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Incorporating Genetic Diversity to Optimize the Plant Conservation Network in the Third Pole

Moses C. Wambulwa[1,2,3] | Guang-Fu Zhu[1,2] | Ya-Huang Luo[1,4] | Zeng-Yuan Wu[2] | Jim Provan[5] | Marc W. Cadotte[6] | Alistair S. Jump[7] | Francis N. Wachira[3] | Lian-Ming Gao[1,4] | Ting-Shuang Yi[2] | Jie Cai[2] | Hong Wang[1] | De-Zhu Li[2,4] | Jie Liu[1,2,6]

[1]CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan, China | [2]Germplasm Bank of Wild Species & Yunnan Key Laboratory of Crop Wild Relatives Omics, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan, China | [3]Department of Life Sciences, School of Science and Computing, South Eastern Kenya University, Kitui, Kenya | [4]Lijiang Forest Biodiversity National Observation and Research Station, Kunming Institute of Botany, Chinese Academy of Sciences, Lijiang, Yunnan, China | [5]Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, Aberystwyth, UK | [6]Department of Biological Sciences, University of Toronto-Scarborough, Toronto, Ontario, Canada | [7]Biological and Environmental Sciences, University of Stirling, Stirling, UK

Correspondence: De-Zhu Li (dzl@mail.kib.ac.cn) | Jie Liu (liujie@mail.kib.ac.cn)

ABSTRACT

Climate change poses a significant threat to the survival of many species. Although protected areas can slow down biodiversity loss, they often lack systematic planning and do not integrate genetic diversity. Genetic diversity is a key prerequisite for species survival and the ability to tolerate new conditions. Using population genetic and distribution data from 96 plant species in the Third Pole (encompassing the Tibetan Plateau and adjacent mountains), we mapped patterns of genetic diversity, projected climate-driven range dynamics and future genetic erosion, and designed an optimal conservation framework for the region. We identified several patches of high haplotype diversity (H_D), with a relatively high number of haplotypes in southeastern Third Pole. Regression models revealed that climate and topography have interacted to shape patterns of genetic diversity, with latitude and precipitation being the best predictors for H_D of cpDNA and nrDNA, respectively. Ecological niche modeling predicted an approximate 43 km northwestward and 86 m upward shift in suitable habitats under future climate scenarios, likely leading to a significant loss of up to 13.19% and 15.49% of cpDNA and nrDNA genetic diversity, respectively. Alarmingly, 71.20% of the newly identified conservation priority areas fall outside of the existing protected areas and planned National Park Clusters. Therefore, we recommend expanding the network by 2.02×10^5 km² (5.91%) in the Third Pole, increasing the total conserved area to 1.36×10^6 km² (39.93%) to effectively preserve the evolutionary potential of plants. This study represents an innovative attempt to incorporate genetic diversity into biodiversity conservation efforts.

1 | Introduction

Climate change poses a significant threat to biodiversity (Boonman et al. 2024), with approximately 40% of plant species at risk of extinction in the coming decades (Antonelli et al. 2020). For example, the 2019 United Nations (UN) report on biodiversity and ecosystem services (IPBES 2019) projects that a 2°C increase in global temperature will lead to the extinction of at least 5% of all species. Indeed, many studies have reported an accelerated loss of species in the Anthropocene, with endemic taxa likely to face the greatest risk (Yu et al. 2022). The most powerful approach to reduce anthropogenic pressure on ecosystems has been the establishment of protected areas, which act as present-day biodiversity refugia (Mi et al. 2023), protecting biodiversity across multiple levels of biological organization. However, there is compelling evidence that more than 27% of the world's protected areas are located in regions where the effects of climate change and land-use change will peak by 2050 (Asamoah et al. 2021). Since the year 2010, many national governments have been expanding their protected areas, but this has not necessarily improved conservation effectiveness (Maxwell et al. 2020) because most existing protected areas were established without systematic evidence-based planning and therefore did not capture key conservation features in target areas during planning phases (Visconti et al. 2019; Xu et al. 2019). Furthermore, the lack of a comprehensive approach that considers all levels of biodiversity (Cadotte and Tucker 2018) contributes to undermining the conservation value of existing protected areas. Consequently, the adoption of a systematic evidence-based approach that considers multiple levels of biological organization during the establishment of protected areas is needed.

The traditional approach to biodiversity conservation has been largely informed by data at the species level, but there is a growing consensus that taxonomic ranks might not always be the most appropriate targets for effective conservation interventions (Cadotte and Tucker 2018; Corlett 2023; Hoban et al. 2020b). Furthermore, much emphasis has been placed on phylogenetic and ecosystem diversity (Hua et al. 2022; Willig et al. 2023; Yang et al. 2019), thus relegating genetic diversity to a subordinate position in conservation programs. Population-level genetic diversity plays a crucial role in maintaining the evolutionary potential of species, enabling them to adapt and persist in changing environments (Steeves et al. 2017). Species respond to climate change by persistence (through genetic adaptation or phenotypic plasticity), range dynamics (shifts, contractions, and expansions), or extinction (Waldvogel et al. 2020). Although range contractions have so far been demonstrated in relatively few of the species that have been assessed (Wiens 2016), such range losses are expected to lead to a significant reduction in intraspecific genetic diversity (Hoffmann et al. 2017). The Convention on Biological Diversity (CBD) and the International Union for Conservation of Nature (IUCN) emphasize the need to elevate the importance of genetic diversity in conservation programs; for example, the first goal of the Global Biodiversity Framework includes the maintenance of genetic diversity by 2050, but this level of biodiversity is rarely considered by most practitioners (Hoban et al. 2020a), except perhaps for restoration programs (Holl et al. 2022). Whenever considered, genetic diversity is often treated in isolation, disconnected from other conservation issues such as climate change,

species diversity and distribution shifts, as well as the threat status of species (Pearman et al. 2024). Against this background, conservation initiatives should adopt integrative macrogenetic approaches at both spatial and temporal scales, since such approaches can support more meaningful practice and policy guidelines around conservation planning (Schmidt et al. 2023), particularly at the regional scale.

Climate change is associated with significant evolutionary dynamics in many taxa, with at least 10% of plant and animal genetic diversity estimated to have already been lost during the Anthropocene (Exposito-Alonso et al. 2022; Leigh et al. 2019). This loss might be greater among genetically diverse taxa than in genetically depauperate taxa (Lyam et al. 2022). With the Global Biodiversity Framework (GBF) goal to conserve at least 90% of all genetic diversity within individual species on the planet (CBD 2021), there is a growing need to understand patterns of standing genetic diversity and its potential loss as climate changes. The growing volume of georeferenced population genetic data across taxa has permitted meta-analyses to test the impact of global change on genetic diversity (Kort et al. 2021; Hu et al. 2021; Miraldo et al. 2016), with most studies generally reporting significant genetic vulnerability. However, most of these investigations were conducted primarily at national or global scales, with a limited focus on key regional biodiversity hotspots. Furthermore, most of these meta-analyses directly retrieved genetic data from published studies without reconstruction of genetic matrices to ensure data standardization. As data availability continues to improve, meta-analyses have the potential to integrate genetic diversity data with changes in species distribution ranges to allow pragmatic and systematic conservation planning. Ecological niche models (ENM) have been widely applied in forecasting the distributions of species under various climate scenarios, as well as in optimizing protected areas (Garzon et al. 2021; Lin et al. 2021). Although probabilistic in nature, these predictive models remain the most reliable for predicting species distributions and extinction probabilities (Zurell et al. 2023). Modeling the spatio-temporal dynamics of species under the ongoing climate change is, therefore, a key research priority, inspired largely by the projection that some ecosystems, including those of the Third Pole, are on the brink of collapse (Liu et al. 2018). Combining predictions on species distributions and genetic diversity can support the adoption of proactive mitigation strategies, which can reduce the loss of terrestrial biodiversity by up to 60% (Warren et al. 2013).

The Third Pole (i.e., Tibetan Plateau *sensu lato*) is an area within the Pan-Tibetan Highland and encompasses the Tibetan Plateau (*sensu stricto*), the Hengduan Mountains, the Himalaya, and part of the Mountains of Central Asia, and has an average elevation of 4054 m (from 88 to 8848 m) and a total area of $3.42 \times 10^6 \, \text{km}^2$ (Liu et al. 2022), with a significant portion located within China (Figure 1A). The region hosts some of the world's key biodiversity hotspots (Mittermeier et al. 2004), supporting at least 18,000 vascular plant species (Liu et al. 2022), with about 20% of the species being endemic to the region (Wen et al. 2014). Despite the high species richness and endemism, the region is highly vulnerable to climate change (Liu et al. 2018), with temperature extremes in the region predicted to intensify with global warming (Yang et al. 2022). Over the past decades, research on the response of species to climate change in the Third Pole has
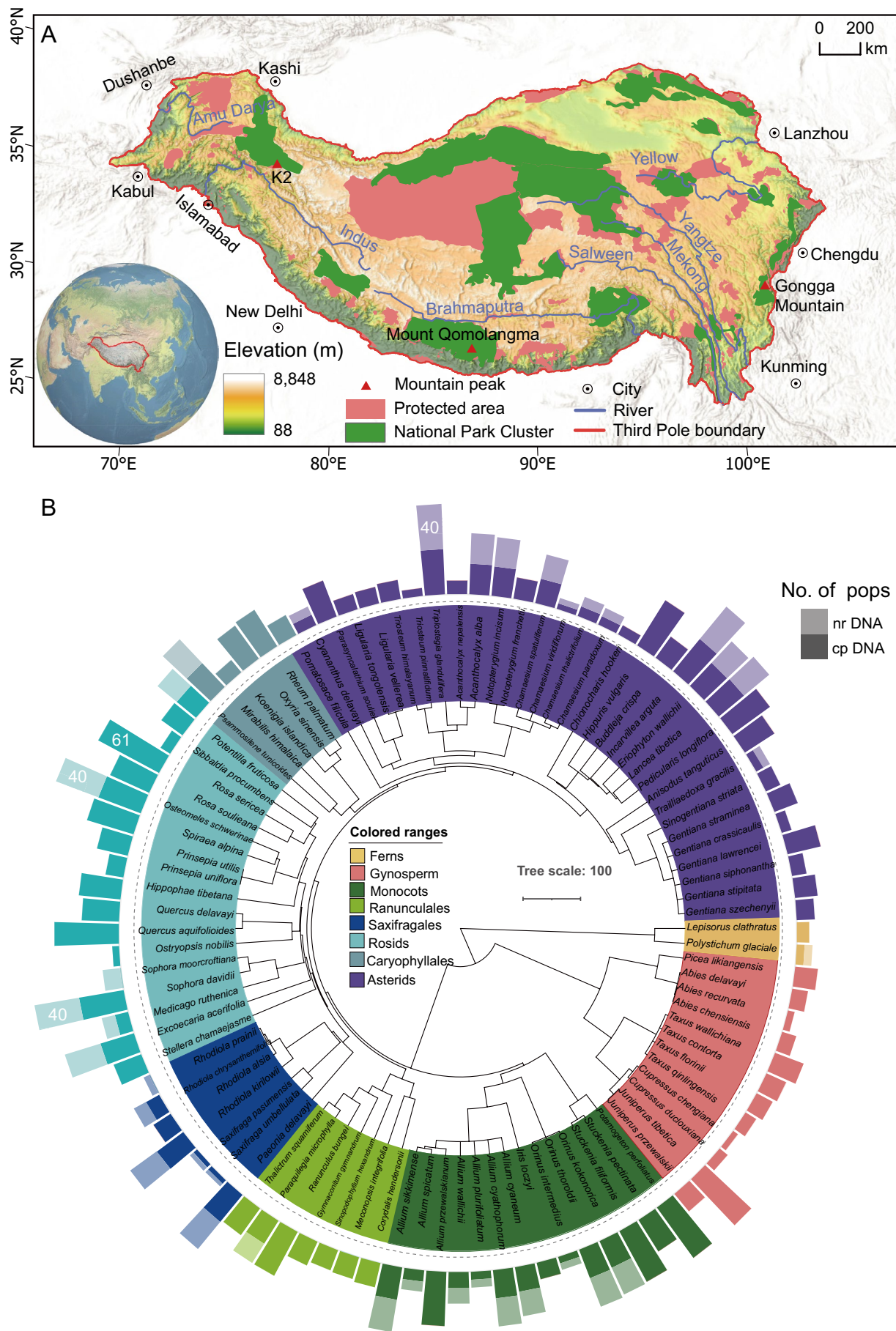
FIGURE 1 | Legend on next page.

FIGURE 1 | The Third Pole region and the 96 plant species included in the meta-analysis. (A) Geographical features (rivers, mountains, and topography) and conservation elements (distribution of Protected areas and National Park Clusters candidates) in the Third Pole. Data on protected areas were sourced from the World Database on protected areas (WDPA) and China's National Nature Reserves (CNNR), while the National Park Clusters were adopted from the delineation by Yang et al. (2023). (B) A phylogenetic depiction of the 96 plant species analyzed in the study, with different colors representing different taxonomic groups. The phylogenetic tree was constructed using V. PhyloMaker2 (Jin and Qian 2022). Bars lengths around the tree are proportional to the number of populations per species, with the maximum number indicated for each dataset. The inner bars indicate species for which cpDNA data were available, while the outer bars indicate species with nrDNA data. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

attracted immense interest from researchers around the world (Chang et al. 2022), but with the majority of studies focusing on single species or just a few congeners; hence, these studies have had limited generalizability and applicability for conservation. The Third Pole hosts a protected area system consisting of at least 50 protected areas, which cover approximately one third of its land area (Li et al., 2018b; Liu et al. 2022) (Figure S1). However, protected areas in the region are mostly fragmented, with inadequate biodiversity and ecosystem services coverage (Xu et al. 2019), underscoring the need to undertake empirically based systematic conservation planning in this region. To address these gaps, Chinese authorities recently proposed the National Park Clusters system (Tang et al. 2023) (Figure S1 and Table S1), which holds great promise for the protection of biodiversity in the region. Furthermore, several studies have attempted to optimize the protected area system in the Third Pole based on conservation features such as phylogenetic diversity, species traits, habitats, ecosystem services, and environmental units (Hu et al. 2023; Hua et al. 2022; Li et al. 2018a, 2020; Saqib et al. 2024; Yang et al. 2019), and identified notable conservation gaps for biodiversity and ecosystem services. For instance, Hu et al. (2023) used species distributions, carbon storage patterns, and geographical environmental variables to assess conservation networks in the Third Pole, demonstrating that at least 20% of protected areas in the region will be lost due to climate change. Parallel assessments of protected area effectiveness have been made at smaller spatial scales in the Third Pole, including the identification of 19 conservation priority areas in Western Himalaya using phylogenetic diversity and endemism, among other metrics (Saqib et al. 2024). Despite the great insights from existing studies, the non-genetic metrics lack the capacity to establish the evolutionary potential of species, which is critically important for adaptation and persistence. Since climate change is projected to disrupt local adaptation in many ecosystems (Anderson and Wadgymar 2020), it is important to enhance the adaptive capacity of conservation networks in the Third Pole by incorporating genetic diversity in the planning process.

Here we combine genetic diversity and species distribution data from published works with geographic information system (GIS) tools to optimize the existing conservation network for plants in the Third Pole. Specifically, this study aimed to (1) map patterns of plant genetic diversity, (2) determine the drivers of plant genetic diversity, and (3) identify conservation priority areas and design an optimal plan to protect the evolutionary potential of plant species in the region. Based on a comprehensive meta-analysis of 96 plant species distributed in the Third Pole, we hypothesize that ongoing climate change will significantly reduce the existing plant genetic diversity. This decline is anticipated to result from an overall reduction of suitable ranges, driven by

a combination of climatic, topographic, and anthropogenic factors. In the context of intensified global efforts to mitigate the effects of climate change, our study provides a robust framework to guide future regional and national policy decisions related to biodiversity conservation.

2 | Materials and Methods

2.1 | Data Collection and Genetic Diversity Analyses

We focus on the Third Pole, which encompasses the Tibetan Plateau and adjacent mountains (Figure 1 and Figure S1), as delineated by Liu et al. (2022). The region exhibits high ecological diversity, with at least 12 vegetation types that range from evergreen broadleaved forests in the southeast to alpine screes in the northwest and central regions (Huang et al. 2023). We conducted a literature search on Google Scholar for articles published between the years 2000 and 2022. We used the following search string: "Tibetan Plateau" OR "Qinghai-Tibet Plateau" OR "Qinghai-Tibetan Plateau" OR "Himalaya" OR "Himalayas" OR "Hengduan Mountains" OR "southwestern China" AND "plant" AND "phylogeography" OR "genetic diversity" AND "chloroplast DNA" OR "nuclear DNA" AND "haplotype". After manual filtering, we retained a total of 129 published articles reporting genetic data for 242 plant species that suited our aim. We then used strict criteria for the inclusion of species or populations in our study: (1) based on occurrence data (from journal articles and databases such as GBIF, NPSRC, iNaturalist, PPBC, GBoWS, BHM; Table S2), 50% of the populations of a given species must be distributed within the Third Pole, (2) a species must have at least four populations with genetic data within the study area, (3) each population must have at least five individuals, (4) each species must have at least two haplotypes, and (5) a species must have at least 12 occurrence points. After applying these criteria, a total of 70 articles reporting genetic data for 96 plant species were retained for subsequent analysis (Tables S3 and S4). We then generated a phylogenetic tree for the 96 species using the R package *V.PhyloMaker2* (Jin and Qian 2022). For the species missing in the database, we added them to the midpoint of their genus or family branch using 'Scenario 3' (Jin and Qian 2022). Of these 96 species, chloroplast DNA (cpDNA) sequence data were available for 92 species (2141 populations), while nuclear DNA (nrDNA) sequence data were available for 38 species (757 populations) (Tables S3 and S4). The majority of the cpDNA sequences were tRNA (trn) intergenic spacers, while the nrDNA sequences were mostly the internal transcribed spacer (nuclear ITS) of the nuclear ribosomal DNA (Table S4). A total of 34 species had both cpDNA and nrDNA data. For each of

the populations of the selected species, geographic coordinates (longitude and latitude) in the articles were recorded. The haplotype information was retrieved from published articles, and the corresponding cpDNA and nrDNA sequences were then downloaded from GenBank (https://www.ncbi.nlm.nih.gov) using the accession numbers provided in the articles (Table S4). Where sequence data for some species were not publicly available, they were obtained directly from the authors (Table S4). To ensure the usage of current and widely accepted taxonomic names, all scientific names were validated using the POWO, Tropicos, and iPlant databases (Table S2). Distribution points were subsequently adjusted to align with the updated species names and their synonyms.

Based on the haplotype data provided in the articles, we reconstructed the population and species sequence matrices. These matrices were aligned using the MAFFT algorithm (Katoh and Standley 2013) implemented in Geneious v2020.0.3 (https://www.geneious.com). The alignments were carefully checked and manually edited as necessary to ensure consistency with the published data. Subsequent population genetic analyses were performed as described in our previous study (Wambulwa et al. 2022). Briefly, we used DnaSP v5.10 (Librado and Rozas 2009) to define populations and to generate species haplotype files. Arlequin v3.5.2 (Excoffier and Lischer 2010) was then used to estimate genetic diversity (haplotype diversity, H_D and nucleotide diversity, π) and population pairwise genetic differentiation (F_{ST}) (Tables S5 and S6). These analyses were conducted separately for the two datasets (cpDNA and nrDNA). Given the high correlation between H_D and π, we selected H_D for all downstream analyses.

2.2 | Spatial Patterns of Species Distribution, Genetic Diversity, and Population Divergence

The locations of the populations, total haplotypes, and private haplotypes were mapped and visualized in ArcGIS Pro v2.9.2 (ESRI, Redlands, CA, USA). Landscape surfaces of genetic diversity (haplotype diversity, H_D) and genetic divergence (F_{ST}) were generated by dividing the study area into $50\,km \times 50\,km$ grids using R scripts in the *terra* R package (Hijmans et al. 2022) and in-house python scripts. We then calculated the mean H_D and F_{ST} for all populations across all species in each grid and performed inverse distance weighted (IDW) interpolation based on the mean values obtained per grid. Interpolation of H_D was performed in R using the *terra* package, while for genetic divergence, the F_{ST} data were first transformed using the Triangulated Irregular Network (TIN) prior to interpolation using a Python script modified from the Genetic Landscapes GIS Toolbox (Vandergast et al. 2011). All in-house python and R scripts used in this study have been deposited at Zenodo (Zhu et al. 2025). All maps were displayed using the Asia-North Albers equal area conic projection (ESRI:102025).

2.3 | Spatial Regression of Genetic Diversity With Explanatory Variables

We extracted 32 explanatory variables, including longitude, latitude, as well as 30 others extracted from six databases (Worldclim, GCAM-Demeter, WoSIS, Human-Footprint, SEDAC, and gHM) at a resolution of 2.5 min. These variables were grouped into four categories: climatic, topographic, edaphic, and anthropogenic factors (Table S7). To explore the effects of these explanatory variables on genetic diversity (H_D), we first conducted Random Forest analysis to rank these predictors based on their relative importance. We then selected the top 10 variables that reduced the mean square error over random permutations and used them as predictors in the subsequent model selection. To mitigate the influence of multicollinearity on the model-building process, we performed a Pearson correlation analysis on these 10 variables. For pairs of variables with a correlation coefficient (r) larger than 0.7 at $p < 0.01$, we excluded the less important variable as determined by the Random Forest ranking. After Pearson's correlation, nine variables were retained for the cpDNA dataset (longitude, latitude, aspect, Bio2, Bio3, Bio15, Hfp, Hii, and Hpd), while eight variables were retained for the nrDNA dataset (longitude, latitude, aspect, Bio2, Bio12, Bio13, Hii, and Hpd) (Table S7). The retained variables were then used in the subsequent regression analysis.

The response variables (haplotype diversity, H_D) were extracted from the interpolated genetic diversity maps of cpDNA and nrDNA at the same spatial resolution as explanatory variables. To examine the effects of the abiotic variables on genetic diversity, we used generalized linear models after standardization of genetic diversity metrics to produce variables with a normal distribution. Model selection was then accomplished by comparing Akaike Information Criterion (AICc) values for all alternative models using the *dredge* function (Barton 2019). Candidate models based on a threshold of $\Delta AICc < 2$ were selected, and model averaging was performed to account for model uncertainty. To quantify the relative contribution of the four categories of variables (climatic, topographic, edaphic, and anthropogenic) on the observed patterns of genetic diversity, we calculated the relative importance of each category. This was done by examining the relationship between the beta coefficient of a given predictor and the sum of the absolute value of the beta coefficients of all predictors. All explanatory variables were scaled prior to modeling analysis to ensure comparability. Additionally, to test whether genetic diversity was associated with species richness, we ran the linear models to assess the effect of species richness on genetic diversity, calculating the adjusted R^2 value for each model. The statistical analyses were performed using the *nlme* package (Pinheiro et al. 2014), *MuMIn* (Barton 2019), and *randomForest* (Liaw and Wiener 2002) packages. All these analyses were performed in R software (version 4.2.3) (R Core Team 2023).

2.4 | Ecological Niche Modeling

We integrated species distribution data from seven sources (Table S2) and applied the *thin* function in the *spThin* package (Aiello-Lammens et al. 2015) to filter the records with a thinning distance of 5 km. This step resulted in a total of 17,972 occurrence points for downstream analyses, with the occurrence density map displayed at $50\,km \times 50\,km$ resolution (Figure S2). Each species had at least 31 occurrence points, except for *Orinus intermedius* (12 points) and *Saxifraga pasumensis* (13 points) (Table S8). For environmental variables, we used the 30 variables mentioned earlier in the regression

analysis (Table S7). After removing highly correlated variables (VIF > 10) using the *vifstep* function in the *usdm* package (Naimi et al. 2014), 14–20 variables were finally retained for each species (Table S7), and a total of 25 variables were retained for subsequent analysis.

Since parameter calibration is critical in ENM analysis, we began by splitting the presence points using the 5-fold cross-validation blockCV's package (Valavi et al. 2018). Next, we calibrated Maxent parameters (17 values of regularization multiplier, and all 31 possible combinations of 5 feature classes) using the *kuenm* R package (Cobos et al. 2019). The final optimized parameters are presented in Table S9. To account for methodological uncertainties in models, we employed five frequently used algorithms for the 96 selected plant species using the *sdm* R package (Naimi and Araújo 2016): generalized linear model (GLM), boosted regression trees (BRT), random forests (RF), support vector machine (SVM), and maximum entropy (Maxent). The calibration region was delimited based on alpha-hull polygons with a 200 km buffer distance using the *getDynamicAlphaHull* function in the *rangeBuilder* package (Davis Rabosky et al. 2016). For each species, we generated 1000 pseudoabsence (background) records in their calibration regions using the *randomPoints* function in the *dismo* package (Hijmans et al. 2022). Resampling by bootstrapping with 10 replications was used to generate the training (70%) and test (30%) datasets. A total of 50 models were fitted per species, resulting in 4800 models across all species. Model performance was evaluated using the area under the curve of the receiver operating characteristic (AUC) and the true skill statistic (TSS). For each species, Models that failed to meet the performance threshold (AUC < 0.8) were excluded. The remaining models were used to characterize the potential distribution of each species during the Last Glacial Maximum (LGM), present, and future (2090-SSP126 and 2090-SSP585). For each species, ensemble models were generated to calculate a consensus potential climatic distribution for the present period based, weighted by AUC scores. The same approach was applied to project the species distribution to the LGM and the future period.

Species probability maps were transformed into binary distribution maps (presence/absence) by maximizing the sum of sensitivity and specificity (max SSS), which has been confirmed to be the best threshold criterion (Liu et al. 2013). To simulate the dispersal of the species in the region, we used MigClim, a cellular automaton designed to simulate both short-distance and long-distance dispersal under future climate change scenarios (Engler et al. 2012). Given the difficulty in obtaining accurate dispersal behavior for each species, we classified the 96 species into seven dispersal categories (Vittoz and Engler 2007), and set the long-distance dispersal maximum distance according to Engler et al. (2009) (Table S10). Dispersal was simulated for each year, except for categories 1–3 (10-year intervals) and category 4 (three-year intervals). MigClim parameters were set as follows: *dispKernel* with a negative exponential dispersal Kernel, *barrierType* defined as weak, *lddFreq* set to 0.01, *iniMatAge* set to 2, and *propaguleProd* defined as c (0.01, 0.08, 0.5, 0.92) (Chauvier-Mendes et al. 2024). Additionally, the GLIMS glacier (Raup et al. 2007) was incorporated as a barrier layer, assuming that permanent glaciers will remain unsuitable for colonization in

the coming decades. We used the potential suitable area from 1970 to 2000 as the initial distribution layer, and 2090 as the habitat suitability layer. To ensure compatibility between the ENM simulation resolution and the MigClim dispersal distance, the ENM results were downscaled to 15 s (approximately 500 m at the equator) using the *disagg* function of the *terra* package. All simulations were repeated three times, and the grids selected in at least two iterations were retained as presence locations.

We then stacked the binary maps for all 96 species for each period to generate the species richness map. Subsequently, we calculated the differences in species richness and beta diversity (turnover and nestedness) between paired periods (LGM-present and present-2090) (Baselga and Orme 2012). To assess dynamic changes in species distribution, we computed the suitability-weighted centroid of the climatically suitable range for each species during each pair of periods (LGM-present and present-2090). The magnitude and direction of the centroid shift were calculated, and the centroids were subsequently converted to the World Mercator projection (EPSG: 3395) to calculate the direction of the shift. The magnitude of the shift was then calculated using the *spDists* function of the *sp* package (Pebesma and Bivand 2005), which calculates true Euclidean distance irrespective of the projection geometry. Additionally, the shift distance and angle were mapped in ArcGIS Pro. Finally, using the *terra* package, we quantified changes in area, elevation, latitude, and longitude for each species across different periods. The results were visualized using the *ggplot2* package (Wickham 2016). All ENM analyses were performed in R software.

2.5 | Potential Loss of Genetic Diversity

By integrating genetic diversity with ENM analysis, we quantified the potential loss of genetic diversity driven by the predicted range contractions. This approach relies on the assumption that genetic variation within populations will be conserved in the future without adaptation and migration (Peterson 2011). Therefore, genetic variations within populations inhabiting unsuitable areas were projected to be lost in the future. This method was previously applied to quantify the loss of genetic diversity in northern plant species (Alsos et al. 2012) and to uncover the cryptic loss of genetic diversity in underwater forests following a marine heatwave (Gurgel et al. 2020). We used a modification of this approach to quantify the potential loss of plant genetic diversity in the Third Pole. Using the range dynamics observed in the ENM analysis, we recalculated the amount of genetic diversity (haplotype diversity, total haplotypes, and private haplotypes) after excluding populations located in unsuitable areas under the two future climate scenarios. Total and private haplotypes expected to be lost in the future were determined for each population and summed; then the percentage of lost haplotypes was computed for each dataset (cpDNA and nrDNA) (Table 1). To avoid the emergence of false private haplotypes in the future, we used the present distribution of private haplotypes as the baseline for the recalculation, allowing private haplotypes in the future only if they existed in the present period. Haplotype diversity (H_D) estimates for the present and the two future climate scenarios were averaged across populations and species. Significant differences between periods were assessed using the paired sample *t*-test.

TABLE 1 | Projected loss of cpDNA and nrDNA genetic diversity based on modelled future species distributions for both 2090-SSP585 and 2090-SSP126 climate scenarios.

Scenario	Marker	S	N	N_L (%)	N_T	N_{TL} (%)	N_P	N_{PL} (%)	H_D	H_{DL}
2090-SSP585	cpDNA	23,815	2141	252 (11.77)	1259	104 (8.26)	728	96 (13.19)	0.735 ± 0.189^a	0.725 ± 0.192^b
	nrDNA	8994	757	90 (11.89)	598	64 (10.70)	368	57 (15.49)	0.743 ± 0.201^a	0.719 ± 0.235^a
2090-SSP126	cpDNA	23,815	2141	204 (9.53)	1259	93 (7.39)	728	72 (9.89)	0.735 ± 0.189^a	0.728 ± 0.197^a
	nrDNA	8994	757	74 (9.78)	598	53 (8.86)	368	47 (12.77)	0.743 ± 0.201^a	0.715 ± 0.235^a

Note: Different superscript letters (a, b) indicate the significant difference based on paired samples *t*-test.
Abbreviations: H_D, genetic diversity (mean ± sd) under present scenarios; H_{DL}, genetic diversity (mean ± sd) under future scenarios; N, number of populations under present scenarios; N_L, number of populations lost under future scenarios; N_P, number of private haplotypes under present scenarios; N_{PL}, number of private haplotypes lost under future scenarios; the percentage value in parentheses represents the proportion of lost populations or haplotypes; N_T, number of total haplotypes under present scenarios; N_{TL}, number of total haplotypes lost under future scenarios; S, number of individuals under current scenarios.

2.6 | Identification of Conservation Priority Areas

To optimize the conservation network in the Third Pole, we divided the region into $10\,km \times 10\,km$ grids as planning units, giving a total of 34,878 planning units. Marginal grids were retained only if at least 50% of the grid area fell within the Third Pole, finally producing 34,161 planning units. For optimization, we used Marxan v4.0.6 (Watts et al. 2009), a decision support model designed to identify conservation priority areas with minimal cost and optimal connectivity, while also outputting an irreplaceability value for each conservation unit. We incorporated three conservation features into the analysis: cpDNA haplotype diversity, nrDNA haplotype diversity, and the current species distribution range target. The presence and absence genetic hotspot data were generated by converting the haplotype diversity raster of each species to a binary raster based on a threshold of > 1.5 standard deviations from the mean (Wambulwa et al. 2022). Human population density data (https://sedac.ciesin.columbia.edu/data/collection/gpw-v4) were $\log_{10}$ transformed and used as an economic cost layer, as areas with higher human intensity incur a greater cost for establishing new conservation units (Ma et al. 2021). The prop parameter was quantified for each species by assigning coefficients to the respective levels based on the International Union for Conservation of Nature (IUCN; https://www.iucn.org/) Red List of Threatened Species, the List of National Key Protected Wild Plants in China (LNKPWP; https://www.gov.cn/zhengce/zhengceku/2021-09/09/content_5636409.htm), and the Convention on International Trade in Endangered Species (CITES; https://checklist.cites.org) (Ma et al. 2022) (Table S11). Species lacking IUCN data were evaluated using the *redlistr* R package (Lee et al. 2019) (Table S12). We then calculated the proportion of conservation features using the formula:

$$COF_B \left[1 + mean \left(COF_I + COF_C + COF_P \right) \right]$$

where COF_B represents the basic coefficient of each species (set at 0.3 for ENM, and at 0.45 for genetic data), while COF_I, COF_C, and COF_P represent coefficients for IUCN, CITES, and LNKPWP, respectively.

Using haplotype diversity data from cpDNA (92 species) and nrDNA (38 species) alongside ENM data for the 96 species in the present period, we incorporated a total of 226 conservation features into Marxan analysis (Table S11). The ArcMarxan plug-in was used to generate Marxan input files and to determine the species penalty factor (SPF) and boundary length modifier (BLM) values. We ran Marxan with 1000 iterations and identified optimal conservation areas based on a selection frequency of > 800. To ensure the functionality and structural integrity of identified priority areas, only optimized areas $\geq 42,000\,km^2$ were considered in our Marxan results.

3 | Results

3.1 | Spatial Patterns of Species Richness and Genetic Diversity

The 96 species selected represent the main evolutionary lineages of vascular plants in the region, including ferns, gymnosperms, monocots, rosids, asterids, Ranunculales, and Caryophyllales (Figure 1B). The sampling richness for both datasets (cpDNA and nrDNA) was highest in the southeast part of the Third Pole (Figure S3). The densest $50 \times 50\,km$ grid for the cpDNA dataset included 25 species, 36 populations, and 423 individuals, while the densest grid for the nrDNA dataset contained 11 species, 18 populations, and 261 individuals (Figure S3). Species richness was found to have a weak effect on genetic diversity (H_D) ($R^2_{adj} = 0.06$ for cpDNA and $R^2_{adj} = 0.002$ for nrDNA), indicating that genetic diversity and species richness in the region are decoupled, thus separately offering novel and complementary information for conservation planning.

Haplotype diversity (H_D) was generally high on the eastern side of the Third Pole, with patches of high nrDNA H_D towards the western and northern parts of the region (Figure 2A,B). Across all populations, we identified a total of 1259 cpDNA haplotypes, of which 728 were private (haplotypes endemic to specific population) (Table S3). For nrDNA, we identified 598 haplotypes, of which 368 were private (Table S3). The distribution pattern of haplotypes was similar for both the cpDNA and nrDNA datasets, with regions such as Lijiang, Dêqên, Nyingchi, and Shangri-La harboring the highest number of haplotypes (Figure 2C–F and Figure S4). For both datasets, F_{ST} values were generally lower in the western part of the study area, likely due to the low number of populations sampled there (Figure S5). However, the highest pairwise F_{ST} values for cpDNA were detected on the Tibetan Plateau, while the highest values for nrDNA were concentrated towards the southeast in the Hengduan Mountains.
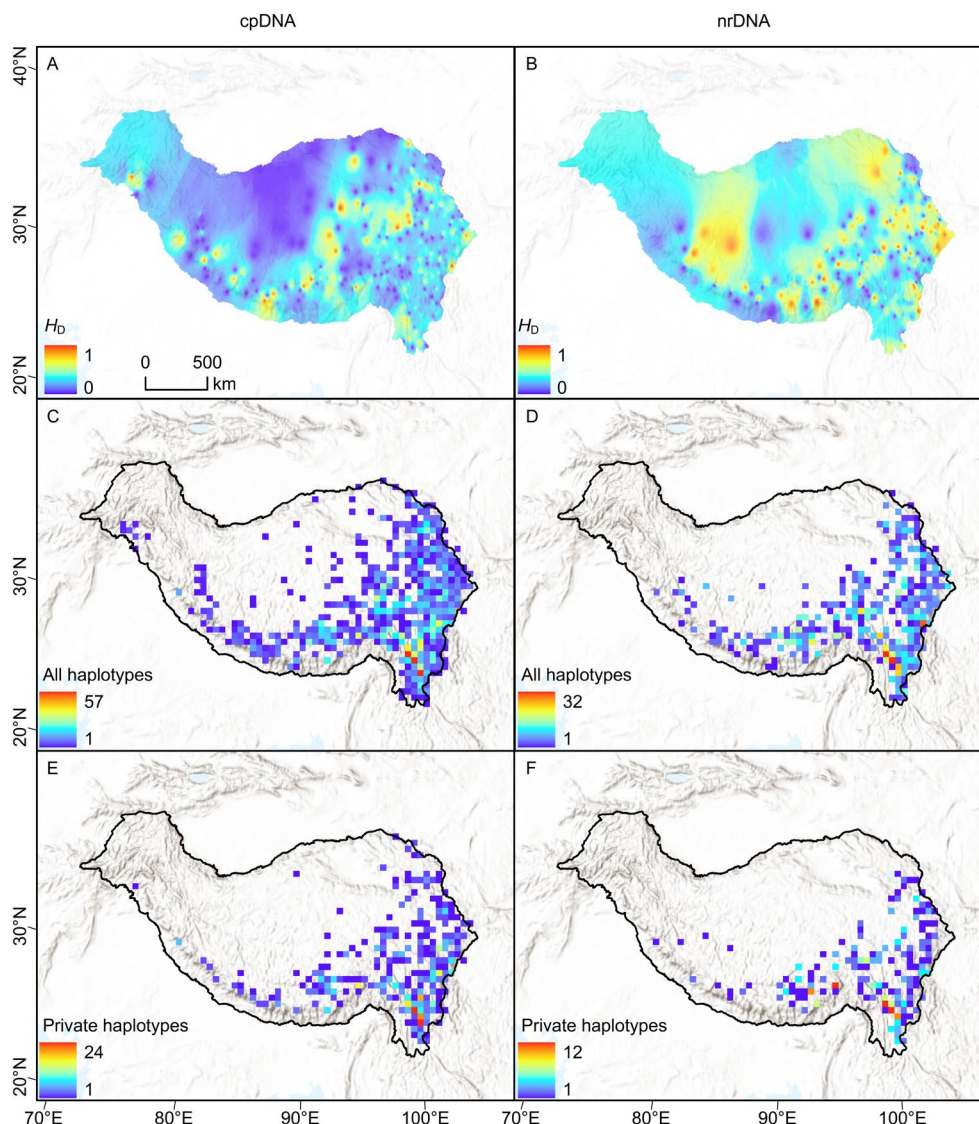
FIGURE 2 | Distribution of genetic diversity in the Third Pole. (A, B) Haplotype diversity (H_D) for cpDNA and nrDNA, respectively. The H_D maps were generated using the inverse distance weighted (IDW) interpolation method implemented using the *terra* R package and python scripts. (C, D) Total haplotypes for cpDNA and nrDNA, respectively. (E, F) Private haplotypes for cpDNA and nrDNA, respectively. All maps were generated at 50 km × 50 km resolution. The total and private haplotypes were mapped and visualized in ArcGIS Pro. Color bars in the bottom-left corner of each subplot indicate levels of haplotype diversity (A and B) or number of haplotypes (C–F), with red denoting the highest values and blue denoting the lowest. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

3.2 | Effects of Abiotic Variables on Genetic Diversity

Random Forest showed that climatic and topographic variables were generally the strongest descriptors of genetic diversity for both cpDNA and nrDNA datasets (Figure S6). After performing correlation analysis on the 10 best explanatory variables, nine and eight variables were retained for the cpDNA and nrDNA datasets, respectively (Figure 3A,B). The same six variables appeared in both selected models explaining genetic diversity: all three topographic variables (longitude, latitude, and aspect), one climatic (Bio2), and two anthropogenic variables (Hii and Hpd). Additional climatic variables for cpDNA included Bio3 and Bio15, while those for nrDNA were Bio12 and Bio13. Notably, the anthropogenic variable Hfp was specific to the cpDNA model.

Linear models showed that topographic and climatic variables accounted for most of the observed genetic diversity, with notable differences between the cpDNA and nrDNA datasets. Topography showed the strongest relative effect (42.54%) in the cpDNA dataset (Figure 3A), while climate had the strongest effect (83.77%) in the nrDNA dataset (Figure 3B). For both genetic datasets, anthropogenic variables had the least relative effect on genetic diversity. In the cpDNA model, latitude showed the strongest negative effect on genetic diversity, while longitude showed the strongest positive effect (Figure 3A). However, Bio13 had the strongest negative effect in the nrDNA model, while Bio12 showed the strongest positive effect. Overall, the strongest effects for the cpDNA and nrDNA models were latitude and Bio13, respectively (Figure 3). Anthropogenic variables had stronger effects on the genetic diversity of cpDNA compared to that of nrDNA. In
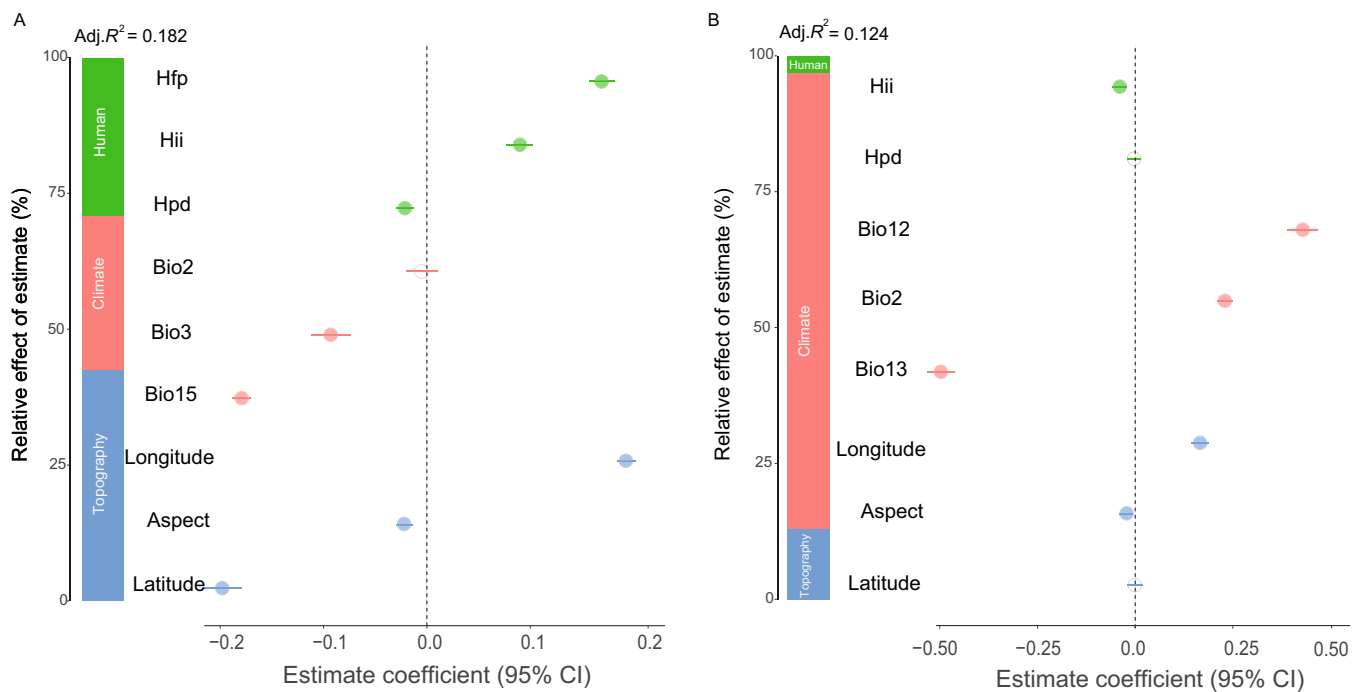
FIGURE 3 | Relative effects of explanatory variables on plant haplotype diversity (H_D) in the Third Pole. (A) Effects of the nine selected variables for the cpDNA sequence dataset. (B) Effects of the eight selected variables for the nrDNA sequence dataset. The colored vertical bars indicate the relative effect of each of the three variable categories: Topographic, climatic, and human variables, expressed as a percentage of explained variance. Plots A and B are based on the best models selected within the set AICc threshold (ΔAICc ≤ 2). The averaged estimated coefficients (standardized regression coefficients) of all selected variables are shown with their corresponding 95% confidence intervals (colored bars). Solid points indicate parameter estimates that were significantly different ($p < 0.05$) from zero (vertical dashed lines) while the hollow points indicate parameter estimates that were not significantly different ($p \geq 0.05$) from zero.

both models, all variables had statistically significant effects ($p < 0.05$), and the selected variables collectively explained 18.2% and 12.4% of the variation in the genetic diversity of cpDNA and nrDNA, respectively (Figure 3).

3.3 | Species Range Dynamics and Changes in Genetic Diversity

Model testing indicated robust predictive power for species distribution, with the lowest AUC and TSS values of 0.841 (mean = 0.892) and 0.574 (mean = 0.683) across species (Table S8). The variables considered showed varying degrees of importance in the ENM model, Bio8 being the most important (Table S13). During the LGM, the species were concentrated towards the eastern (Hengduan Mountains) and the southern (Himalaya) edges of the Third Pole (Figure S7A). The present distribution shows significant northeastward range expansion since the LGM, coupled with range contractions in the Himalaya and the Hengduan Mountains (Figure 4A and Figure S7B). On average, species moved northeastward from the LGM to the present, with a mean shift angle of 63.00° and mean shift distance of 139.30 km (Figure 4B). Future (2090-SSP585) species distribution area was comparable to that observed for the present distribution (Figure S7C,D), although most species appeared to shift toward the Tibetan Plateau, with further loss of range in the Himalaya (Figure 4C). This projected range contraction was also associated with the loss of a substantial proportion of populations (11.77% for cpDNA

and 11.89% for nrDNA under the SSP585 scenario; Table 1). Our results predicted an overall northward shift of species from the present to the future (2090-SSP585), with a mean shift angle of 79.10° and a mean shift distance of 42.64 km for the SSP585 scenario (Figure 4D). Species range dynamics under the optimistic scenario (SSP126) were generally consistent with the SSP585 scenario, but with minimal shifts, averaging a shift angle and distance of 60.23° and 20.55 km respectively (Figure S8). Across all transitions (LGM-present, present-2090), species range contractions and northward shifts suggest a potential net loss of species in the Hengduan Mountains and the Himalaya (Figure 4A–D). Changes in species beta diversity, turnover, and nestedness were higher for the LGM-present than for the other transitions (Figure S9). These changes were generally minimal in the southeastern part of the Third Pole but appeared to peak towards the western periphery, especially for the present-2090 transitions. Notably, beta diversity and nestedness were higher than turnover along the southern Himalayan border, highlighting complex shifts in species composition.

The mean longitude remained generally stable from LGM (97.58°) to 2090 (~97.9°), while latitude increased steadily from 30.44° during LGM to 31.06° and 31.16° in 2090-SSP126 and 2090-SSP585 respectively (Figure 4E and Figure S8E). The mean elevation for the species distributions during LGM was 3383.8 m, which steadily increased to 3611.7 m in the present period and to 3646.3 m and 3697.6 m in the 2090-SSP126 and 2090-SSP585 scenarios, respectively. The total average land area
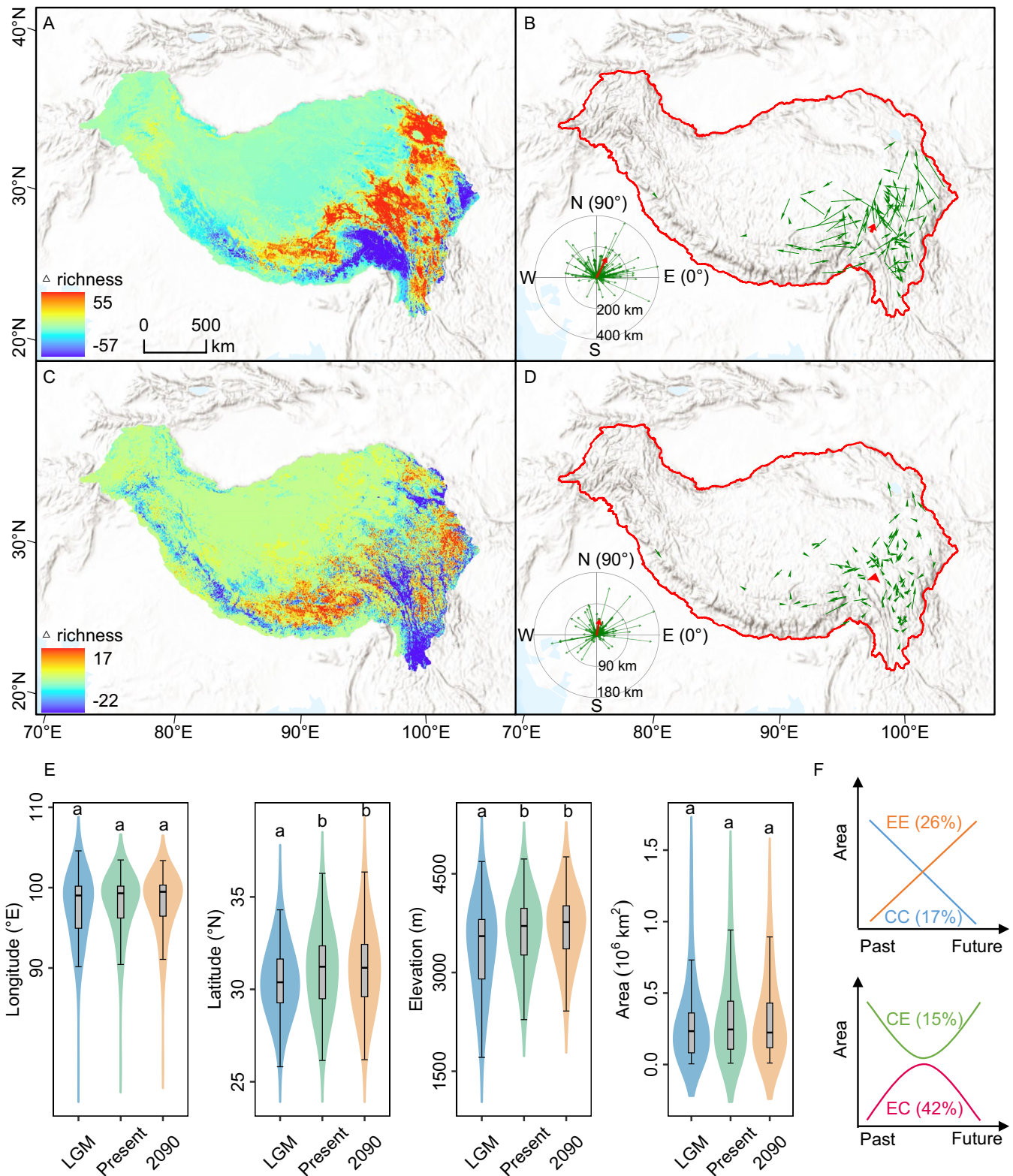
FIGURE 4 | Legend on next page.

covered by species during LGM was about $3.02 \times 10^5 \, \text{km}^2$ and was projected to increase to $3.34 \times 10^5 \, \text{km}^2$ in the present period, then decrease marginally in both 2090-SSP126 ($3.28 \times 10^5 \, \text{km}^2$) and 2090-SSP585 ($3.23 \times 10^5 \, \text{km}^2$) scenarios (Figure 4E and Figure S8E). Under the pessimistic SSP585 scenario, most species (42%) are expected to experience an expansion-contraction (EC pattern), expanding their ranges from the LGM to the

present, and subsequently contracting by 2090. A substantial proportion of species (26%) are projected to expand their ranges from LGM to the future, following an expansion-expansion (EE) pattern (Figure 4F). This pattern was consistent with the SSP126 climate projection, where 40% of the species showed the EC pattern while 29% showed the EE pattern (Figure S8F and Table S14).

FIGURE 4 | Spatiotemporal changes in species distribution in the Third Pole. (A) Change in species richness from the Last Glacial Maximum (LGM) to the present. (B) Species shift direction and distance from the LGM to the present, with green arrows representing shifts of the 96 species, and the red arrow showing the mean shift angle (63.00°) and mean shift distance (139.30 km). (C) Projected changes in species richness from the present to future (2090-SSP585 climate scenario). (D) Species shift direction and distance from the present to the future (2090-SSP585), with a mean shift angle of 79.10°, and a mean shift distance of 42.64 km. (E) Violin-boxplot illustrating the dynamic changes from the LGM to the future (2090-SSP585) across four dimensions: Longitude, latitude, elevation, and area. Different letters (a, b) indicate statistically significant differences ($p < 0.05$). (F) Schematic representation of range dynamics patterns for species potential distribution area from the past (LGM) to the future (2090-SSP585). EE denotes expansion-expansion, CC contraction-contraction, CE contraction-expansion, and EC expansion-contraction (see Table S14 for details). The percentage figures indicate proportions of species projected to follow the respective patterns. Map lines delineate study areas and do not necessarily depict accepted national boundaries. Results for the 2090-SSP126 scenario are provided in Figure S8.

Consistent with our ENM results above predicting a reduction in total distribution area, our analysis indicated a substantial future decline in genetic diversity in the Third Pole in the future, with varying degrees of vulnerability across species and areas (Figures S10 and S11; Table S15). Under the 2090-SSP585 scenario, the region is projected to lose a considerable proportion of total haplotypes (8.26% and 10.70% for cpDNA and nrDNA, respectively) and private haplotypes (13.19% for cpDNA and 15.49% for nrDNA) (Table 1). On the other hand, the optimistic scenario 2090-SSP126 projected slightly lower but still substantial losses, with total haplotypes decreasing by 7.39% and 8.86% for cpDNA and nrDNA, respectively, and a private haplotype loss of 9.89% and 12.77% for cpDNA and nrDNA, respectively (Table 1). Furthermore, our results indicated a clear decrease in genetic diversity (H_D) from the present to future periods, with the cpDNA data for the SSP585 scenario showing a statistically significant reduction in H_D (Table 1).

3.4 | Conservation Priority Areas and Network Optimization

Based on the calibration results from Marxan, the best SPF and BLM values were 1.3 and 0.03, respectively (Figure S12). A total of 2837 grids were ultimately included in the optimization protection area. Our Marxan analysis identified 15 conservation priority areas covering 2.84×10^5 km^2, which is approximately 8.3% of the Third Pole total area (Table 2 and Table S16). These priority areas include Pan-Three Parallel Rivers, Boshula Mountains, Minshan, Amne Machin-Nanshan (Qinghai), Noijin Kangsang, Lancang River Source, Hoh Xil, Brahmaputra Grand Canyon, Manaslu-Annapurna, Kohistan, Ngawa, Langtang, Riyueshan (Qinghai), Banma, and Burang in descending order of area size (Figure 5 and Figure S13; Table 2). These areas varied widely in size, ranging from 4.20×10^3 km^2 (Burang) to 6.62×10^4 km^2 (Pan-Three Parallel Rivers). Most of these areas were located toward the eastern edge of the Third Pole, with one isolated conservation priority area (Kohistan) in the western part of the region (Figure 5). Overall, only 8.17×10^4 km^2 (28.80%) of the existing conservation network, comprising both protected areas and National Park Clusters, overlaps with the newly identified priority areas (Table S16). Furthermore, 7.14×10^4 km^2 of the newly identified priority areas overlap with the existing protected areas, meaning that 74.83% of the newly identified areas lie outside of the existing protected areas (Table 2). The overlap area between the identified priority areas and National Park Cluster areas was 3.89×10^4 km^2, leaving 86.29% of the conservation priority areas outside of the existing National Park

Clusters (Table 2). Strikingly, 71.20% of the identified conservation priority area is located outside the current conservation network (protected areas + National Park Clusters) in the Third Pole (Table S16).

4 | Discussion

The Kunming-Montreal Global Biodiversity Framework (GBF) Target 3 aspires to protect at least 30% of terrestrial and marine areas by 2030 (CBD 2022). However, recent studies indicate that achieving such ambitious spatial targets alone, without enhancing the effectiveness of protected areas, is not likely to mitigate biodiversity loss (Arneth et al. 2023). Accordingly, leveraging multi-species genetic data across landscapes offers a more effective approach to developing global conservation policies, going beyond single species conservation programs that will certainly be unsustainable in the long term (Schmidt et al. 2023). Ignoring genetic diversity in conservation planning has exacerbated concerns about the ineffectiveness of protected areas in safeguarding critical biodiversity features in the Third Pole and surrounding areas (Ren et al. 2019). We mapped the genetic diversity of 96 plant species across the Third Pole and determined the factors shaping these patterns. Advancing from previous methodologies, we incorporated genetic diversity to assess the vulnerability of plant species in the region and formulated an optimal conservation plan for the Third Pole.

4.1 | Patterns of Genetic Diversity and Potential Climate Refugia

The southeastern part of the Third Pole generally harbored the highest level of genetic diversity, including both H_D and haplotype number. This finding aligns with previous studies that demonstrated high genetic variation of plants in the Hengduan Mountains (Fan et al. 2018; Qiu et al. 2011; Wambulwa et al. 2022; Yu et al. 2019). While this pattern might be partially attributed to the more species sampling in the Hengduan Mountains, our generalized linear models indicated a weak correlation between species richness and genetic diversity, suggesting the influence of other landscape-related factors. The observed spatial incongruence between patterns of cpDNA and nrDNA genetic diversity likely reflects the difference in the mode of inheritance. In most of the species analyzed, cpDNA inheritance is primarily seed-mediated, whereas nrDNA is seed and pollen-mediated. For instance, the relatively less rugged landform towards the west and north of the Third Pole should permit higher pollen

TABLE 2 | The 15 newly identified priority areas (coded A to O in descending order of area size) and the proportion of their overlap area with existing protected areas (PA) and National Park Clusters (NPC) (see also Figure 5).

Code	Name	Identified priority areas[*] (×100 km²)	Extant protected areas (×100 km²) (%)	National Park Clusters (×100 km²) (%)	Total overlap area (×100 km²) (%)
A	Pan-Three Parallel Rivers	662	131 (19.79)	96 (14.50)	45 (6.80)
B	Boshula Mountains	383	22 (5.74)	0 (0)	0 (0)
C	Minshan	373	87 (23.32)	32 (8.58)	16 (4.29)
D	Amne Machin— Nanshan (Qinghai)	242	108 (44.63)	2 (0.83)	0 (0)
E	Noijin Kangsang	217	27 (12.44)	0 (0)	0 (0)
F	Lancang River Source	205	83 (40.49)	0 (0)	0 (0)
G	Hoh Xil	119	106 (89.08)	90 (75.63)	85 (71.43)
H	Brahmaputra Grand Canyon	115	0 (0)	1 (0.87)	0 (0)
I	Manaslu-Annapurna	108	73 (67.59)	91 (84.26)	67 (62.04)
J	Kohistan	95	1 (1.05)	0 (0)	0 (0)
K	Ngawa	84	0 (0)	0 (0)	0 (0)
L	Langtang	75	73 (97.33)	75 (100)	73 (97.33)
M	Riyueshan (Qinghai)	66	0 (0)	2 (3.03)	0 (0)
N	Banma	51	3 (5.88)	0 (0)	0 (0)
O	Burang	42	0 (0)	0 (0)	0 (0)
	Total[†]	2837	714 (25.17)	389 (13.71)	286 (10.08)

Note: Area estimates are based on the number of 10 km × 10 km grid cells, with only cells with overlap areas exceeding 50% included. Proportions of PAs and NPCs within the identified priority areas are indicated in parentheses after the overlap area values.

*Identified priority areas were used as the denominator when calculating the proportions of extant protected areas, National Park Clusters, and the total overlap area. The calculations were performed per row.

†A total of 8.17×10^4 km² (28.80%) of the newly identified areas overlap with existing protected areas or National Park Clusters, while 2.02×10^5 km² (71.20%) lie outside the extant conservation network.

dispersal; hence, the relatively high nrDNA haplotype diversity areas in the western and northern peripheries. Cautiously, such a pattern might result from rough interpolation in regions with sparse sampling, a common challenge reported in the literature (e.g., Fan et al. 2018; Hu et al. 2021; Terzer et al. 2024; Yu et al. 2019).

We identified suitable species distribution areas in the Hengduan Mountains from the LGM to 2090. Coupled with the observed high genetic diversity and the high number of private haplotypes in the area, this finding highlights the long-term stability of the Hengduan Mountains, further suggesting their potential as a key climatic refugium for plant species in the region under ongoing climate change. The Hengduan Mountains' long-term stability could be favored by the high landscape heterogeneity (Chang et al. 2023), which fosters high habitat diversity and niche divergence, thereby enhancing species persistence over time. However, our analysis also indicated that the area might lose a higher proportion of unique haplotypes in the future, emphasizing the urgency for conservation interventions in the Hengduan Mountains. Similarly, conservation interventions are required in the Himalaya, where many of the species analyzed

were projected to experience a steady loss of range from the LGM to the future.

The projected general range shift toward the north (Figure 4D) is consistent with the widely observed trend of species migrating to higher latitudes in response to a warming climate. The significant temperature rise reported in mountain ecosystems such as the Third Pole (Liu et al. 2018) has meant that species in the region must shift their ranges northward to track their (cooler) thermal niches. However, our results indicate a relatively short shift distance for most species, suggesting that they are likely to persist in their current habitats. This finding is consistent with the observed low beta diversity, turnover, and nestedness for transitions between the present and 2090 (Figure S9). Despite the limited range shifts, conservation efforts should prioritize higher latitude areas of the Third Pole. These areas, characterized by high genetic diversity (Figure 2A,B) and high cpDNA F_{ST} (Figure S5A), represent evolutionary 'hotspots' with considerable potential to foster lineage diversification and bolster species resilience in the face of climate change. For species distributed in the Himalaya and the southern edge of the Hengduan Mountains,
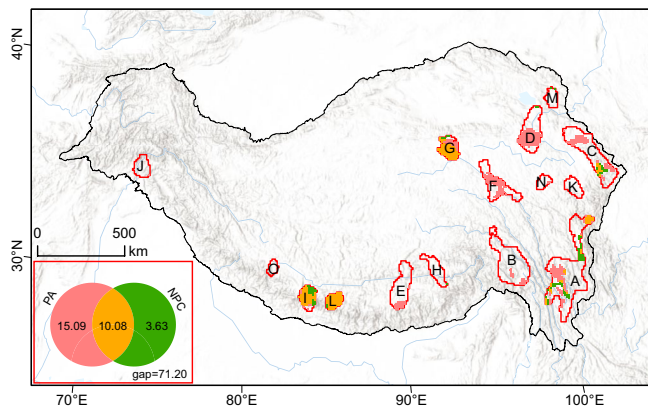
FIGURE 5 | Optimization of conservation networks in the Third Pole using a systematic conservation planning approach in Marxan. Each color in the Venn diagram at the bottom left corner represents a specific type of conservation area combinations (Table 2). Extant protected areas and planned National Park Clusters within the newly identified priority areas are shown in pink and green, respectively. Areas of overlap between the identified priority areas, extant protected areas, and National Park Clusters are shown in orange. The percentage figures in parentheses indicate the proportion of the identified priority areas overlapping with extant Protected area (15.09%), National Park Clusters (3.63%) or both (10.08%), amounting to a total of 28.80% of the identified priority areas within the existing conservation network, leaving a 71.20% conservation gap. The 15 conservation priority areas (each of size ≥ 4200 km²) are displayed with a red outline and labelled with letters (A–O) in descending order of area size. These priority areas are: (A) Pan-Three Parallel Rivers; (B) Boshula Mountains; (C) Minshan; (D) Amne Machin-Nanshan (Qinghai); (E) Noijin Kangsang; (F) Lancang River Source; (G) Hoh Xil; (H) Brahmaputra Grand Canyon; (I) Manaslu-Annapurna; (J) Kohistan; (K) Ngawa; (L) Langtang; (M) Riyueshan (Qinghai); (N) Banma; (O) Buran. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

where future range reductions are projected, we recommend data-driven *ex situ* conservation measures as well as taxon-targeted assisted migration strategies.

4.2 | Determinants of Plant Genetic Structure in the Third Pole

Topography was the best predictor of cpDNA genetic diversity, with longitude showing the strongest positive effect and latitude showing the strongest negative effect. This pattern likely reflects the high genetic diversity in the southeastern area (Hengduan Mountains), which gradually decreases northward and westward. The longitudinal pattern is consistent with a previous finding by Yu et al. (2019) and can be attributed to the recolonization of some species from the Hengduan Mountains to the Tibetan Plateau and Himalaya during the warm Interglacial periods (Qiu et al. 2011). This process likely caused gradually decreasing genetic diversity along the westward dispersal routes due to founder effects. The latitudinal trend is consistent with a previous global-scale study, which reported decreasing population-level genetic diversity with increasing distance to the equator (Miraldo et al. 2016). This latitudinal gradient of genetic diversity might be caused by the historical glacial oscillations that reduced the genetic diversity of poleward-expanding

species, as demonstrated for the northern hemisphere (Hewitt 2000). Additionally, the occurrence of glacial refugia at lower latitudes and recolonization of higher latitudes after the LGM (Capria et al. 2024) likely contributed to this latitudinal pattern. However, our finding diverges from studies reporting a positive relationship between genetic diversity and latitude (Hirao et al. 2017) or no effect at all (Kort et al. 2021), suggesting that our results might have been influenced by the smaller spatial scale of the study. With most species investigated here concentrated in the Hengduan Mountains, it is possible that the mixing of genetically divergent lineages in the region could obscure broader patterns across the wider Third Pole area. Any relationship between genetic diversity and latitude/longitude is likely to be complex and may require sampling at larger spatial scales and the inclusion of additional information, including phenology and phylogenetic diversity in models to explore potential causal links and the underlying mechanisms.

nrDNA genetic diversity was most strongly influenced by climatic variables, with Bio13 (precipitation of wettest month) showing the strongest negative effect and Bio12 (annual precipitation) showing the strongest positive effect (Figure 3B), accentuating the central role of precipitation in shaping genetic diversity patterns in the region. The negative relationship between precipitation and nrDNA genetic diversity is consistent with a global meta-analysis of plant species using nrDNA markers (Kort et al. 2021). Conversely, the strongly positive effect of Bio12 is consistent with a southeast-to-northwest precipitation gradient across the Third Pole and corroborates a previous study (Wambulwa et al. 2022), which also suggested a positive relationship between annual mean wet day frequency and genetic diversity. Interestingly, Bio2 (mean diurnal temperature range) was included in both cpDNA and nrDNA models, exerting a stronger positive effect in the nrDNA model. This suggests that greater temperature variation may enhance plant genetic diversity. This result is consistent with a previous study (Kort et al. 2021), which found that temperature stability since the Mid-Holocene was negatively associated (albeit marginally) with plant genetic diversity at a global scale.

Anthropogenic variables had the least relative effect on both cpDNA and nrDNA genetic diversity, suggesting low anthropogenic pressure in the region, as previously reported (Li et al., 2018c). This low relative effect may be explained by the fact that agricultural and built-up land accounts for less than 1% of the Third Pole total land area (Dong et al. 2023). However, despite the relatively weak association, the role of anthropogenic activities in shaping genetic diversity in the region cannot be overlooked (Yan et al. 2024). The lower effect of anthropogenic variables might stem from the complex ways genetic diversity responds to human activities. Factors such as species-specific traits, the type of genetic diversity parameter used, and geography often confound this relationship (González et al. 2020). Nonetheless, the stronger relationship observed between some anthropogenic variables (e.g., Hfp, Human footprint; Hii, human influence intensity) and genetic diversity suggests a notable influence of human activities on plant genetic structure in the Third Pole. Specifically, Hfp and Hii showed a relatively strong positive association with the genetic diversity of cpDNA, suggesting a link between human activities and enhanced seed-mediated dispersal. Human-mediated dispersal often introduces

new genetic variants into populations, thereby increasing population-level genetic diversity. However, some studies (e.g., Almeida-Rocha et al. 2020) have highlighted the negative effect of increased human activities on the genetic diversity of terrestrial species (Almeida-Rocha et al. 2020). Conversely, the relatively weak association between Hii and Hpd and the genetic diversity of nrDNA might result from the weak role of humans in pollen movement.

4.3 | Optimization of Conservation Networks in the Third Pole

Although our paired samples *t*-test indicated that only cpDNA might experience a significant loss of haplotype diversity (H_D), our analysis suggests that the Third Pole risks losing up to 13.19% for cpDNA and 15.49% for nrDNA genetic diversity by 2090. These findings underscore the need for urgent mitigation measures. Despite the region hosting relatively large national protected areas (Figure S13) (Liu et al. 2022), only about one-third of the newly identified priority areas overlap with the existing conservation network in the Third Pole (Table S16), thus highlighting a significant conservation gap in the region. Conservation gaps of climate refugia on the Tibetan Plateau have been revealed based on various environmental diversity indicators (Hua et al. 2022); however, these gaps differ from those identified using genetic diversity in our work. Our results indicate that the hotspots of genetic diversity and species richness differ. Given the substantial amount of plant genetic diversity projected to be lost in the region (Table 1), it is important to optimize conservation networks in the Third Pole based on the conservation gaps identified in our study. We identified 15 areas that require prioritization for the conservation of plants in the Third Pole, but some of these (e.g., Pan-Three Parallel Rivers, Kohistan/northwest Zanda, and Lancang River Source) had been proposed earlier (Hu et al. 2023). The identified areas were generally in agreement with the conservation priority areas for biodiversity conservation and key ecological function zones in the region (Cao et al. 2015), validating the rationality of our planning approach. The newly identified priority areas represent locations of high conservation value that also harbor high evolutionary potential, owing to the high levels of genetic diversity and private haplotypes they harbor. This high potential for evolution should confer the much-needed adaptive capacity for species in a changing world. Without considering genetic diversity, previous similar attempts have failed to pinpoint evolutionary "hotspots" in the region that are highly susceptible to anthropogenic activities and climate change. Consequently, we propose the optimization of the protected area and National Park Cluster systems based on the conservation priority areas identified here. We recommend adding an area of $2.02 \times 10^5 \, \text{km}^2$ to the current network, which represents approximately 5.91% of the total area of the Third Pole, to effectively preserve the evolutionary potential of plants. This addition would increase the conserved proportion to $1.36 \times 10^6 \, \text{km}^2$ (39.93%) in the Third Pole, compared to the existing protected areas at $8.73 \times 10^5 \, \text{km}^2$ (25.54%) or the National Park Clusters alone at $6.56 \times 10^5 \, \text{km}^2$ (19.21%) (Figures S1 and S13; Table S16). Moreover, the new protected area should be established in the relatively small priority areas that have little or no overlap with existing protected areas/ National Park Clusters (e.g., Ngawa and Riyueshan).

Our Marxan analysis showed that the conservation priority areas are mostly located in the eastern part of the Third Pole (i.e., Hengduan Mountains), consistent with an earlier study (Xue et al. 2021), which identified conservation priority areas in the southeastern Third Pole based on species richness, species complementarity, and spatial phylogenetics. These identified areas are geographically distinct from the existing protected areas and the National Park Clusters, which are generally located in the central and northern regions (Figure S1). Notably, only 28.80% ($8.17 \times 10^4 \, \text{km}^2$) of the identified conservation priority area ($2.84 \times 10^5 \, \text{km}^2$) overlaps with the current conservation network area (Figure 5 and Figure S13), emphasizing a major conservation gap for plants in the Third Pole but also offering a scientific basis for the optimization of conservation networks in the region. For example, when combined, large protected areas such as Qiangtang, Sanjiangyuan, and Hoh Xil and national parks like Yangtze River Source, Qilian Mountains, and Mount Qomolangma collectively account for a significant portion of the total nature reserve area ($> 8.00 \times 10^5 \, \text{km}^2$). However, their effectiveness in protecting the evolutionary potential of plant species may be limited due to their central locations with low genetic diversity. Conversely, smaller isolated patches might be more effective than single large reserves in biodiversity conservation (Fahrig 2020). However, our ENM results suggested that the area encompassing these large protected areas and national parks will also harbor suitable habitats for a relatively high number of species in the future (Figure 4C); hence, these large areas should also be maintained to act as climatic refugia.

National Park Clusters had a higher spatial mismatch with the identified priority areas compared to protected areas (Figure 5). This discrepancy may reflect the different conservation priorities—integrity and authenticity—emphasized by the National Park Cluster system (Tang et al. 2023, and references therein). Moreover, a recent study showed that major national park candidates in the Third Pole, such as Pamir-Kunlun Mountains, Three-River Source, and Qiangtang, have significantly improved in their habitat quality in the last decade (Yang et al. 2023), painting a favorable outlook for national park clusters in the region. Despite the significant threat posed by future climate change on protected areas globally, our data showed significant overlap between the newly identified priority areas and the extant protected areas in the region. This suggests that protected areas in the Third Pole are generally well-positioned to buffer against future loss of species but might not fully safeguard plant genetic diversity. Therefore, to comprehensively protect plant species in the region, the newly identified conservation priority areas should be annexed to the existing protected areas and National Park Clusters network. For example, small protected areas (e.g., parts of Sanjiangyuan, Three Parallel Rivers and Sichuan Giant Panda Sanctuaries) and national parks (e.g., Giant Panda, Minya Konka, Zorgai, Gaoligong Mountains, Qinghai Lake, and Shangrila) in the eastern Third Pole should be adjusted to accommodate the new priority areas. While the expansion of existing protected areas to cover the newly identified areas is a desirable strategy, previous studies have shown that improved management rather than expansion of existing protected areas could be more effective and less costly (Adams et al. 2019). Nonetheless, the proposed priority areas in the current study have a total area of $2.84 \times 10^5 \, \text{km}^2$; around $2.02 \times 10^5 \, \text{km}^2$ lies outside the existing conservation areas (Figure 5), a reasonable size that balances

conservation needs with the financial implications of establishing new areas. More importantly, incorporating the new priority areas into the existing protected networks will increase the total protected area to 39.93% of the total area of the Third Pole (Figure S13), surpassing Target 3 of the Kunming-Montreal Global Biodiversity Framework (GBF), which aims to protect at least 30% of the world's ecosystems by 2030 (CBD 2022).

We acknowledge that the disproportionate distribution of genetic data in the study area may impact the reliability of our results, as is often the case in meta-analyses (Gurevitch et al. 2018). The 96 species selected based on our inclusion criteria were mostly distributed in the central and eastern parts of the Third Pole, with limited representation from the western side. This uneven distribution, coupled with varying sampling densities, may pose challenges for interpolation. Furthermore, the selected species spanned a wide range of families and orders across the Tree of Life, introducing potential variability due to differences in life history and reproductive traits, which could be a potential source of additional variation in the meta-analysis. Ideally, a more uniform set of DNA sequence markers would have strengthened our analysis. For example, using consistent loci for cpDNA and nrDNA across the 96 species could minimize the variation arising from differences in the inheritance mechanisms between the neutral and adaptive loci. However, this ambition was unrealistic as the loci used in previous phylogeographic studies varied widely, and hence our study utilized different types of loci (comprising genes, introns, and intergenic spacers). As more genomic data are generated in the region, future meta-analyses should overcome these drawbacks and possibly expand the analysis to include additional branches of the Tree of Life. Indeed, our dataset only represents a fraction of the plant diversity in the Third Pole; hence, more work remains to be done.

Despite the above limitations, we integrated genetic data, species distribution modeling, and a systematic conservation planning tool to optimize the protection of plant species in the Third Pole, one of the world's most vulnerable ecosystems. Our analysis indicated that plant genetic diversity in the Third Pole is spatially structured, with high genetic diversity areas restricted to the southeastern edge of the region. While more even data availability across the region would be beneficial for a deeper eco-evolutionary understanding of its biodiversity, we recommend that the southeastern part of the Third Pole be prioritized for conservation, as it currently falls outside the existing protected area and National Park Cluster system. By incorporating genetic diversity as a conservation feature, we identified conservation priority areas that can allow for a more holistic approach to bio-diversity management that considers and protects the adaptive potential of plant species in the region. Our findings broaden the knowledge base established by earlier studies that identified priority areas for conservation. Future work in the region should aim to utilize consistent genomic data to map range-wide genomic diversity and to explore genomic responses associated with environmental change, especially for the most threatened species. Spatial analyses that quantify the amount of phylogenetic and functional diversity for all plants will provide further insight into the ecosystem processes and responses to climate change in the region. Furthermore, predictive models should be interpreted in the context of ecologically meaningful processes, such as species demographics and phenology. We therefore recommend that future similar meta-analyses consider phylogenetic diversity, life history characteristics, and other functional traits.

Author Contributions

Moses C. Wambulwa: data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing – original draft, writing – review and editing. **Guang-Fu Zhu:** data curation, formal analysis, methodology, software, validation, visualization, writing – original draft, writing – review and editing. **Ya-Huang Luo:** data curation, formal analysis, investigation, methodology, validation, visualization, writing – original draft, writing – review and editing. **Zeng-Yuan Wu:** methodology, visualization, writing – review and editing. **Jim Provan:** validation, visualization, writing – review and editing. **Marc W. Cadotte:** investigation, validation, writing – review and editing. **Alistair S. Jump:** methodology, validation, visualization, writing – review and editing. **Francis N. Wachira:** investigation, validation, writing – review and editing. **Lian-Ming Gao:** supervision, validation, writing – review and editing. **Ting-Shuang Yi:** supervision, validation, writing – review and editing. **Jie Cai:** data curation, methodology, writing – review and editing. **Hong Wang:** conceptualization, project administration, supervision, validation, writing – review and editing. **De-Zhu Li:** conceptualization, project administration, supervision, validation, writing – review and editing. **Jie Liu:** conceptualization, data curation, funding acquisition, methodology, project administration, supervision, writing – original draft, writing – review and editing.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data, code, and ESRI Shapefile of the identified protected areas that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.14908392 and the National Tibetan

Plateau/Third Pole Environment Data Center at https://doi.org/10.11888/HumanNat.tpdc.302146. Occurrence data was obtained from the Global Biodiversity Information Facility (GBIF) at https://doi.org/10.15468/dl.arz7nb, the National Plant Specimen Resource Center (NPSRC) at https://www.cvh.ac.cn/, iNaturalist at https://www.inaturalist.org/, the Plant Photo Bank of China (PPBC) at http://ppbc.iplant.cn/, the Germplasm Bank of Wild Species (GBoWS) at https://pdbms.iflora.org.cn/home, and the Biodiversity of the Hengduan Mountains and Adjacent Areas of South-Central China (BHM) at http://hengduan.huh.harvard.edu/fieldnotes.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.