to the current modeled extent. In contrast, *L. proskorjakovii* and *L. vvedenskyi* showed strong mid-century expansion followed by pronounced contraction by 2070. Suitable habitat for *L. proskorjakovii* increased from 614,628 km² to approximately 9.9 million km² by 2050, but subsequently declined to 187,272 km² by 2070. Similarly, *L. vvedenskyi* increased from 994,032 km² to approximately 17.5 million km² by 2050 before declining to 742,932 km² by 2070. *Lagochilus inebrians* also exhibited a transient response, increasing from 93,960 km² under current conditions to 918,864 km² in 2050, followed by a return to near-current levels (94,932 km²) by 2070 (Suppl. material 1: Fig. S7).

The contrasting trajectories of *L. olgae* and *L. proskorjakovii* can be interpreted in relation to differences in their modeled climatic niches and present ecological distributions. For *L. olgae*, temperature seasonality (BIO4) was by far the dominant predictor, accounting for 48.7% of model contribution, whereas precipitation of the driest month (BIO14) and annual precipitation (BIO12) contributed 12.3% and 9.1%, respectively. The species occurs on stony and gravelly slopes of the lower and middle mountain zones of the Nuratau Range. The progressive expansion predicted for *L. olgae* therefore suggests that climatic conditions analogous to its current temperature-seasonality envelope may become available across a larger geographic area under future climate conditions. Nevertheless, this represents an expansion of modeled climatic suitability rather than evidence of actual range expansion, because dispersal limitations, substrate availability, biotic interactions, and anthropogenic pressures were not explicitly incorporated into the models.

In contrast, *L. proskorjakovii* showed a more distributed dependence on moisture and temperature variables, particularly BIO14 (21.4%), BIO12 (17.2%), and minimum temperature of the coldest month (BIO6; 15.1%). This extremely rare narrow endemic is restricted mainly to dry, stony and gravelly slopes of the middle mountain zone of the Nuratau Range. Its strong expansion by 2050 followed by severe contraction by 2070 suggests that mid-century climatic conditions may temporarily increase the geographic extent of analogous climatic environments, whereas later-century conditions increasingly depart from the climatic envelope represented by its present occurrences. Its narrow geographic distribution may further constrain its ability to track such rapidly shifting suitable conditions.

A similar transient pattern was observed for *L. vvedenskyi*, for which precipitation of the driest month (BIO14; 35.6%) was the strongest predictor. As a rare Kyzylkum endemic associated with eroded slopes of isolated low mountains, the

species occupies geographically fragmented habitats, potentially limiting its capacity to exploit the extensive climatic suitability projected for 2050. *Lagochilus inebrians*, despite an even stronger dependence on BIO14 (41.8%) and BIO12 (22.5%), currently occupies a broader range of habitats, including clayey and stony slopes, piedmont plains, gravelly substrates, and foothills. Its return to near-current suitable area by 2070, following the strong 2050 expansion, indicates substantial temporal redistribution rather than simple long-term stability.

Overall, these results demonstrate that the four *Lagochilus* species are unlikely to respond uniformly to climate change. Their contrasting projections are associated with differences in the climatic variables defining their modeled niches, their geographic restriction, and their present habitat distributions. Particularly important is the distinction between the sustained expansion predicted for *L. olgae* and the transient mid-century expansion followed by late-century contraction predicted for *L. proskorjakovii* and *L. vvedenskyi*. These species-specific trajectories emphasize that projected increases in climatically suitable area should not automatically be interpreted as realized range expansion, especially for narrow endemics with restricted distributions and potentially limited dispersal opportunities.

Conservation implications

The projected fragmentation and upward shifts of suitable habitats emphasize the importance of mountain ecosystems for biodiversity conservation. Conservation strategies should prioritize climatically stable refugial zones within the Nuratau system and maintain connectivity between fragmented habitat patches.

Species with narrow environmental niches, such as *L. proskorjakovii*, appear particularly vulnerable to increasing aridity and warming. Integrating ecological niche modeling with conservation planning frameworks can improve the identification of priority conservation areas under future climate scenarios (Araújo et al. 2011; Pacifici et al. 2015).

Conclusion

This study provides a comparative ecological niche modeling analysis of four *Lagochilus* species in Central Uzbekistan under current and future climate scenarios. The results demonstrate that species distributions are strongly influenced by climatic factors, particularly precipitation of the driest month and temperature seasonality, confirming the dominant role of water availability and thermal variability in shaping plant niches in arid environments.

Despite partial geographic overlap, the studied species exhibit clear ecological differentiation, indicating distinct climatic preferences and niche segregation. Future projections under the SSP245 scenario suggest contrasting responses among taxa. *Lagochilus olgae* shows a substantial expansion of suitable habitat, whereas *L.*

proskorjakovii and *L. vvedenskyi* display peak suitability in 2050 followed by marked declines by 2070, reflecting potential habitat instability. In contrast, *L. inebrians* remains relatively stable, suggesting broader ecological tolerance to changing climatic conditions.

The persistence of climatically suitable areas within the Nuratau Mountains across all scenarios highlights the importance of this region as a potential long-term refugium for endemic and range-restricted species. These findings emphasize that narrowly distributed taxa are more vulnerable to climate change, while widespread species may possess greater adaptive capacity.

Overall, climate change is likely to increase ecological divergence among *Lagochilus* species rather than promote niche convergence. From a conservation perspective, priority should be given to preserving climatically stable mountain habitats and maintaining landscape connectivity to support species persistence under future environmental change.

Further research integrating genetic data, dispersal mechanisms, and population dynamics will be essential for improving predictions of species responses and for developing effective conservation strategies for the endemic flora of Central Asia.

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Supplementary material 1

Figure S1. Jackknife test of variable importance for the MaxEnt models of *Lagochilus inebrians* and *Lagochilus proskorjakovii*

Figure S2. Jackknife test of variable importance for the MaxEnt models of *Lagochilus olgae* and *Lagochilus vvedenskyi*

Figure S3. Response curves of key environmental variables and model performance for *Lagochilus inebrians* under current climatic conditions (1970–2000)
Figure S4. Response curves of key environmental variables and model performance for *Lagochilus olgae* under current climatic conditions (1970–2000)
Figure S5. Response curves of key environmental variables and model performance for *Lagochilus proskorjakovii* under current climatic conditions (1970–2000)
Figure S6. Response curves of key environmental variables and model performance for *Lagochilus vvedenskyi* under current climatic conditions (1970–2000)
Figure S7. Projected changes in suitable habitat area for four *Lagochilus* species under current (1970–2000) and future climatic conditions (2050 and 2070; SSP245 scenario)

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