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Impacts of permafrost degradation on the richness of human-used plant species in the High Mountain Asia

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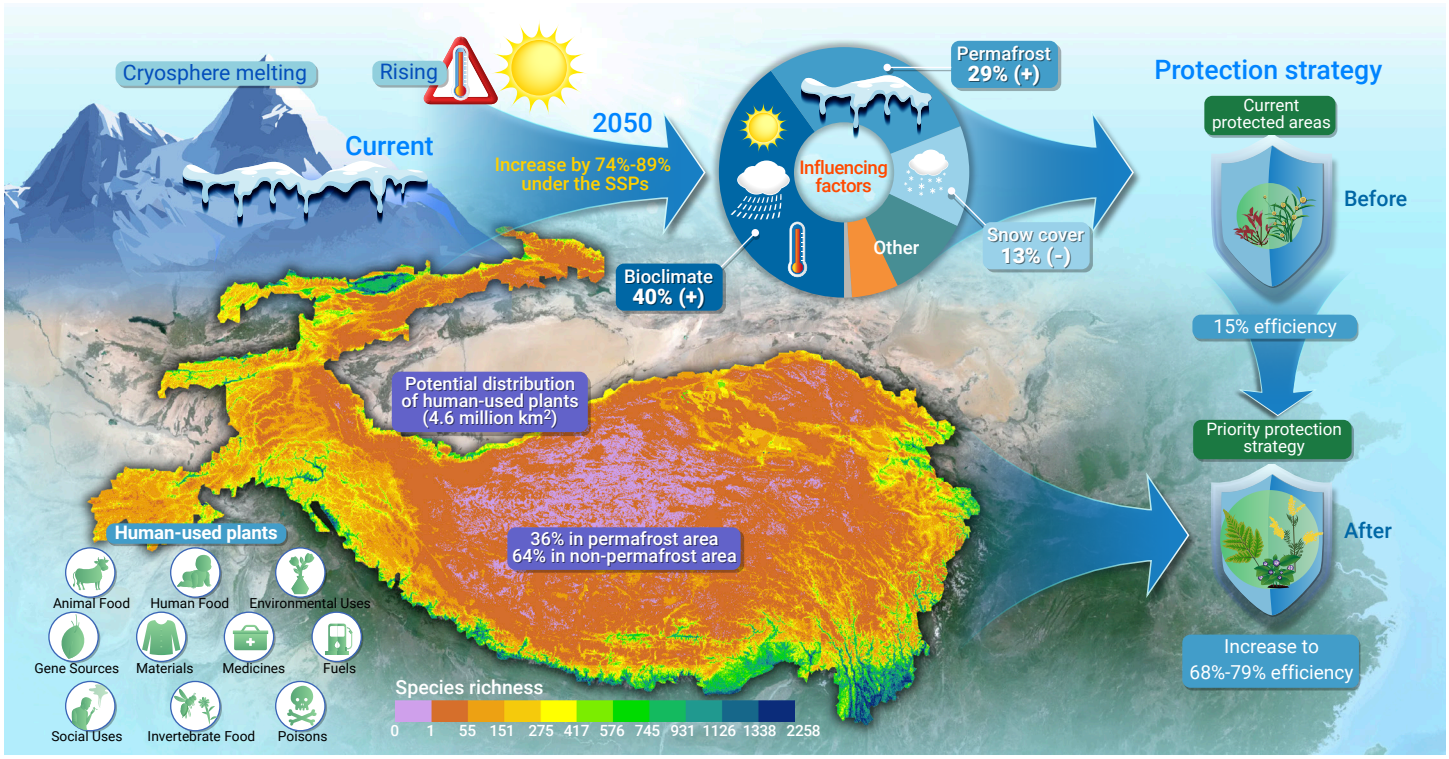
GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Approximately 36% of human-used plant species richness is distributed in permafrost areas.
- An obvious elevation-dependent pattern is found in future changes of plant species richness.
- Effects of bioclimatic, permafrost and snow cover on the plant richness are 40%, 29% and 13%, respectively.
- Our priority strategies will increase the conservation efficiency to 68%-79%.

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Climate warming has accelerated the melting of cryosphere, substantially affecting the plants biodiversity in global cold regions. However, the spatiotemporal patterns of human-used plants and their responses to climate change remain uncertain. Here, by synthesizing 3,716 investigated plant species from ten use categories in the High Mountain Asia, we show that the potential distribution area of human-used plants species richness is 4.6 ± 0.2 million km^2, of which 36% is located in permafrost areas. The change in plant species richness shows an obvious elevation-dependent pattern, and this is most obvious in permafrost regions. The area of regions with increasing species richness of human-used plants is projected to increase by 74%-89% by 2050 under the Shared Socioeconomic Pathways. Among them, bioclimatic factors, permafrost and snow cover have the greatest impacts on species richness, with respective standardized effects of 40%, 29% and 13%. Based on the conservation gaps of human-used plants, our proposed priority protection strategies will increase conservation efficiency to 68%-79% relative to current natural reserves. These findings highlight the cryosphere melting substantially influences plant biodiversity, and underscore the urgent need to integrate these impacts into the Convention on Biological Diversity.

INTRODUCTION

Biodiversity provides essential goods and services, such as food, medicine, materials, and fuel that sustain human life and well-being, with human-used plant species being crucial for social benefits and sustainable development.[1,2] Currently, biodiversity loss remains one of the most serious environmental issues under climate change.[3] Recent global biodiversity assessments predict that up to one million species or more may face the risk of extinction in the future.[4] Notably, changes in the cryosphere also have far-reaching implications for plant diversity and local livelihoods.[5,6] High-altitude regions are undergoing rapid climatic warming, which is accelerating the melting of cryosphere, as evidenced by glacier retreat, diminished snow cover and permafrost degradation (e.g., active layer thickening).[7,8] However, the changes and drivers of human-used plant species in high-altitude regions remain poorly understood.

The plant species abundance and composition have substantial changes in the high-altitude ecosystems (very high confidence), partly due to the retreat of cryosphere (high confidence).[6] The habitats of plant species are also influenced by the thawing of permafrost (medium confidence), and snow cover (high confidence). Specifically, the impact of permafrost degradation is gaining recognition for its significant role in plant biodiversity by altering soil water-heat balance.[9] On the one hand, permafrost thaw can decrease soil surface moisture content due to active layer deepening, thereby influencing vegetation growth.[10] On the other hand, permafrost degradation promotes the release of nutrients, which enhances plant root depth expansion, consequently increasing human-used plant species richness.[11,12] In addition, reduced snow cover has a negative impact on the reproductive fitness of some plant species (high confidence).[13] However, based on the site-scale monitoring efforts, litter is known about the overall changes in human-used plant species richness. Thus, there is a growing urgent need to systematically explore the impact of cryosphere retreat on the species richness of human-used plants.

Additionally, it is crucial for understanding the trend of elevational gradient changes in plant species richness. This is because climate warming occurs more rapidly at higher elevations, and this phenomenon is known as elevation-dependent warming.[14] This uneven warming has reshapes the cryospheric conditions, especially the stability of permafrost, thereby generating an elevation-dependent degradation pattern.[15] Taken together, climate and permafrost affect soil habitats, thereby shaping the elevational patterns of plant species richness. In recent years, the elevational gradient distribution of species richness have drawn increasing attention.[16] In mountain ecosystems, species richness presents two pattens: one is that it decreases with the increase of altitude, and the other is that it peaks in the middle of altitude.[17] However, it remains unclear how climate change and permafrost dynamics affect the elevational gradient of human-used plants.

Notably, although protection strategies for plant biodiversity have attracted global attention,[18,19] these strategies are seldom implemented in high-altitude cold regions due to several constraints, such as the lack of quantified changes in human-used plants, in some case, limited awareness of policy-making and local communities. Particularly, previous natural reserves have not adequately considered the impact of current rapidly melting of cryosphere as well as the trends in altitudinal gradient. Therefore, it is essential to identify priority protection strategies for human-used plant species by integrating cryosphere changes, further contributing to the goals of the Convention on Biological Diversity.

High Mountain Asia (HMA) including the Tibetan Plateau and the surrounding high Asian mountain ranges, is a vital water source for nearly 2 billion people.[20] This region is warming at a rate approximately double the global average.[21] The permafrost covers approximately 45% of the HMA region and is undergoing severe degradation,[22] with the mean annual ground temperature (MAGT) rising at a rate of 0.20–0.34°C/10a, active layer thickness (ALT) increasing at 19.5 cm/10a,[23,24] and permafrost area declining at a rate of 0.066 × 10^6 km^2/10a over the past 30 years.[25] At lower elevations, there is high confidence that the duration of snow cover has generally declined with great spatial variations since the middle of the 20th century. At higher elevation, snow cover trends are generally insignificant (medium confidence).[6] Notably, the diversification of alpine species has markedly accelerated during both orogenesis and the intensification of the Asian monsoon.[26] Currently, this region supports 19,485 species of wild vascular plants across 2,535 genera in 282 families.[27] There is a pressing need to understand their responses to cryosphere retreat and corresponding human intervention strategies.

This study aims to address the following questions: (1) What are the spatial patterns and underlying drivers of human-used plant diversity across the HMA region? (2) What are the existing conservation gaps regarding human-used plant species, and in what ways can protection strategies be optimized to maximize their effectiveness? To address the questions, we first synthesized data on 3,716 human-used plant species across 10 categories in the HMA region, including human food, vertebrate food, invertebrate food, materials, fuel, social uses, poisons, medicines, environmental uses, and genetic resources (Figure 1). Based on the actual distribution of each species, we integrated 36 environmental variables, such as bioclimate, permafrost, snow,

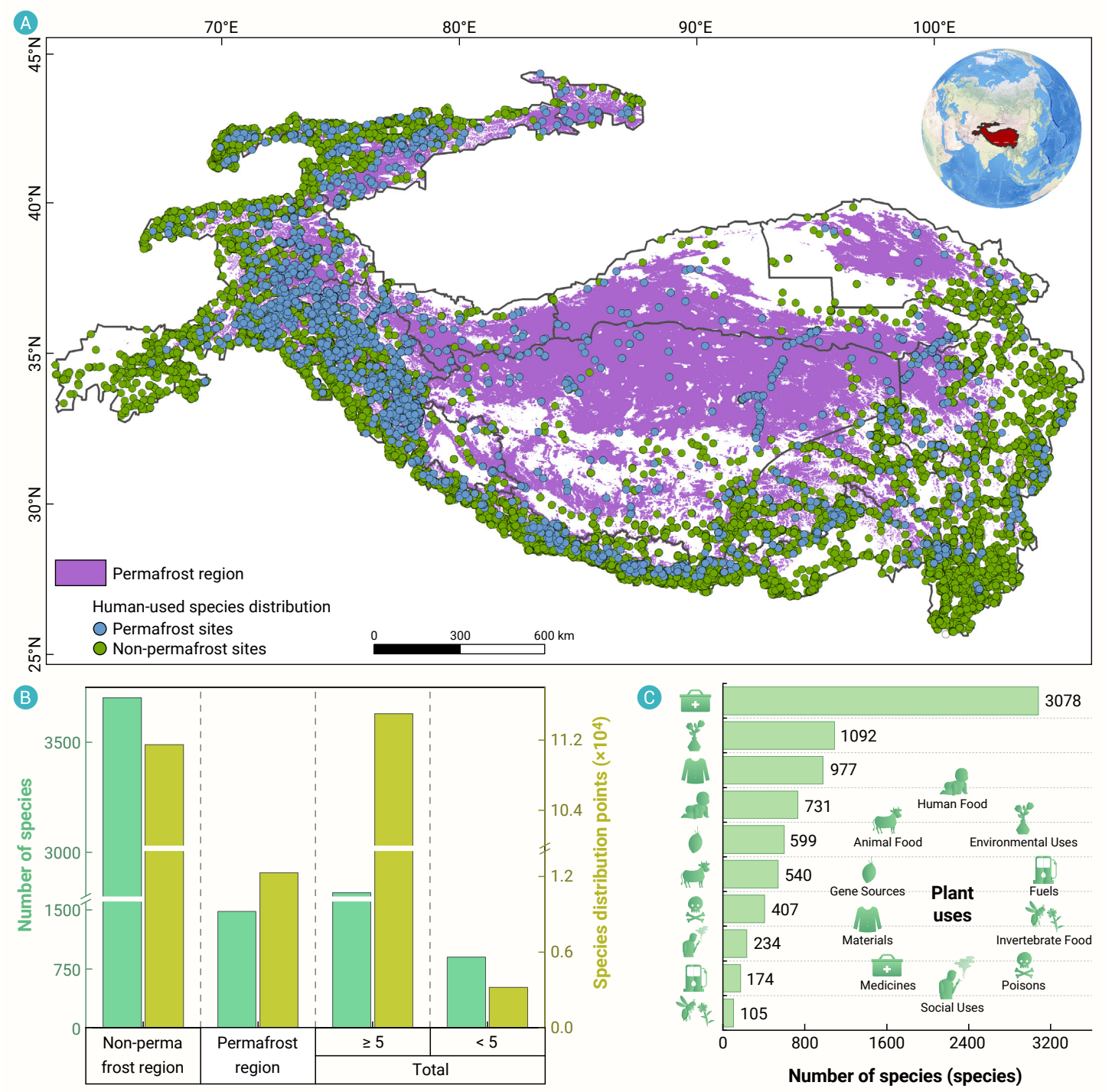

Figure 1. Sample distribution of human-used plants in the High Mountain Asia region (A) Actual sample distribution of the human-used plant species from the Global Biodiversity Information Facility (GBIF), Community for Naturalists and Botanical Information and Ecology Network (BIEN). (B) Distribution of human-used plant species in the permafrost and non-permafrost regions. The distribution of permafrost is from the literature.[22] The threshold of ≥ 5 denotes species exhibiting five or more verified distribution records, whereas values < 5 correspond to species with fewer than five documented occurrence points. (C) Sample number of the human-used plants in 10 categories.

terrain, soil, and human activities, and utilized four individual and two ensemble species distribution models to examine the spatial distribution of human-used plant species richness and its changes under Shared Socioeconomic Pathways (SSP1-2.6, SSP5-8.5) by 2050. Meanwhile, we explored the elevation-dependent patterns in the changes of human-used plant species richness. Furthermore, we quantified the contributions of environmental variables to the plant species richness and examined their response to permafrost thaw. Finally, we identified conservation priority areas for human-used plants using the Zonation 5.0 model, and assessed the effectiveness of protection strategies.

MATERIALS AND METHODS

Our study area is located in the High Mountain Asia (HMA), including the Tibetan Plateau and the surrounding high Asian mountain ranges. The vector boundary of this region was delineated based on the National Tibetan Plateau Scientific Data Center (https://data.tpdc.ac.cn/), with consideration of mountain-range integrity. The study area covers the geographical coordinates ranging from 63.6°E to 104.4°E in longitude and 25.7°N to 44.5°N in latitude. Our study first compiled and processed the datasets of human-used species distribution and 13 environmental variables to ensure consistency for multicollinearity. We then applied a suite of single and ensemble models to simulate the distributions of human-used species, producing projections under

both current and future climate scenarios. Subsequently, the patterns of regional species richness were estimated by overlaying species distribution models. In addition, we explored the elevational pattern and key environmental drivers using statistical and interpretive approaches. Finally, a conservation prioritization model was employed to conduct systematic planning and delineate critical conservation areas (Figure S1).

List of human-used plant species

Based on the "World Checklist of Useful Plant Species",[28] we define "human-used plant" as described by Pironon et al.[2] Specifically, the term "human-used plant" refers to vascular terrestrial plant species that provide documented material and non-material benefits to humans, which are publicly accessible. Human-used plants may be wild, introduced, cultivated, or weedy, and their uses may offer direct benefits (e.g., food, medicine, material) or indirect benefits (e.g., contributions to environmental services such as water, soil, or air quality protection). Their uses may have been documented over different time periods (from prehistory to contemporary times), scales (from local to global, by individuals or societies), and economic levels (from local personal use to commercial enterprise). While all plants may have effective or potential uses, human-used plants are those with documented human use in the scientific literature. The list of utilized plants was compiled from the dataset using the methodology outlined in the references and will not be reiterated.[2] We employed an adapted version of level 1 of the Economic Botany data standards, incorporating the ten subsequent plant use categories (Table S1):

Human-used plant occurrence data

We compiled occurrence records for each human-used plant species from the following three databases: (i) the Global Biodiversity Information Facility (GBIF, http://www.gbif.org; accessed March–April 2024), using the function "get_gbifid" from the R package "taxize" for species name matching, followed by the function "occ_download" from the R package "rgbif" to download the records; (ii) iNaturalist (https://www.inaturalist.org; accessed March 2024), using the function "get_inat_data" from the R package "rinat"; and (iii) the Botanical Information and Ecology Network (BIEN, version 4.2, https://bien.nceas.ucsb.edu/bien; accessed March 2024), using the function "BIEN_occurrence_species" from the R package "BIEN". First, we corrected geographic reference errors using the World Checklist of Vascular Plants (WCVP) and reduced biases by eliminating records located outside known species distributions.[29] Further, we used the metadata information saved from the original data source, retaining only (i) the records collected since 1945 and removing (ii) the records whose latitude or longitude coordinates exceed the study area; (iii) no decimal (i.e. rounding off the coordinates); (iv) equal coordinates (i.e. latitude equal to longitude); (v) coordinates located around the centroids of countries, provinces, capitals and plant institutions. We then cleaned the data using the R package "CoordinateCleaner" to ensure data quality.[30] To minimize sampling bias and spatial autocorrelation,[31] we aggregated densely clustered occurrence records into 30-arc-second (~1 km^2) grid cells, retaining a single record per species per cell. This procedure was implemented using the R package "ENMTools".

After data cleaning, we obtained occurrence records for 3,716 human-used plant species in the HMA region. Among them, 3,078 species were used for medicine, 1,092 for environmental purposes, 977 for materials, 731 for human food, 599 for genetic resources, 540 for animal food, 407 for poisons, 234 for social uses, 174 for fuels, and 105 for invertebrate food (Figure 1C). The final occurrence dataset comprised 123,782 records.

Environmental variable data

We assembled an original set of environmental variables related to climate, permafrost, snow cover, terrain, soil, and human activity (Table S2). Among them, bioclimatic variables and snow cover days (SCD) were provided by the Climatologies at High Resolution for the Earth's Land Surface Areas (CHELSA v.2.1; https://chelsa-climate.org).[32] Permafrost-related variables include active layer thickness (ALT), mean annual ground temperature (MAGT), freezing degree-days (FDD), and thawing degree-days (TDD).[33] This dataset explicitly accounts for topography-driven thermal heterogeneity by integrating physically informed machine-learning approaches with rigorous observational validation, constituting a 1-km resolution permafrost product with high predictive accuracy and clear physical plausibility and practical usability.[33] Terrain variables include elevation, slope, topographic position index (TPI), topographic ruggedness index (TRI), and topographic wetness index (TWI). These variables were calculated from a Digital Elevation Model (DEM) provided by the Global Multi-resolution Terrain Elevation Database (GMTED;http://www.earthenv.org).[34] Soil variables were from the Harmonized World Soil Database (HWSD v.2.0; https://www.fao.org), including available water capacity (AWC), organic carbon content (ORG_CARBON), sand, silt, clay, and pH_water. We considered the human influence index (Hii), which was produced by the Wildlife Conservation Society (WCS) and the Columbia University Center for International Earth Science Information Network (CIESIN) (Last of the Wild, v2; https://beta.sedac.ciesin.columbia.edu).

For the selection of environmental variables: we firstly assessed the extent to which each variable explained the variance using principal component analysis (PCA), applying the "dudi.pca" function from the R package ade4. Simultaneously, we performed correlation analysis to examine the relationships among variables using the "quickcor" function from the R package ggcor. We then calculated the variance inflation factor (VIF) to quantify multicollinearity using the "vif" function from the R package car. For variable pairs with correlation coefficients $|r| > 0.8$, the variable with the highest VIF value was excluded. Although a single variable was selected instead of the principal component, the correlation between the variables may not have been fully considered, which could introduce bias into the analysis results. Ultimately, we estimated 13 environmental variables: temperature annual range (TAR), mean temperature of the wettest quarter (MTWQ), precipitation seasonality (PS), precipitation of the coldest quarter (PCQ), ALT, MAGT, TDD, SCD, Slope, TWI, Sand, pH_water, and Hii (Figure S2). They are widely recognized as crucial influencing factors in shaping plant species distributions.[2,35] These data were selected for the current period (1981-2010s) and future period (2041-2070s) under the SSP1-2.6 and SSP5-8.5 scenarios. We selected SSP1-2.6 and SSP5-8.5 to bracket the lower and upper bounds of future radiative forcing,36 enabling us to assess whether a high-emissions pathway (SSP5-8.5), relative to a sustainability-oriented mitigation pathway (SSP1-2.6), is associated with a higher risk of triggering key cryospheric tipping points before 2050.[37,38]

Species distribution modelling

Species Distribution Modelling (SDM) comprises a suite of biological methods that integrates species occurrence data with relevant environmental variables to assess habitat suitability for a given species.[39] Although numerous SDM techniques are available, each method has inherent strengths and limitations, arising from differing algorithms and theoretical assumptions, with performance being highly dependent on the quality of input data.[40] To enhance predictive accuracy, we employed an ensemble modelling approach rather than relying on a single algorithm.[41] The R-based platform Biomod, developed in 2003, has since gained widespread recognition and adoption.[41,42] We selected the Biomod2 version 3.5.1 for its two key advantages: first, it supports five model integration methods and ten model validation metrics. Second, it allows flexible customization of model ensembles, enabling adjustments to initial conditions, model types, parameters, and boundary settings to optimize predictive performance.

Four individual models of generalized additive models (GAM), generalized boosted models (GBM), Maximum Entropy Models (MAXENT), and random forests (RF) show high simulation performance in plant species richness patterns.[43] Although these models have some limitations in capturing ecological processes, they can reveal the nonlinear responses of human-used plant species to the changes in climate and environmental factors. To enhance the simulation precision of species distribution and reduce uncertainty, we selected the model with a true skill statistic (TSS) greater than 0.4 for constructing ensemble models. Specifically, we constructed two ensemble models-EMca and EMwmean-using the "committee.averaging" and "prob.mean.weight" functions from the R package "biomod2". For the input distribution data, certain models in Biomod2 require presence-absence datasets, including pseudo-absence points. We generated pseudo-absence data using the random method via the "PA.strategy" function in "biomod2". To evaluate model performance, we randomly partitioned the occurrence

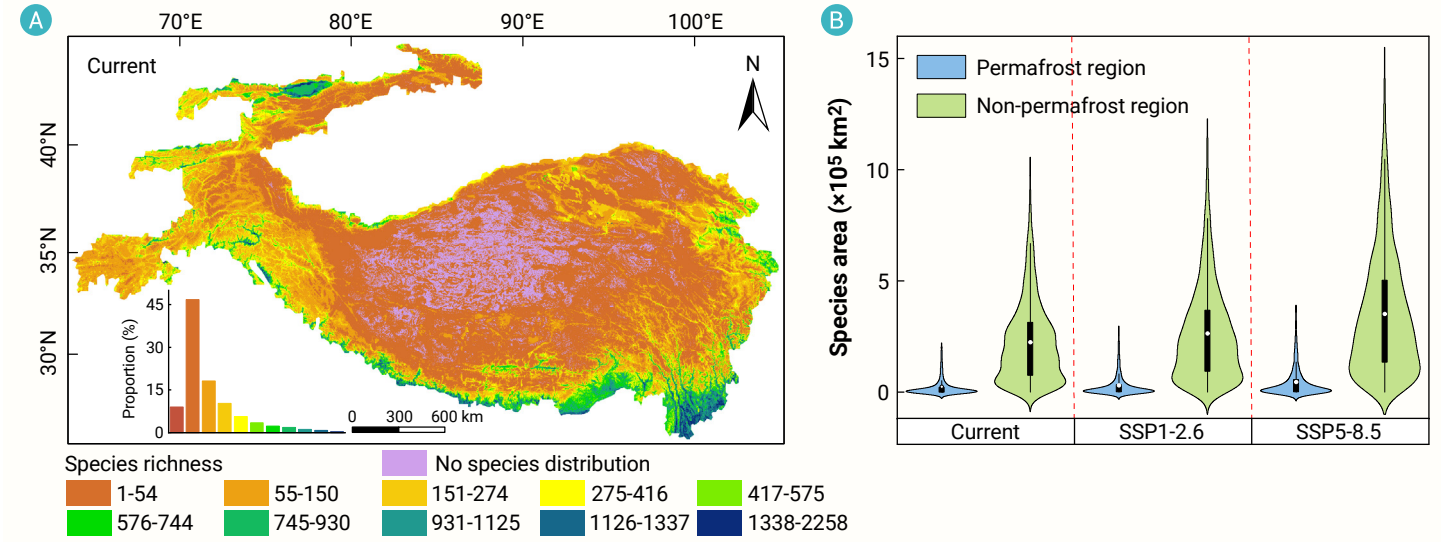

Figure 2. Distribution of human-used plant species richness (A) Current distribution of human-used plant species richness. The bar chart shows the proportion of each classification level. (B) Changes in human-used plant species in different regions at current and under SSP1-2.6 and SSP5-8.5 scenarios by 2050.

dataset, allocating 70% of the data for model calibration (training) and the remaining 30% for evaluation (testing).[44] In accordance with SDM reliability requirements, we excluded species with fewer than five recorded occurrences, resulting in a final dataset of 2,815 species. Finally, we simulated the potential distribution of each species under both current and future climate scenarios (SSP1-2.6 and SSP5-8.5) using the SDM.

Model evaluation

We selected the Area Under the Curve (AUC), TSS, and Cohen's Kappa index (Kappa) as the metrics for evaluating model performance.[45] AUC represents the area under the Receiver Operating Characteristic (ROC) curve and is independent of the prevalence of species distribution points or threshold values. The curve is plotted with the false positive rate (i.e., the probability of predicting presence when the actual state is absence) on the x-axis and the true positive rate (i.e., the probability of correctly predicting presence when the actual state is presence) on the y-axis.[46] TSS quantifies the model's ability to differentiate between positive and negative predictions. While it is independent of the prevalence of distribution points, it is sensitive to the threshold value.[45] The Kappa statistic reflects the accuracy of predictions relative to random occurrence, with its value influenced by the prevalence of distribution points and the threshold value (Figure S2).

Projection of species richness

We analyzed the evaluation metrics of GAM, GBM, MAXENT, RF, EMca, and EMwmean (Figure S3). To assess species richness across space, we employed a "Stacked-Species Distribution Models" (S-SDMs) approach, which involves stacking individual species distribution maps derived from SDMs.[47] Threshold (binary) maps were used to estimate species richness.[48] In general, the sensitivity-specificity difference minimizer and the sensitivity-specificity sum maximizer criteria yielded the most accurate predictions.[49] Consequently, this study utilized the Maximum Training Sensitivity Plus Specificity (MTSS) generated by the model. Ultimately, we estimated the potential species richness for all human-used plants and for 10 utilization categories under both current conditions and future scenarios (SSP1-2.6 and SSP5-8.5).

Analyses of influencing factors

To examine the variations in human-used plant species richness along elevation, we fitted Generalized Additive Models (GAM) between elevation and species richness.[50] Model fitting was conducted using our predicted species richness estimates per grid cell as the response variable, with a penalized cubic regression spline applied to the elevation of the grid cells as a smooth term, using the "bam" function from the R package "mgcv". To better visualize the differences among use categories, we considered species richness across all human-used plants as a baseline and represented the deviation of the elevational pattern for each use category from this baseline. We assessed (dis-)similarities and clustering among the elevational profiles of each use by constructing dendrograms using the "hclust" function from the R package "stats".

To quantify the effects of environmental variables on the potential species richness of human-used plants, we conducted a three-step analysis. First, we evaluated the overall influence of each driving factor, including bioclimate (TAR, MTWQ, PS, and PCQ), permafrost (ALT, MAGT, and TDD), snow cover (SCD), terrain (Slope and TWI), soil (SAND and PH_water), and human (Hii) factors on the species richness of utilized plants in both the HMA and permafrost regions using the R package "plspm".[51] The model fit was assessed using the Goodness of Fit (GOF), and the model was considered well-constructed when the GOF > 0.4.[52] Second, we calculated the contribution and average feature importance of each environmental variable to species richness in human-used plants in both the HMA and permafrost regions using the Python package "shap". Key environmental variables affecting species richness were identified where the Mean Shapley Value exceeded 30 in the HMA region and 5 in the permafrost region. Finally, we generated the partial dependence plot using the "pdp" function from the R package "iml", illustrating the impact of major environmental variables on species richness in human-used plants in both the HMA and permafrost regions.

Conservation Priority Area Identification

Based on the current simulated distribution of human-used plant species in the HMA region, we conducted spatial planning for multi-species conservation using the Zonation 5.0 model.[53] The Zonation 5.0 is a widely adopted spatial conservation planning framework that establishes priority areas based on biodiversity representation, habitat connectivity, and ecological integrity. The model generates a hierarchical priority map, enabling decision-makers to reconcile conservation value with real-world implementation constraints. The model was run using core-area cell and edge removal rules, with a warp factor set to "1" to optimize results, while other parameters were maintained at their default values.[49] Given the variations in species conservation needs, it is crucial to consider each species based on its conservation value when designing protection strategies. To address this, we assigned weights to the species in the Zonation 5.0 model. First, base weights were assigned based on the number of uses of each species: species with a single use were assigned a weight of 0.1, with an additional 0.1 added for each subsequent use. Second, geographical distribution weights were calculated using the entropy method, with species having smaller distribution ranges receiving higher weights.[54] Finally, the two weight categories were combined to derive a comprehensive weight value for each human-used plant species.

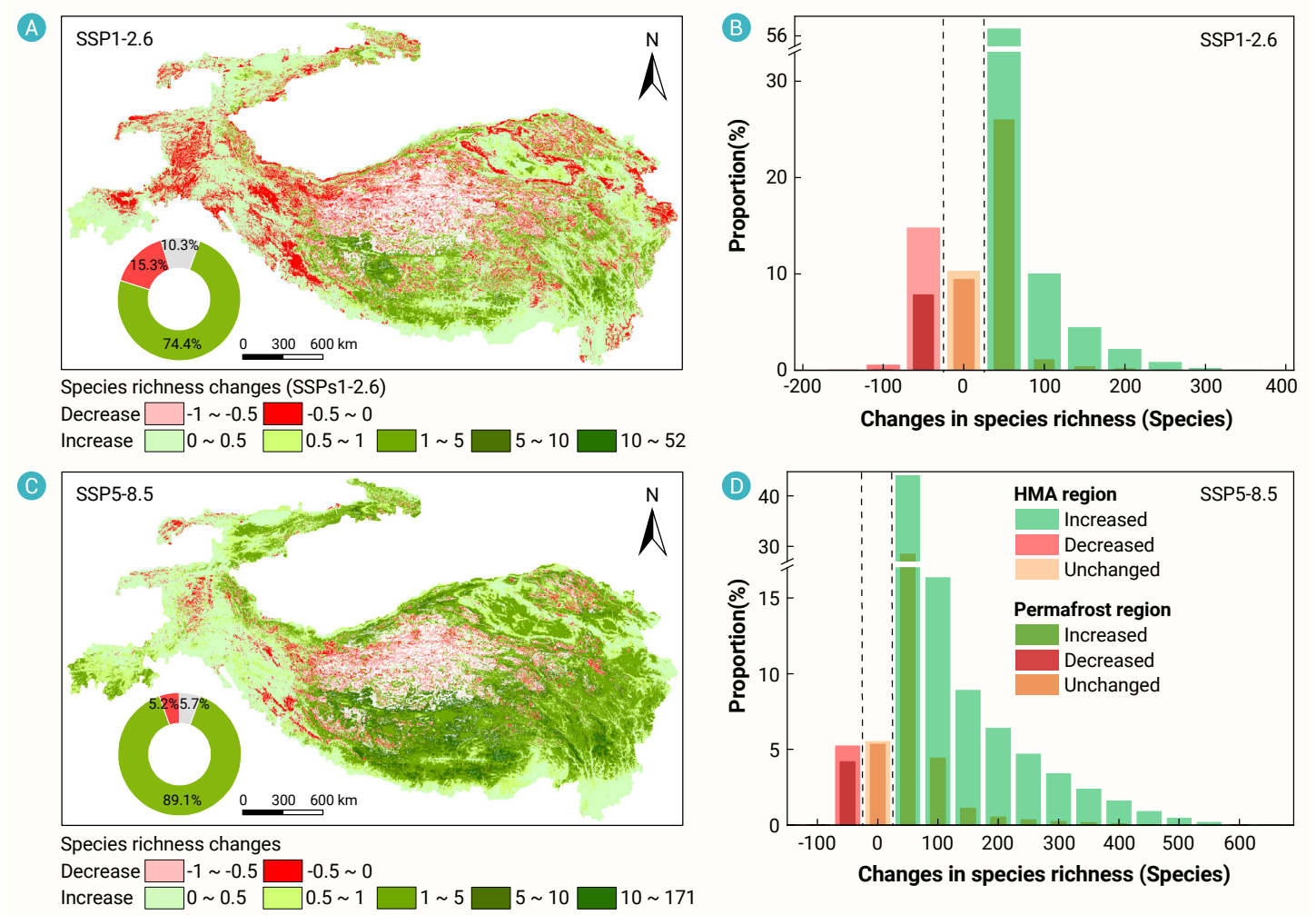

Figure 3. Future human-used plant species richness (A-B) Changes in human-used plant species richness by 2050 under the SSP1-2.6. (C-D) Changes in human-used plant species richness by 2050 under the SSP5-8.5. The pie charts represent the proportions of increases (green), decreases (red), and no changes (gray). In the bar charts, the dark bars indicate the permafrost region, whereas the light bars represent the entire HMA region.

We calculated the conservation priority (i.e., conservation value, ranging from 0 to 1) for human-used plants at each grid cell in the HMA region. The top 30% areas with the highest conservation priority were designated as conservation priority areas (CPAs) for human-used plants. Based on the traditional 10% conservation target and the Aichi Biodiversity targets, these CPAs were classified into three levels: Level 1 (conservation value ≥ 0.9), Level 2 (0.83 ≤ conservation value < 0.9), and Level 3 (0.7 ≤ conservation value < 0.83).[55]

Optimization of the protected area system

We identified overlapping areas of current PAs and three CPAs in the HMA region as conservation gaps for human-used plants, excluding areas with high anthropogenic intensity (HMc ≥ 0.4).[56] Using the previously established classification criteria for CPAs, these conservation gaps were categorized into three levels: Level I, Level II, and Level III. We developed three optimization strategies for existing PAs: Strategy A: PAs + (Level I conservation gaps), Strategy B: PAs + (Level I + II conservation gaps), and Strategy C: PAs + (Level I + II + III conservation gaps). To evaluate the conservation efficiency of the PAs or the three conservation strategies for each human-used plant, we performed a spatial overlay to determine the overlapping area and subsequently calculated the percentage of each species' distribution range within this region. Additionally, for each species, we applied the criterion that at least 10% of the species' suitable habitat must be covered by existing PAs or the conservation strategy to assess whether the species is effectively protected.[57]

RESULTS AND DISCUSSIONS

Spatiotemporal distribution of human-used plant species

To show the distribution of human-used plant species richness in the HMA, we analyzed 3,716 species from 1,293 genera across 220 families of human-used plants (Figure S4) and compiled 123,782 georeferenced occurrence records (Figure 1A). Additionally, we classify human-used plants into 10 utilization categories.[2,28] Using four individual species distribution models and two ensemble models (EMca and EMwmean) for each human-used plant species (Figure S2) (see Materials and Methods), our results suggest that the potential distribution area for species richness of human-used plants in the HMA is (4.6 ± 0.2) ×10^6 km^2, with approximately 36% in permafrost regions (Figure 2A). Notably, the medicinal plants account for 97% ± 1% of the total human-used plant distribution area. This highlights the dominance of medicinal plants in biodiversity and their critical role in supporting local livelihoods in the HMA region. The spatial distribution patterns of species richness across the 10 utilization categories correspond to the total human-used plant distribution (Figure S5). Among them, the highest richness of human-used plant species is found in the Himalayas, Hengduan Mountains, and western Tian Shan Mountains, which also serve as the hotspots for vascular plant diversity, tree species richness,[58,59] and global biodiversity.[60,61] However, compared to non-permafrost regions, human-used plant species in permafrost areas exhibit a smaller distribution area (Figure 2B), leading to lower species richness, with only 10% of total species abundance distributed in these regions. This is attributed to harsh environmental constraints, including low temperatures, extreme precipitation variability, and nutrient deficiencies at high altitudes.[62] Our study shows the uneven distribution patterns of human-used plant species richness due to the permafrost distribution.

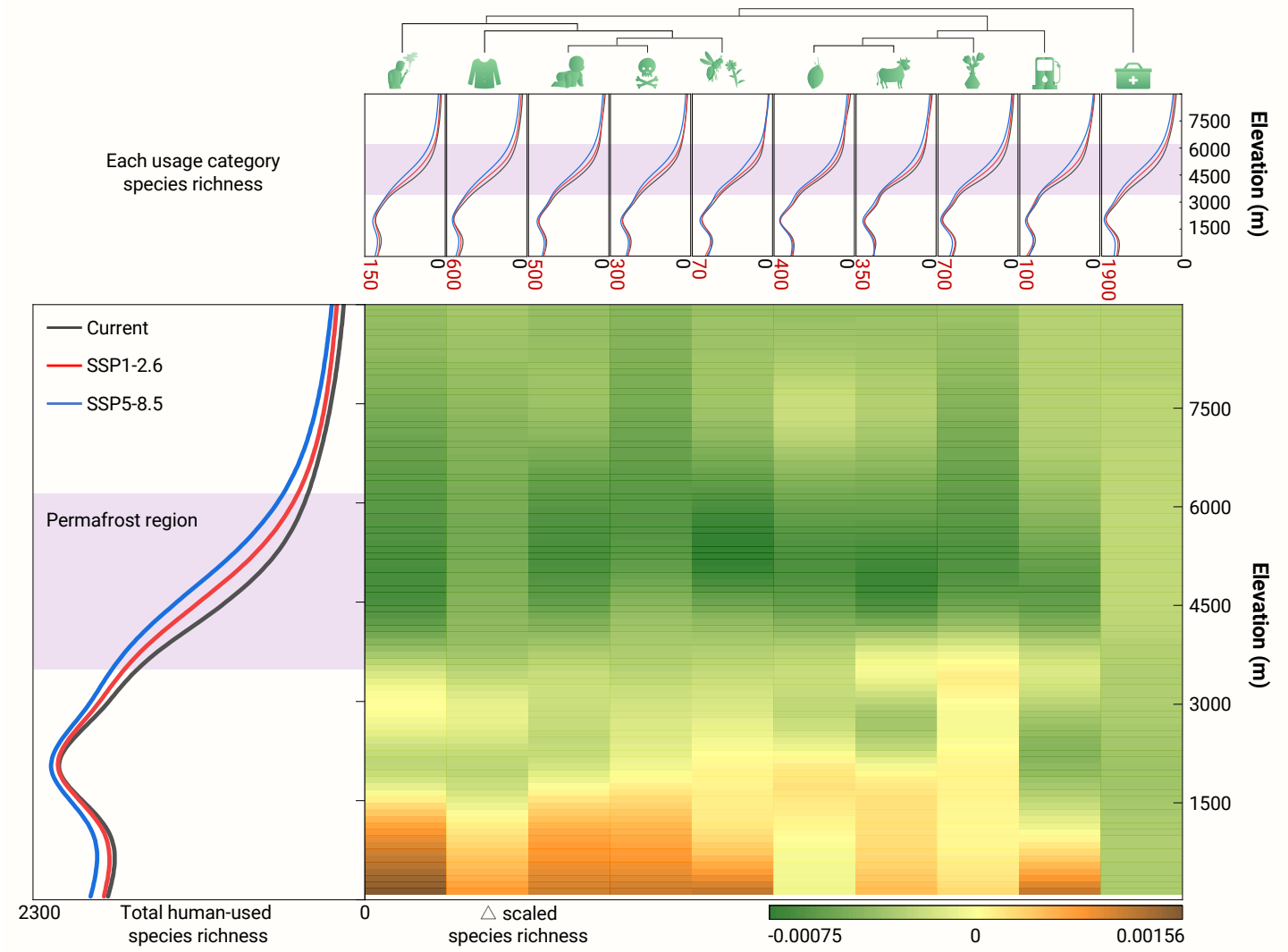

Figure 4. Changes in human-used plant species richness with elevation Changes in human-used plant species richness across 10 categories with elevation. The curve on the left represents the elevational distribution of all human-used plant species richness. The dendrogram in the top 10 orders uses categories according to the (dis-)similarity of their species richness elevation profiles. The curves underneath the dendrogram correspond to the species richness elevational profile for each use category. The heatmap shows the elevational variation in the deviation of utilized plant species richness for the 10 plant-use categories. The colors indicate higher (orange) or lower (green) proportions of human-used plant species richness for a given use relative to the total human-used plant species richness.

Under future climate scenarios, the environmental variables (MAGT, ALT, TDD) influencing human-used plant species richness show an upward trend under two shared socioeconomic pathway (SSP) scenarios, SSP1-2.6 and SSP5-8.5 (Figure S6). Conversely, the variables (SCD, PS, PCQ) that negatively affecting human-used plant species richness generally display a declining trend (Figure S7). We further estimate future changes in human-used plants using the established species distribution models. Furthermore, the distribution area of human-used plant species richness is projected to increase to 84% ± 6% and 89% ± 4% by 2050 under the SSP1-2.6 and SSP5-8.5 scenarios, respectively (Figure S8). Moreover, the distribution areas of 10 categories of plant species richness also exhibit an overall expansion trend under future climate scenarios (Figure S9). Notably, under the SSP1-2.6, the areas with increasing species richness account for 74% ± 9% of the HMA region (with 28% ± 5% in permafrost region), while the areas with decreasing species richness account for 15% ± 8% (with 8% ± 3% in permafrost region) (Figures 3A-B). Under the SSP5-8.5 scenario, the areas with increasing species richness account for 89 ± 9% of the HMA region (with 35% ± 5% in permafrost region), whereas areas with decreasing species richness account for approximately 5% ± 3% (with 4% ± 2% in permafrost region) (Figures 3C-D).

To further assess the robustness of our findings, we compare the results of different models under the SSP1-2.6 and SSP5-8.5. We find that, whether an ensemble or a single model is applied, the areas of human-used plant richness projected to increase substantially exceed those projected to decline, with the pronounced trend under the SSP5-8.5 (Figure S10). Overall, approximately 40% of the increase in human-used plant species richness is attributed to the changes in the permafrost region, owing to higher increasing rates of air temperature in these regions compared to the global average.[63] In contrast to previous studies,[11,12] our study examines the crucial role of permafrost in influencing future changes in human-used species richness. Our findings provide the first quantitative evaluation for the changes in human-used plants species richness across the HMA region.

Elevation-dependent patterns

Furthermore, our results indicate that the richness of human-used plant species follows a unimodal elevational pattern, reaching its peak at approximately 2,100 m a.s.l. (Figure 4), which aligns well with the hump-shaped pattern that species richness peaks at mid-elevations.[64] The richness of human-used plant species declines at the high-altitudes, mainly due to the unique environmental conditions in the region severely restricting the adaptation and survival capabilities of many species, such as low temperatures, nutrient-poor soils, and habitat limitations.[65] Compared with the current distribution, the plant species richness increases the most within the altitude range of 3,500 to 6,000 m a.s.l. under the SSP1-2.6 and SSP5-8.5 scenarios, and this area overlaps with the distribution of permafrost (Figure 4). The result implies that sensitivity of plant species richness in permafrost regions

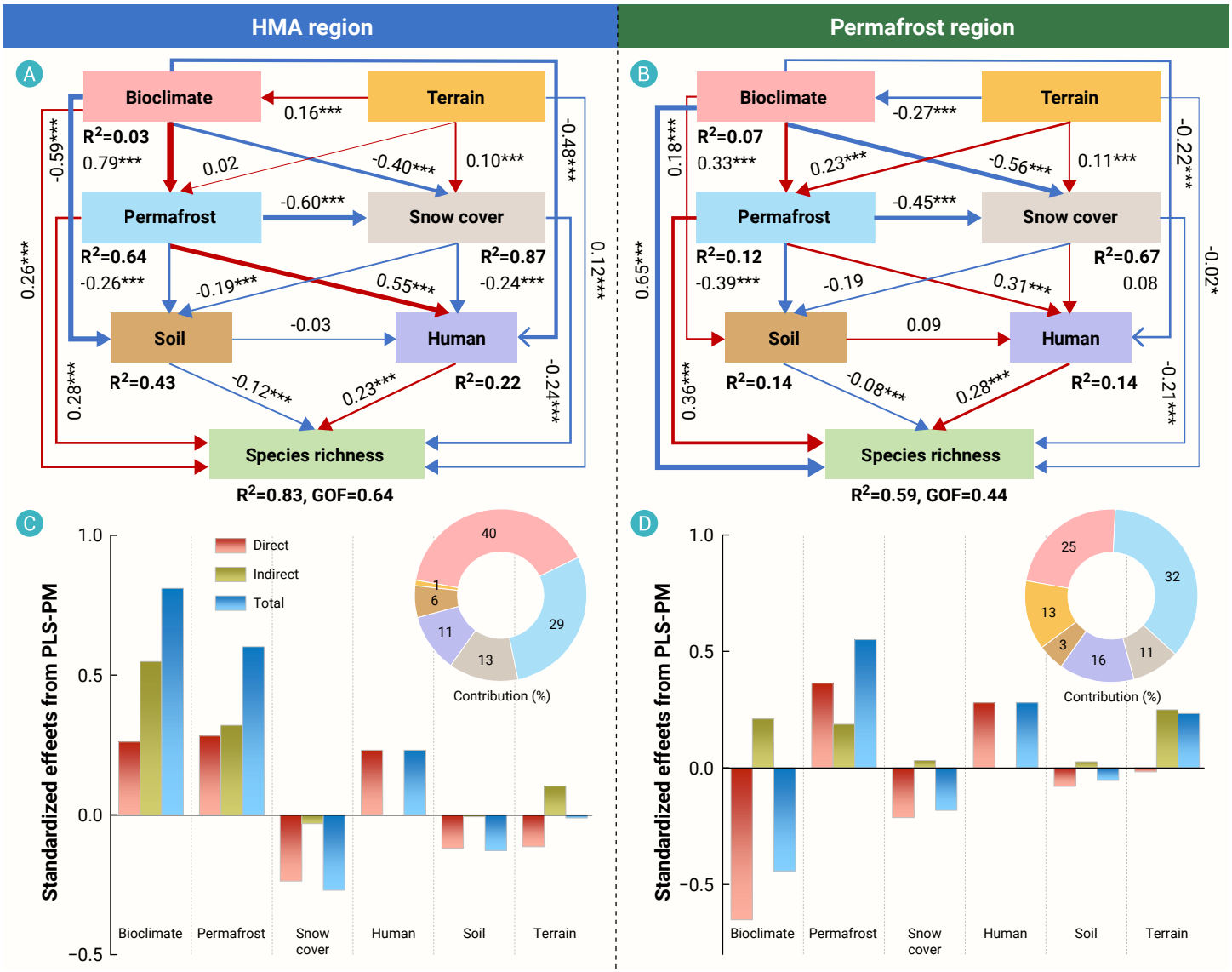

Figure 5. Environmental determinants of human-used plant species richness (A-B) The interpretations of six categorical factors to the human-used plant species richness using PLS-PM in the whole HMA region (A) and permafrost region (B). Larger path coefficients are shown as wider arrows, and red and blue colors represent positive and negative effects, respectively. The goodness of fit (GOF) indicates the overall model fit. Asterisks indicate significant correlations *P < 0.05; **P < 0.01; ***P < 0.001. (C-D) Standardized direct, indirect and total effects for human-used plant species richness in the HMA region (C) and permafrost region (D). The rings indicate the total contributions of six categorical factors.

to climate change is higher than other regions. Despite each usage category contains a large number of species in its hotspots, the elevational pattern of medicinal plants is most similar to the overall distribution of human-used plant (Figure 4). Notably, the potential species increase reaches a peak near the altitude of 4,500 m a.s.l., which occurs mainly in the discontinuous permafrost zone. It was shown that the discontinuous permafrost zone exhibits heightened sensitivity to climatic warming.[66] The results imply that the changes in human-used plant species richness are elevation-dependent and show a strong spatial association with the distribution of permafrost in the HMA region.

Drivers of human-used plant changes

To explore the underlying mechanisms of driving changes in human-used plant species, we quantify the impacts of six major categories including 13 environmental variables (see Materials and Methods). The results indicate that the species richness in the entire HMA region is significantly positively correlated with bioclimatic factors, permafrost and human activities, and is negatively correlated with snow cover, soil, and terrain (Figure 5A). Notably, different with the HMA region, the species richness in the permafrost regions is negatively correlated with the bioclimatic factors (Figure 5B). This is consistent with the positive response of Arctic plant species diversity to temperature rise and the weakened or even negative correlation observed in regions with greater temperature variability.[67] In the HMA region, bioclimatic factors, permafrost, and snow cover have the greatest direct and overall impact on the species richness, with the standardized effects of 0.81 (40%), 0.60 (29%), and −0.27 (13%), respectively (Figure 5C). Moreover, the indirect effects of bioclimatic factors are greater than the direct effects, indicating that temperature and precipitation are not only the key factors driving the changes in the richness of human-used plant species,[68,69] but also indirectly enhance species richness by influencing permafrost hydrothermal conditions. In the permafrost region, bioclimatic factors, permafrost variables, and snow cover had standardized effects of −0.44 (25%), 0.55 (32%) and -0.18 (11%), respectively (Figure 5D). The divergent effects of permafrost and snow cover on plant species richness are due to the fact that a reduction in snow cover accumulation can shorten the duration of snow melting, thereby promoting plant growth.

For instance, snow cover days (SCD) is shown as the most significant variable (Figure 6A), indicating that a shorter duration of snow cover can increase the availability of water and nutrients for plants,[70] thereby enhancing species richness. In addition, reduced snow depth attenuates soil thermal insulation, triggering extreme cooling and intensified freeze–thaw cycles that ultimately compromise human-used plant diversity via root damage and frost

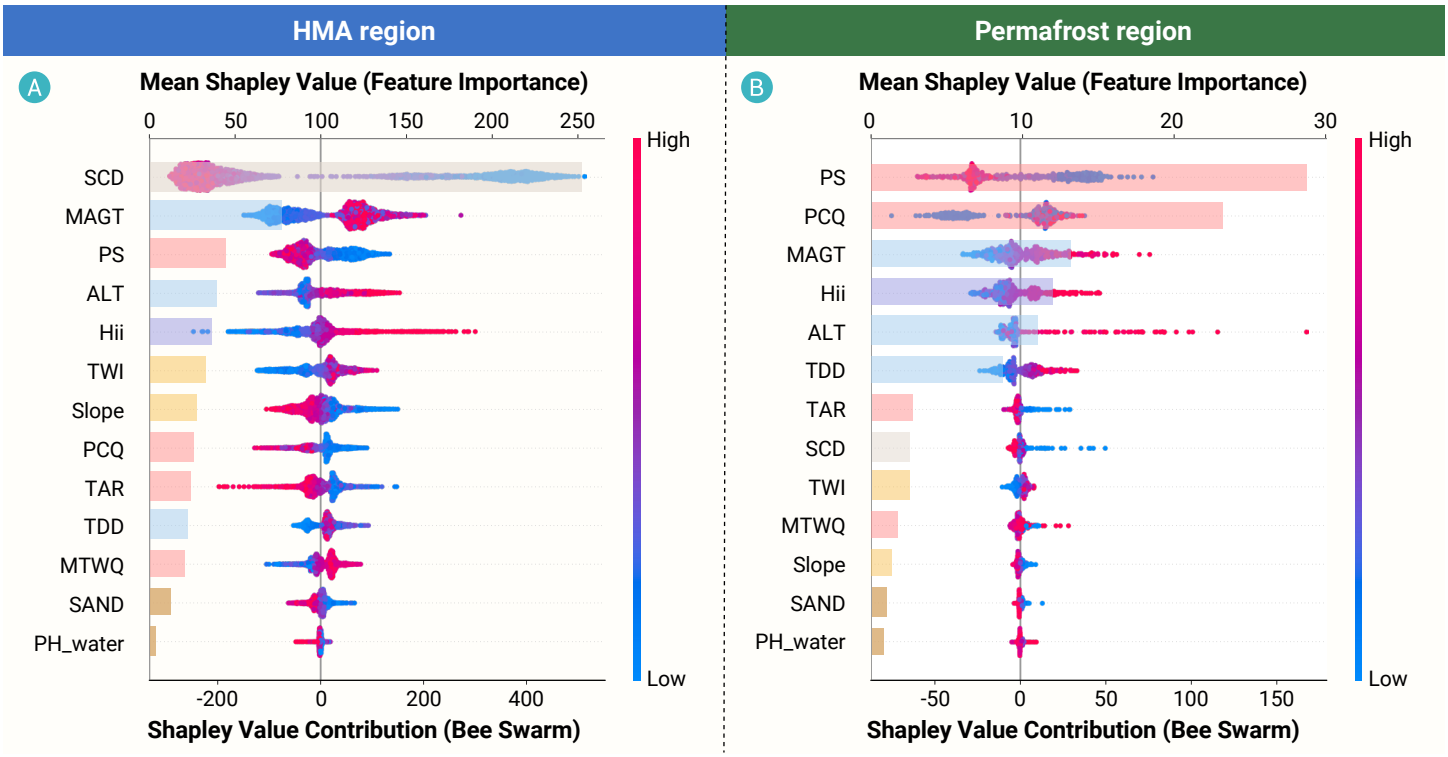

Figure 6. Contributions of various environmental variables to the human-used plant species richness In the HMA region (A) and permafrost region (B). The bee swarm plot and the feature importance histogram illustrate each feature's contribution to model predictions and its average importance, respectively. The bee swarm plot shows the distribution of SHAP values for each feature along the lower X-axis, with color indicating the magnitude of the feature value, whereas the histogram presents the average SHAP value for each feature on the upper X-axis, ranked by importance. (SCD: Snow Cover Days, MAGT: Mean Annual Ground Temperature, PS: Precipitation Seasonality, ALT: Active Layer Thickness, Hii: Human Influence Index, TWI: Topographic Wetness Index, Slope: Slope, PCQ: Precipitation of Coldest Quarter, TAR: Temperature Annual Range, TDD: Thawing Degree-Days, MTWQ: Mean Temperature of Wettest Quarter, SAND: Sand, PH_water: pH in water.)

drought.[71] While the positive effect of permafrost is that the increase in soil moisture and the release of nutrition caused by permafrost degradation can promote the growth of human-used plant.[9]

Specifically, in the permafrost regions, precipitation seasonality (PS) is the most important variable, indicating that the temporal distribution of precipitation plays a crucial role in the changes of human-used plant diversity (Figure 6B).[72] Our study further presents the response curves of key environmental variables to the species richness of human-used plants (Figure S11). The results identify a response threshold of human-used plant diversity to the active layer thickness (ALT) of permafrost. When the ALT exceeds 350-360 cm in depth, there is a significant positive effect on species richness, whereas richness stabilizes when the ALT reaches 450-600 cm in depth (Figure S11). This occurs because the permafrost layer acts as an aquitard, substantially limiting hydraulic connectivity and downward water infiltration; consequently, it preserves soil moisture and sustaining nutrient cycling within the rooting zone to support plant growth.[73] Meanwhile, short-term deepening of the active layer releases meltwater that enhances water availability,[11] thereby promoting plant richness in the HMA region. However, long-term permafrost degradation induces excessive deepening of the active layer, rendering soil moisture increasingly susceptible to downward percolation. Meanwhile, enhanced evapotranspiration further desiccates surface soils,[74,75] and these two factors collectively constrain plant growth. In addition, abrupt permafrost thaw can trigger the formation of thermokarst landscapes, such as thaw slumps and thermal erosion gullies, which directly damage vegetation and ultimately reduce plant species richness.[76] Thus, the impacts of permafrost thaw on plant species are dependent on multiple time scales. Taken together, cryospheric factors (including permafrost and snow cover) account for approximately 42% of the changes in human-used plants richness in the HMA region, exceeding the influence of bioclimatic factors. These findings suggest that cryospheric factors are the crucial drivers of human-used plant biodiversity in the HMA region.

Protection strategies

Based on the changes in human-used plant diversity, we further propose conservation priority areas (CPAs) strategies using the Systematic Conservation Planning approach and Zonation 5.0 model (see Materials and Methods). The results reveal that CPAs for human-used plants at Levels 1, 2, and 3 account for 10%, 7%, and 13% of the HMA areas, respectively (Figure S12). We find that approximately four-fifths of the identified CPAs are not covered by current protected areas (PAs), highlighting the significant gaps for protecting human-used plants in the HMA region, particularly in the discontinuous permafrost regions, which are more vulnerable to climate warming.

By overlaying the spatial distributions of established CPAs and PAs, while excluding areas disturbed by human activities, we identified conservation gaps for human-used plants at Levels I, II, and III, which cover approximately 7.5%, 5.7%, and 10.6% of the HMA region, respectively. Compared to current PAs, the Level I conservation gap is primarily located in the Central-Eastern Himalayas, central and southern Hengduan Mountains, and western Tian Shan Mountains, while the Level II and III conservation gaps largely extend from the Level I gap (Figure 7A). Therefore, we propose three optimized conservation strategies for human-used plants: Strategy A: PAs + (Level I conservation gap), Strategy B: PAs + (Level I+II conservation gap), and Strategy C: PAs + (Level I+II+III conservation gap).

The results indicate that Strategies A, B, and C have the average conservation efficiencies of 71% ± 21%, 81% ± 16%, and 90% ± 10% for total human-used plants, respectively, particularly 68%-79%, 79%-86%, and 88%-91% for 10 utilization categories. The implementation effects of our strategies are significantly higher than those of current PAs (average 15%) (Figure 7B & Table S3). To inform future policymaking and local communities, we estimate the conservation efficiency of these strategies under SSP1-2.6 and SSP5-8.5 scenarios. The results show that Strategies A, B, and C have average conservation efficiencies of 64%-68%, 75%-79%, and 87%-89% for total human-used plants by 2050, respectively (Tables S4-S5). The three strategies can protect at least 99.6% of human-used plants. Taken together, compared to current PAs, our optimization strategies enhance the conservation effectiveness of human-used plants in the HMA region.

Considering regional biodiversity conservation alongside future socioeconomic development, achieving optimal conservation effectiveness with mini-

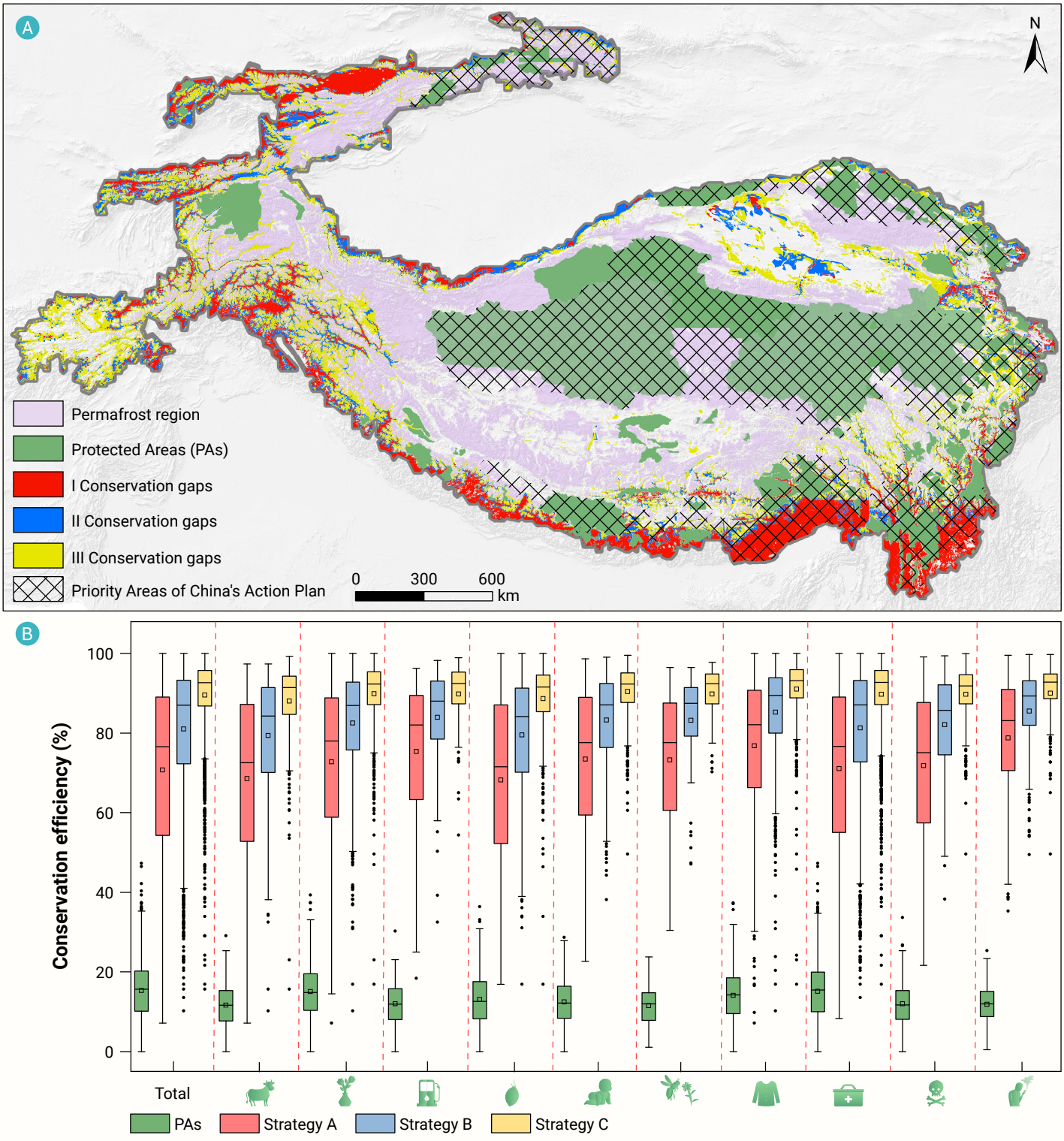

Figure 7. Distribution of conservation gaps and implementation effects of strategies (A) Compared with current PAs, the distribution of conservation gaps for human-used plants in the HMA region. The boundaries of PAs in this study are from the World Database on Protected Areas (WDPA; https://www.protectedplanet.net) and the China Nature Reserve Specimen Resource Sharing Platform (https://www.bhq.papc.cn). Priority area of China's action plan boundaries from the Ministry of Ecology and Environment of the People's Republic of China (https://www.mee.gov.cn). (B) Conservation efficiency of different strategies for human-used plants. Strategy A: PAs + I conservation gaps; Strategy B: PAs + (I+II conservation gaps); Strategy C: PAs + (I+II+III conservation gaps).

mal PAs is a fundamental principle of systematic conservation planning for regional PAs optimization.[57,77] Thus, this study identifies Strategy A as the optimal solution, with Level I conservation gaps (7.5% of the HMA areas) incorporating into current PAs. The identified conservation gaps in this study demonstrate high conservation effectiveness, with the Level I conservation gap requiring more attention in optimizing HMA protected areas, such as the Central-Eastern Himalayas, the central and southern Hengduan Mountains, and the western Tian Shan Mountains. These areas align with global biodiversity hotspots and current conservation gaps for endemic, endangered, and perennial plants.[78-80] Moreover, the Level I conservation gap strongly overlaps with the seven global biodiversity conservation priority templates, specifically with the Level I Conservation Priority Zones and Level I Cost-Effective Zones.[81] Notably, nearly half (49.8%) of the Level 1 conservation gaps identified in this study are located in China. The "Action Plan Priority Areas" outlined

in China's Biodiversity Conservation Strategy and Action Plan cover 70.4% of the country's Level 1 conservation gap areas, indicating that Strategy A is in alignment with national conservation strategies and is likely to receive policy support. This suggests that our protection strategy for human-used plants in high-altitude cold regions will contribute to the goals of the Convention on Biological Diversity by integrating the impact of cryosphere retreat.

Limitations and feasibility

Our study has some limitations that are crucial to consider when interpreting our findings. First, our definition of "human-used plants" is grounded in their documented relationship with human use. We analyzed 3,716 human-used plants species belonging to 1,293 genera and 220 families and compile 123,782 geographic reference records. These species include wild, cultivated, introduced, or even regarded as weeds.[2] This study solely focuses on the abiotic driving factors that affect the potential distribution of human-used plants species richness such as bioclimatic factors, permafrost conditions, snow cover, human activities, terrain and soils, without considering biotic processes such as interspecific competition, invasion dynamics or functional trait variations. However, these complex ecological processes may affect species distribution and community composition, leading to uncertainties in predictions.

Additionally, although our analysis incorporated comprehensive species occurrence records and various environmental variables,[82] and adopted a multi-model framework, our projections indicate that climate change and cryosphere retreat are expected to drive significant changes in species distributions, thereby affecting regional biodiversity.[83,84] Nevertheless, the positive effects of permafrost degradation mainly reflect the short- to medium-term ecological responses. These models have limited capabilities in simulating the complex feedback in ecosystem dynamics, which would affect the accuracy of long-term ecological predictions. For instance, they often rely on the assumption of "ecological niche conservatism", which means that the niche of plant species remains stationary over time and cannot adapt to climate fluctuations.[85] However, plant species may change their ecological niches through adaptive evolution or phenotypic plasticity,[86] thereby increasing the uncertainty of models. Although principal component analysis and variance inflation factor were employed to reduce multicollinearity, the inherent covariation among elevation, climate variables, and cryospheric conditions indicates that certain residual confounding effects are likely unavoidable. Thus, this limitation should be taken into account when interpreting the elevational patterns identified in this study. Given that residual collinearity may affect the interpretation of SHAP values, the ranking of environmental drivers still requires a more in-deep understanding of the underlying mechanisms. Notably, our results identify statistical associations between species richness patterns and permafrost-related gradients, rather than establishing direct hydrothermal or cryogenic process controls. Future integration of process-based models will be essential to elucidate these causal mechanisms. Furthermore, this study did not fully integrate the impact of abrupt permafrost thaw, including thaw slump, thermal erosion, and thermokarst lakes, which may exert an influence on the effects of permafrost degradation.[76] However, current observational data on vegetation changes during the development of thermokarst landscapes are limited.[11,12,71] Thus, future research should strengthen relevant observations to provide a systematic understanding of plant species' responses to climate change. These efforts will provide a robust foundation for biodiversity conservation and ecosystem management.

Our proposed priority protection strategies demonstrate substantial feasibility, which is underpinned by their high spatial congruence, enhanced conservation effectiveness, and alignment with policy frameworks. The identified Conservation Priority Areas exhibit considerable overlap with global biodiversity hotspots and several international conservation priority frameworks, thereby highlighting their ecological importance and strategic value.[87] Notably, the Level I conservation gaps are closely aligned with the priority regions specified in China's national biodiversity conservation action plan, which in turn increase the likelihood of policy adoption and targeted resource allocation. Furthermore, Systematic Conservation Planning has been consistently validated for its capacity to optimize conservation outcomes under resource constraints, thereby providing a robust methodological basis for our strategies.[88] Although our protection strategies have incorporated the impacts of cryosphere retreat and aim to promote the objectives of the Convention on Biological Diversity, they remain subject to various sources of uncertainty. First, socio-economic constraints, including implementation costs, land-use competition, and stakeholder acceptance, pose significant challenges to the feasibility of the proposed strategies, particularly in high-altitude cold regions.[89] Second, uncertainties in ecosystem dynamics must be considered: permafrost degradation and habitat shifts driven by climate change may undermine the future suitability of priority conservation areas, introducing temporal sensitivity into the current spatial planning.[90] Additionally, variations in the intensity of human activities, such as grazing expansion and infrastructure development, may further destabilize fragile ecosystems, thereby exacerbating the uncertainty of conservation outcomes.[91] To enhance the feasibility of these strategies, future efforts should integrate a multi-dimensional socio-economic evaluation framework to quantify the social value of human-used plants and the broader ecosystem benefits of conservation. Strengthening community-based management and benefit-sharing mechanisms, such as ecotourism and sustainable resource use, could foster local engagement, reduce potential conflicts, and improve the long-term sustainability of the strategies.[92,93] Our study underscores that the changes in human-used plant biodiversity are substantially influenced by cryosphere retreat, highlighting the urgent need to incorporate these impacts into future conservation strategies for cold regions.

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AUTHOR CONTRIBUTIONS

C.M. and J.S. designed the study, interpreted the results and wrote the paper. J.S. analyzed all the data and finished the figures. M.M., Y.J., K.L and Y.W. helped to make the figures. T.D., X.M., C.Z., P.L. and X.D. contributed to the discussion of the study and improved the paper. R.L., Sonam Wangchuk provided advice, ideas, and discussion. All authors contributed to the discussion and revision of the paper. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

All data needed to evaluate the conclusions are present in the paper and/or the Supplementary Information.

SUPPLEMENTAL INFORMATION

It can be found online at https://doi.org/10.59717/j.xinn-geo.2026.100221.