

Legal protection biases and gaps for China's threatened vascular plants

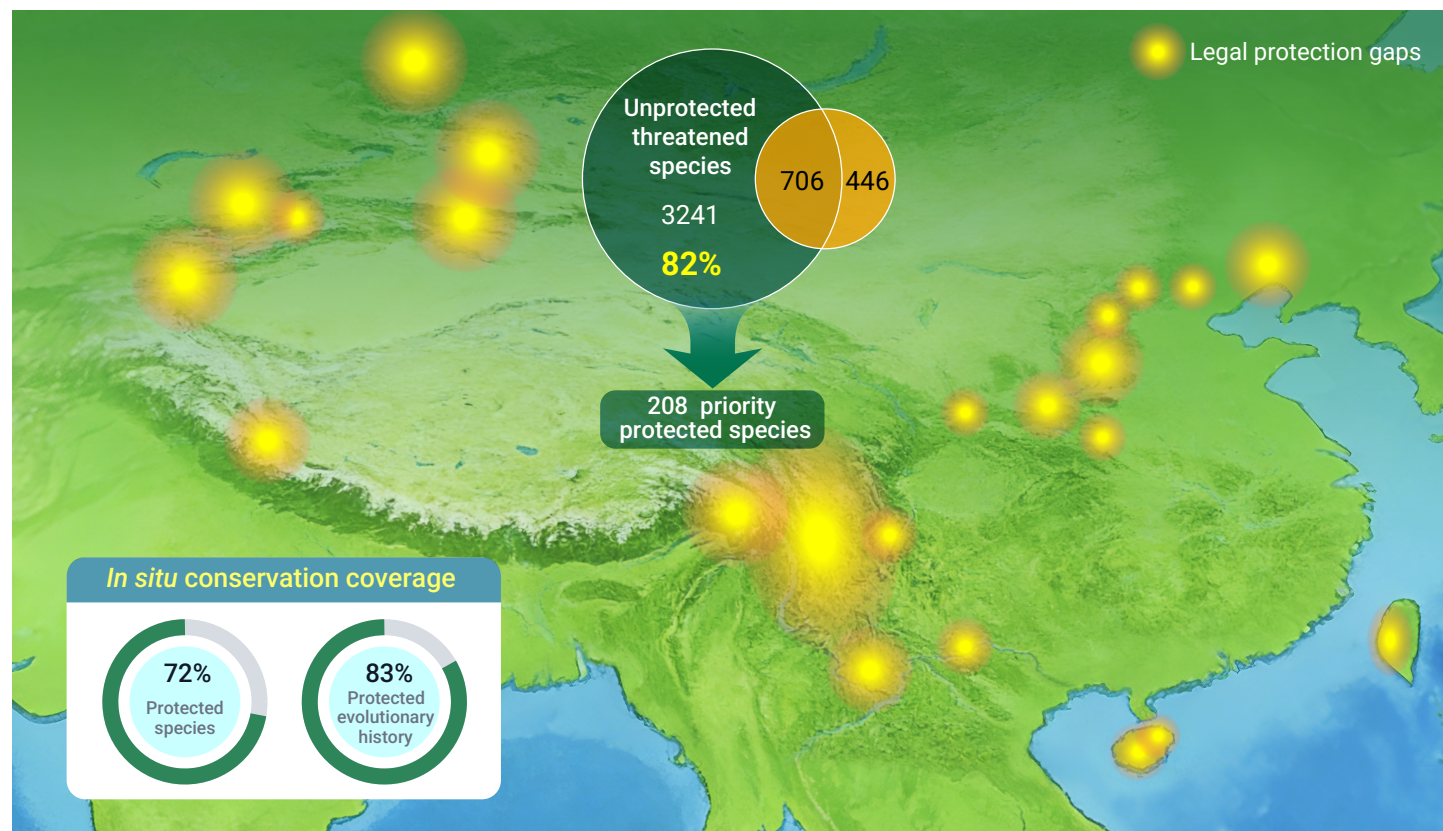
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GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Over 80% of China's threatened vascular plants remain legally unprotected.
- A total of 208 species were identified as high-priority candidates for legal protection.
- Legal protection gaps spatially overlap with diversity hotspots of unprotected threatened species.
- National nature reserves safeguard the majority of species and evolutionary history in gap regions.

Legal protection biases and gaps for China's threatened vascular plants

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With over 10% of its flora threatened, China faces a growing plant extinction crisis. While the List of National Key Protected Wild Plants (Legal Protection List) currently provides legal protection to over 1,100 plant species, its overall coverage and effectiveness remain uncertain. Here, we integrated the vascular plants in China's Threatened Species List and the Legal Protection List to assess the legal protection of 4,393 key species. Using > 110,000 distribution records and a comprehensive phylogeny, we evaluated the taxonomic and phylogenetic distribution of legally protected versus unprotected species and projected their responses to future climate change. We also assessed spatial variation in the effectiveness of legal protection using a newly developed Legal Protection Index (LPI). Our results indicate that legal protection extends to only 18% of threatened species. Unprotected species are phylogenetically clustered and disproportionately vulnerable to future climate, highlighting 208 species as high-priority candidates for legal protection. Regions with the highest taxonomic and phylogenetic diversity—Southwestern China, Hainan, and Taiwan—exhibit the lowest effectiveness of legal protection, representing critical protection gaps. However, a positive finding is that 72% of species and 83% of evolutionary history in these regions are already safeguarded through *in situ* conservation, although nationwide, 1,195 threatened species remain neither legally protected nor conserved in nature reserves. These findings highlight spatial and evolutionary gaps in China's legal protection system and offer a roadmap for prioritizing climate-resilient and evolutionarily informed conservation strategies.

INTRODUCTION

Global biodiversity is experiencing exceptionally rapid declines, prompting widespread concern that the sixth mass extinction may already be underway.^{1–3} Current extinction rates are estimated to be approximately 1,000 times higher than background rates, highlighting the urgent need for effective conservation actions.⁴ Among the most prominent and widely used tools informing conservation planning and practices is the International Union for Conservation of Nature (IUCN) Red List of Threatened Species,^{5,6} which has assessed the threat status of more than 169,400 species to date (<https://www.iucnredlist.org>; accessed May 9, 2025). However, despite its global authority, the IUCN Red List essentially remains an advisory reference and decision-making tool for policymakers, lacking mandatory enforcement to address the multiple drivers of biodiversity loss, such as habitat destruction and human exploitation, particularly at the regional level.⁷

This gap between global assessment and local enforcement is particularly relevant in a megadiverse country like China. China's highly heterogeneous topography, climate, and ecosystems support over 30,000 vascular plant species (Figure S1).⁸ Nearly 4,000 of these species have been assessed as threatened under the IUCN Red List Categories and Criteria⁹ (henceforth: Red List), highlighting an urgent need for effective conservation interventions. In a forward-looking policy move as early as 1999, China issued the *List of National Key Protected Wild Plants* under the *Regulation of the People's Republic of China on the Protection of Wild Plants* to provide legal protection

for rare and endangered species.¹⁰ The list was substantially updated in September 2021 according to the latest scientific assessments (henceforth: Legal Protection List).¹¹ The current list legally protects 455 explicitly designated species and 40 higher taxonomic ranks (e.g., families, genera), encompassing over 1,100 species in total.¹² Species included in this list receive prioritized attention from government agencies and protected area managers. It also strictly prohibits unapproved collection and trade of listed species, with violations subject to legal penalties.^{12,13} While *in situ* conservation in China is primarily delivered through the protected area network,^{14,15} the government-issued protection list provides a critical, complementary layer of species-specific legal protection. This safeguard is particularly vital for species outside formal reserves, as it offers a universal legal shield against threats such as illegal harvesting and habitat destruction.^{12,13} Previous studies have often treated the Red List and the Legal Protection List in isolation, focusing on spatial diversity patterns or conservation gaps for each list separately.^{13,16–19} However, their distinct yet complementary functions within the broader conservation framework underscore the necessity of integrated, comparative analyses to fully understand and optimize their collective effectiveness.

Beyond simply counting species, a more comprehensive approach to conservation must consider evolutionary history. Phylogenetic diversity (PD), which represents the total evolutionary history of a set of species, provides a complementary metric, illuminating the evolutionary processes underpinning biodiversity and offering a novel perspective for evaluating the evolutionary impacts of legal protection.^{20–22} This evolutionary perspective is central to the emerging concept of conservation evolutionary biology, which advocates a shift from static, “museum-style” preservation towards dynamically safeguarding evolutionary processes.²³ Previous studies have revealed highly uneven geographic distributions of threatened species,^{16,18,24} suggesting that the effectiveness of legal protection may likewise exhibit pronounced spatial heterogeneity—a pattern that remains insufficiently quantified, particularly regarding geographic legal protection gaps. Last but not least, given the pivotal role of *in situ* conservation in halting biodiversity loss, assessing the extent to which legal protection gaps across multiple biodiversity dimensions are effectively buffered by China's current protected area network may provide valuable guidance for future conservation planning.

Climate change has become increasingly central to biodiversity conservation research, particularly given the accelerated extinction risks predicted with global warming.^{25–28} Species distribution models (SDMs) are widely used to assess species responses to future global change.^{18,25,26} For example, a recent study found that China's current Red List underestimates both the number and threat levels of endemic woody plants,²⁵ further implying that the current legal protection framework may similarly fail to adequately cover future-threatened species. Moreover, previous studies have indicated that plants of different life forms or taxonomic lineages vary considerably in their vulnerability to climate change.^{29,30} However, whether these vulnerabilities to climate impacts differ between legally protected and unprotected threatened species remains unclear, thereby limiting the effective integration of climate-change responses into conservation strategies.

In this study, we combined the Red List and the Legal Protection List to generate a non-redundant checklist of 4,393 vascular plant species, herein collectively defined as China's Key Vascular Plants.^{9,11} These species were subsequently classified, according to their threat status and legal protection status, into three mutually exclusive categories: protected threatened species (PTS), protected non-threatened species (PNTS), and unprotected threatened species (UPTS) (Figure S2). We then integrated 110,900 geographic distribution records with the most comprehensive phylogeny of Chinese vascular plants available and applied a newly proposed Legal Protection Index (LPI). Specifically, we addressed the following three questions: (1) do UPTS tend to face higher extinction risk than PTS? (2) is the effectiveness of legal protection uneven across space and between richness- and phylogeny-based measures? and (3) do current *in situ* conservation measures adequately cover the legal protection gaps revealed by the LPI?

MATERIALS AND METHODS

Legal protection status of threatened vascular plants

The list of threatened vascular plant species in China was derived from the *China Biodiversity Red List—Higher Plants* (2020).⁹ We defined threatened species to include the three IUCN-designated threatened categories (Critically Endangered, CR; Endangered, EN; and Vulnerable, VU). Taxonomic names were standardized according to the *Catalogue of Life China: 2024 Annual Checklist* (<http://www.sp2000.org.cn/>), resulting in a final list of 3,947 threatened species with 166 lycophytes and ferns (pteridophytes), 109 gymnosperms, and 3,672 angiosperms.

In China, the *List of National Key Protected Wild Plants* (Legal Protection List) serves as legal basis for conservation actions.^{12,13} The most recent version of the list was officially issued on September 7, 2021.¹¹ It includes 455 species and 40 higher-level taxa (families, genera, or sections). We compiled the final list by standardizing all entries to accepted species names, resulting in 1,152 vascular plant species.

To assess legal protection status, each threatened species was classified as protected or unprotected based on inclusion in the Legal Protection List. This yielded two categories: protected threatened species (PTS, $n = 706$) and unprotected threatened species (UPTS, $n = 3,241$). In addition, 446 legally protected species were not included in the Red List. These were retained in our analyses as protected non-threatened species (PNTS), given their recognized economic, ecological, or genetic value.¹² Collectively, these three categories form China's Key Vascular Plants, comprising 4,393 species that were used for subsequent analyses (Figure S2). Furthermore, we assessed the endemism status of these species using two sources: Huang et al.'s checklist of endemic seed plants and Zhou et al.'s checklist of pteridophytes.^{31,32} Finally, 2,295 species (52.2%) were identified as endemic.

To evaluate the diversity and proportion of PTS, PNTS, and UPTS across plant families, we identified the top ten families with the highest number of species in each category and compared their proportional compositions. We also compared the distribution of the three categories across major clades of the tree of life. For PNTS, we further examined the IUCN Red List threat categories assigned to these species.

Phylogenetic signals of legal protection status

Phylogenetic analyses were conducted based on the most comprehensive species-level tree of life of Chinese vascular plants to date, reconstructed by the authors (unpublished data), including 16,585 species native to China. This tree was then matched to our species list of China's Key Vascular Plants, and a pruned subtree (hereafter, T_{actual}) containing 2,112 species (~48.1% of the total) was extracted using the R package *ape*.^{33,34} The resulting tree was visualized using iTOL (<https://itol.embl.de/>).³⁵ To account for incomplete sampling, we constructed a complete phylogenetic tree (T_{complete}) including all 4,393 species by grafting the species lacking sequence data onto T_{actual} using the "scenario 3" algorithm in the R package *V.PhyloMaker*.³⁶

We quantified phylogenetic signals in the distribution of PTS, PNTS, and UPTS using Fritz's D-values.³⁷ For each analysis, species assigned to a given category (e.g., PTS) were coded as 1 and all others as 0. D-values were calculated using the *phylo.D* function in the R package *caper*.³⁸ A D-value of 1 indicates a random distribution (no phylogenetic signal), whereas a D-value of 0 corresponds to the expectation under Brownian motion evolution (strong

phylogenetic signal). Values between 0 and 1 indicate an intermediate level of signal, with lower values reflecting stronger phylogenetic clustering. Two p-values were derived from 999 permutations: p_0 ($D > 0$) tests whether the observed D deviates from the Brownian motion model, and p_1 ($D < 1$) tests deviation from a random distribution. Phylogenetic signal analyses were repeated on T_{complete} to assess the robustness of the results.

Species distribution data

Our distribution data included 110,900 county-level records for 4,379 species, primarily obtained from Zhao et al.³⁹ (see supplemental materials and methods for details). Furthermore, because recently described species may lack comprehensive survey data, we examined whether the year of species description biased the availability of distribution data. Publication years were compiled for all species and compared across PTS, PNTS, and UPTS. The results showed no significant bias in species description dates among the three categories, indicating that data availability was not strongly influenced by recency of description (Figure S3).

County-level data were projected using the Albers equal-area projection and subsequently aggregated into 100×100 km grid cells.^{24,40} Grid cells with land areas smaller than 5,000 km² were excluded. The final dataset comprised 81,537 occurrence records across 941 grid cells.

Species range under current and future climate scenarios

Geographic range size serves as a key metric for informing conservation strategies.^{41,42} Based on the gridded distribution dataset, a species was considered to occupy the full area of any grid cell in which it was recorded.^{24,43} This commonly used approach may overestimate range size. However, as the method is applied uniformly across species and categories, it is unlikely to substantially bias comparisons among groups. Range size was thus calculated as the total area of all occupied grid cells.^{24,43} We examined the distributions of $\log_{10}$ -transformed range sizes for PTS, PNTS, and UPTS, with statistical significance evaluated using Kruskal-Wallis and Wilcoxon tests. To test the robustness of our results for transboundary species, we repeated all range size analyses using only the endemic species (Figure S4).

We modeled the distributions of 3,942 threatened species (PTS and UPTS) under present and future climatic scenarios using our county-level data and 19 bioclimatic variables (at 10-minute resolution) obtained from the *WorldClim* (ver. 2.1, <http://www.worldclim.org/>).⁴⁴ Future climate projections were derived from the BCC-CSM2-MR model under two Shared Socioeconomic Pathways (SSPs) from the Coupled Model Intercomparison Project Phase 6 (CMIP6), representing moderate (SSP1-2.6) and extreme (SSP5-8.5) warming scenarios for the 2070s (2061–2080).^{18,19,25}

In China, existing databases with coordinate records show pronounced spatial gaps, sampling biases, and taxonomic misidentifications, which together limit the reliability and representativeness of coordinate-based SDMs.^{45–47} By contrast, county-level records compiled from expert-curated floras and checklists offer more complete coverage and more reliable identifications, and have been proven effective for large-scale biodiversity studies.^{13,25,40,48} We therefore constructed SDMs using Mikrubi with county-level data as input,⁴⁹ and conducted a sensitivity analysis based on coordinate records. Detailed methods and results of this complementary analysis are provided in the Supplemental information (Table S1).

Using the raster outputs of SDMs from Mikrubi, we assessed trends in range size changes (i.e., contraction, expansion, or stability) for each threatened species (PTS and UPTS). For each pixel, we compared species presence probabilities under two future climate scenarios to current values. Pixel-level comparisons were coded as follows: +1 if future probability exceeded the present, 0 if equal, and –1 if lower. For each species, these values were summed across all occupied pixels under both scenarios. A total score greater than 0 indicated potential range expansion, less than 0 indicated contraction, and equal to 0 indicated range stability. Additionally, we further examined variation in projected distributional responses between endemic and non-endemic species, among different growth forms, and across major phylogenetic clades. Growth form data were primarily sourced from Lu et al.,⁴⁰ with missing values for 892 species supplemented using trait descriptions from the *Flora of China*.⁸ These analyses were conducted in R using the *terra* and *dplyr* packages.^{50,51}

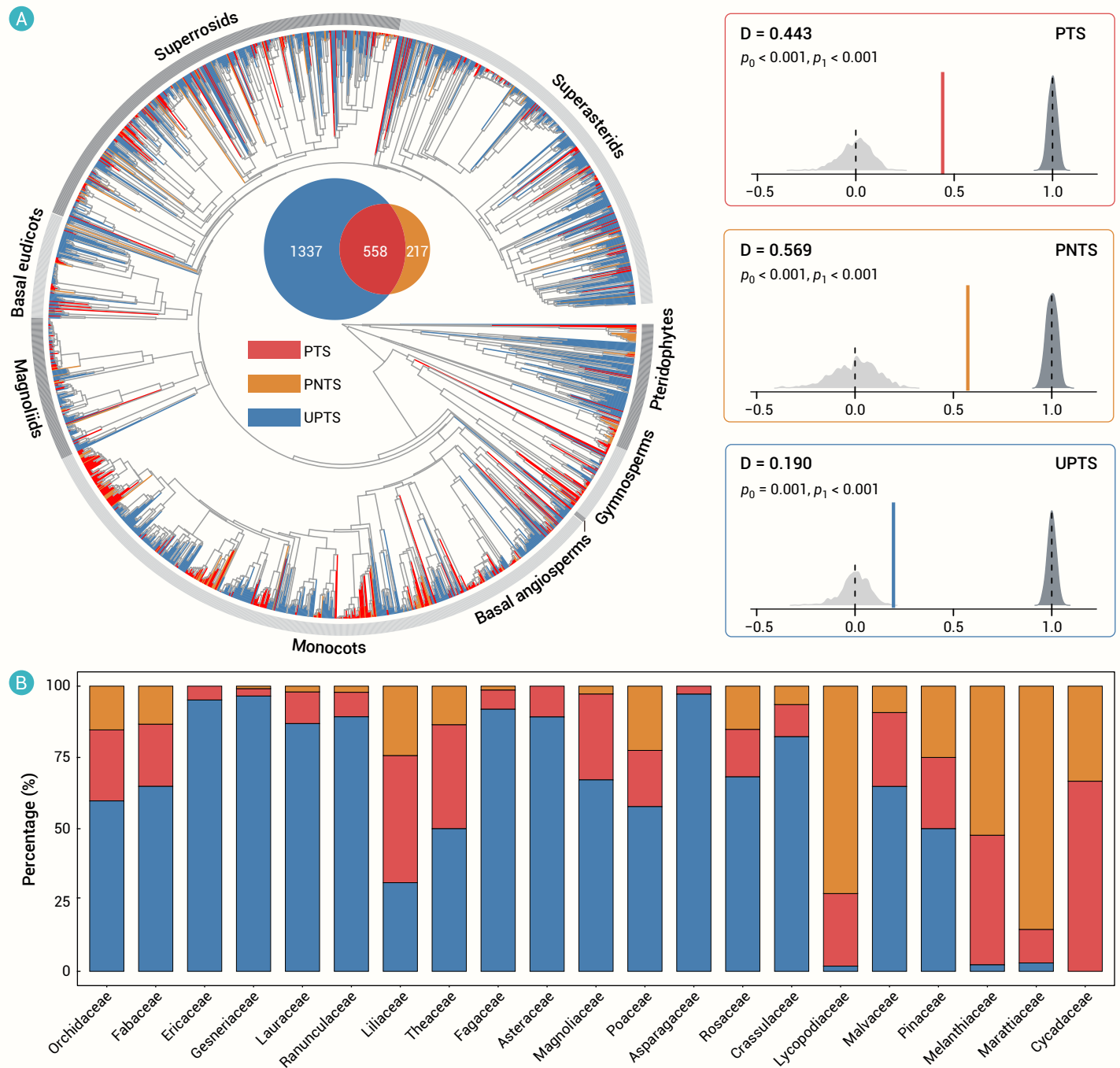


Figure 1. Phylogenetic signals and legal protection of China's Key Vascular Plants (A) The phylogeny of China's Key Vascular Plants with molecular sampling ($n = 2112$), where red branches represent protected threatened species (PTS), orange branches protected non-threatened species (PNTS), and blue branches unprotected threatened species (UPTS). The Venn diagram as an inset shows the number of three categories of species and their relative relationships. On the right are simulated diagrams of phylogenetic signals for three categories of species, with the distribution of Fritz's D values assumed to be a Brownian motion (gray) and a random model (dark gray), respectively. (B) Proportions of PTS, PNTS, and UPTS within the top ten families for each category, ranked by species number in descending order.

Spatial analysis of diversity

We calculated three biodiversity metrics of PTS, PNTS, and UPTS: species richness (SR), phylogenetic diversity (PD), and the standardized effect size of PD (SES.PD). SR was computed as the total number of species per grid cell using the R package *vegan*.⁵² Faith's PD was calculated using the R package *phyloregion*,^{53,54} which sums the branch lengths connecting all species present in each cell on the T_{actual} .²⁰ SES.PD was computed to control for the effect of species richness. This was done by randomly shuffling taxon labels across the tips of the phylogeny 999 times per grid cell to generate a null distribution of expected PD values. For each cell, the mean expected PD (PD_{random}) and its standard deviation (SD_{random}) were calculated. SES.PD was

then defined as $(PD_{\text{observed}} - PD_{\text{random}})/SD_{\text{random}}$, where PD_{observed} is the observed phylogenetic diversity.^{40,55} Grid cells with fewer than 10 species were excluded from SES.PD analysis due to statistical unreliability. Hotspots were defined as the top 5% of grid cells with the highest SR, PD, or SES.PD values.²⁴

Spatial assessment of legal protection effectiveness

To assess the potential spatial variation in the coverage of threatened species and evolutionary history by the Legal Protection List, we developed a new metric, Legal Protection Index (LPI). LPI was calculated at both taxonomic and phylogenetic levels. The richness-based LPI (LPI_{SR}) was calcu-

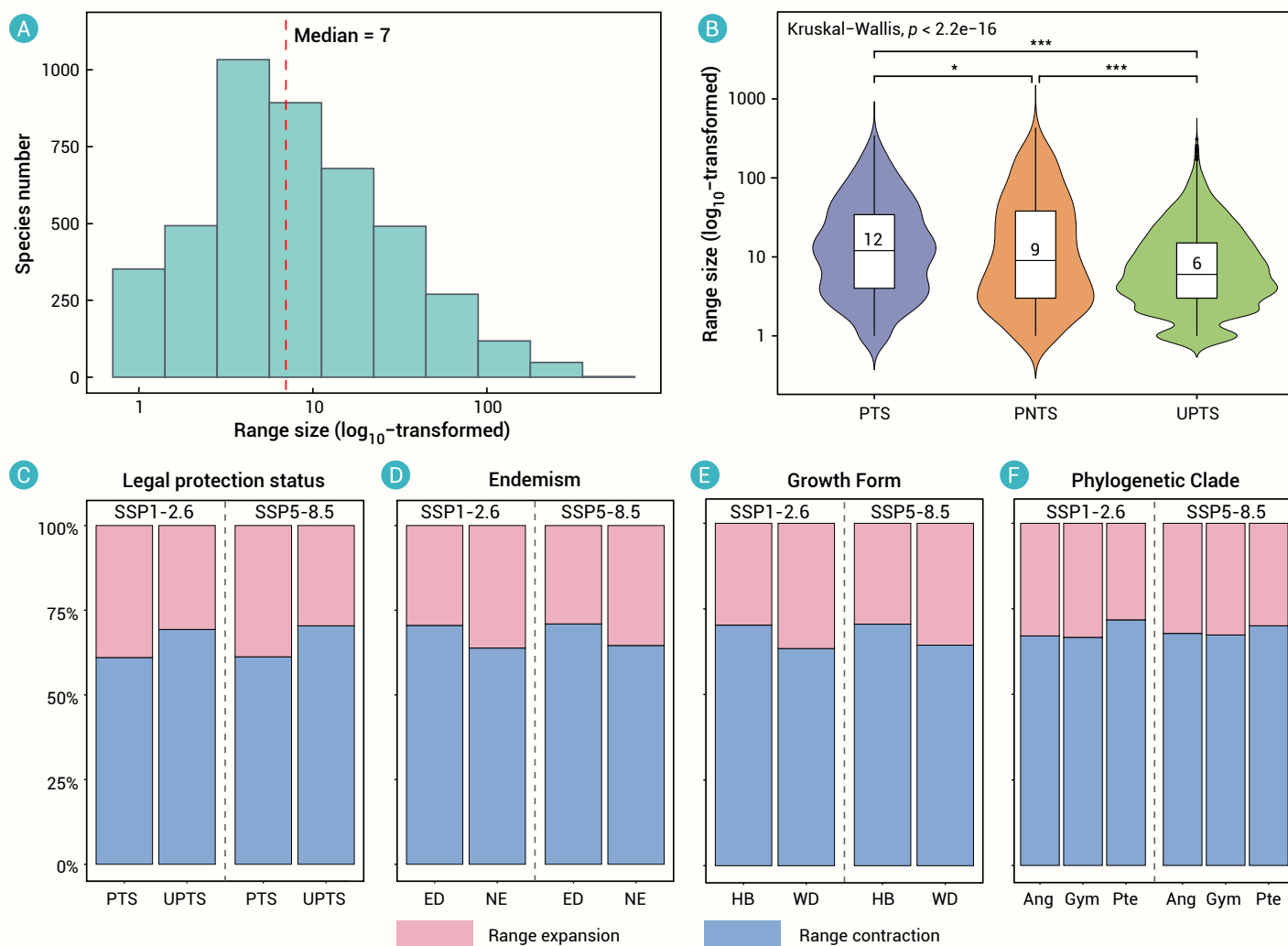


Figure 2. Current status and future changes of species range sizes (A–B) Current status of species range sizes for China's Key Vascular Plants. (A) Frequency distribution of species range sizes. (B) Comparison of range size distributions among PTS, PNTS, and UPTS, with the numbers in the box representing the median. Asterisks indicate statistical significance (* $p < 0.05$ and *** $p < 0.001$) for the Wilcoxon tests. (C–F) Relative proportions of species with range contractions and expansions as simulated under two future climate scenarios (SSP1-2.6 and SSP5-8.5), categorized by (C) legal protection status, (D) endemism, (E) growth form, and (F) phylogenetic clade. PTS, protected threatened species; PNTS, protected non-threatened species; UPTS, unprotected threatened species; ED, endemic species; NE, non-endemic species; HB, herbaceous species; WD, woody species; Ang, angiosperms; Gym, gymnosperms; Pte, pteridophytes.

lated as the difference in proportional richness between legally protected (PTS and PNTS) and unprotected (UPTS) species within each grid cell:

$$LPI_{SR} = \frac{SR_{PTS} + SR_{PNTS} - SR_{UPTS}}{SR_{PTS} + SR_{PNTS} + SR_{UPTS}}$$

where SR_{PTS} , SR_{PNTS} , and SR_{UPTS} represent the number of PTS, PNTS, and UPTS in each cell, respectively. LPI_{SR} values range from -1 to 1, with -1 indicating that all species in a grid cell are unprotected (i.e., UPTS only), and 1 indicating that all are protected (i.e., PTS and/or PNTS only). To account for evolutionary history, we repeated the above calculation using PD in place of SR, yielding the phylogeny-based index (LPI_{PD}). Moreover, we recalculated LPI using only PTS as the protected category to assess sensitivity to the calculation strategy (see supplemental materials and methods for details). Grid cells with fewer than 10 species were excluded from calculations to reduce statistical bias. Grid cells with the lowest 5% of LPI_{SR} or LPI_{PD} values were further designated as legal protection gaps.

To evaluate the spatial consistency between LPI_{SR} and LPI_{PD} , we used the modified t -test in the SpatialPack package of R.⁵⁶ The correlation coefficient (r) quantified spatial consistency, with higher value indicating greater consistency. Similarly, we further assessed the relationship between LPI and diversity metrics (SR, PD, and SES.PD of China's Key Vascular Plants) to explore how LPI varies as a dependent variable of overall biodiversity levels across all grid cells.

To evaluate the extent to which legal protection gaps are covered by *in situ* conservation, we overlaid the legal protection gaps with the geographic layer of national nature reserves in China. These cells with $\geq 10\%$ of their area (i.e., ≥ 1000 km²) overlapping with reserves were considered to be effectively protected *in situ*.^{18,40} We then quantified protected proportions of land area, number of UPTS, and PD.

RESULTS

Phylogenetic signals and distribution patterns across the tree of life

Our analysis based on Fritz's D values revealed non-random phylogenetic distributions for protected threatened species (PTS), protected non-threatened species (PNTS), and unprotected threatened species (UPTS), each influenced to varying extents by phylogenetic relationships (Figure 1A). Specifically, the D values for PTS, PNTS, and UPTS were 0.443, 0.569, and 0.190, respectively, indicating distributions that are neither entirely phylogenetically conserved nor completely random. Among these, UPTS exhibited the lowest D value ($D = 0.190$, $p_0 = 0.001$, $p_1 < 0.001$), reflecting the strongest phylogenetic signal and significant phylogenetic clustering, suggesting that closely related species are more likely to share an unprotected status. The intermediate D value for PTS ($D = 0.443$, $p_0 < 0.001$, $p_1 < 0.001$; Figure 1A) indicated a moderate phylogenetic signal, whereas PNTS had the highest D value ($D = 0.569$, $p_0 < 0.001$, $p_1 < 0.001$), closest to a random distribution. Additionally, phylogenetic analyses across the full sampling of 4,393 species further

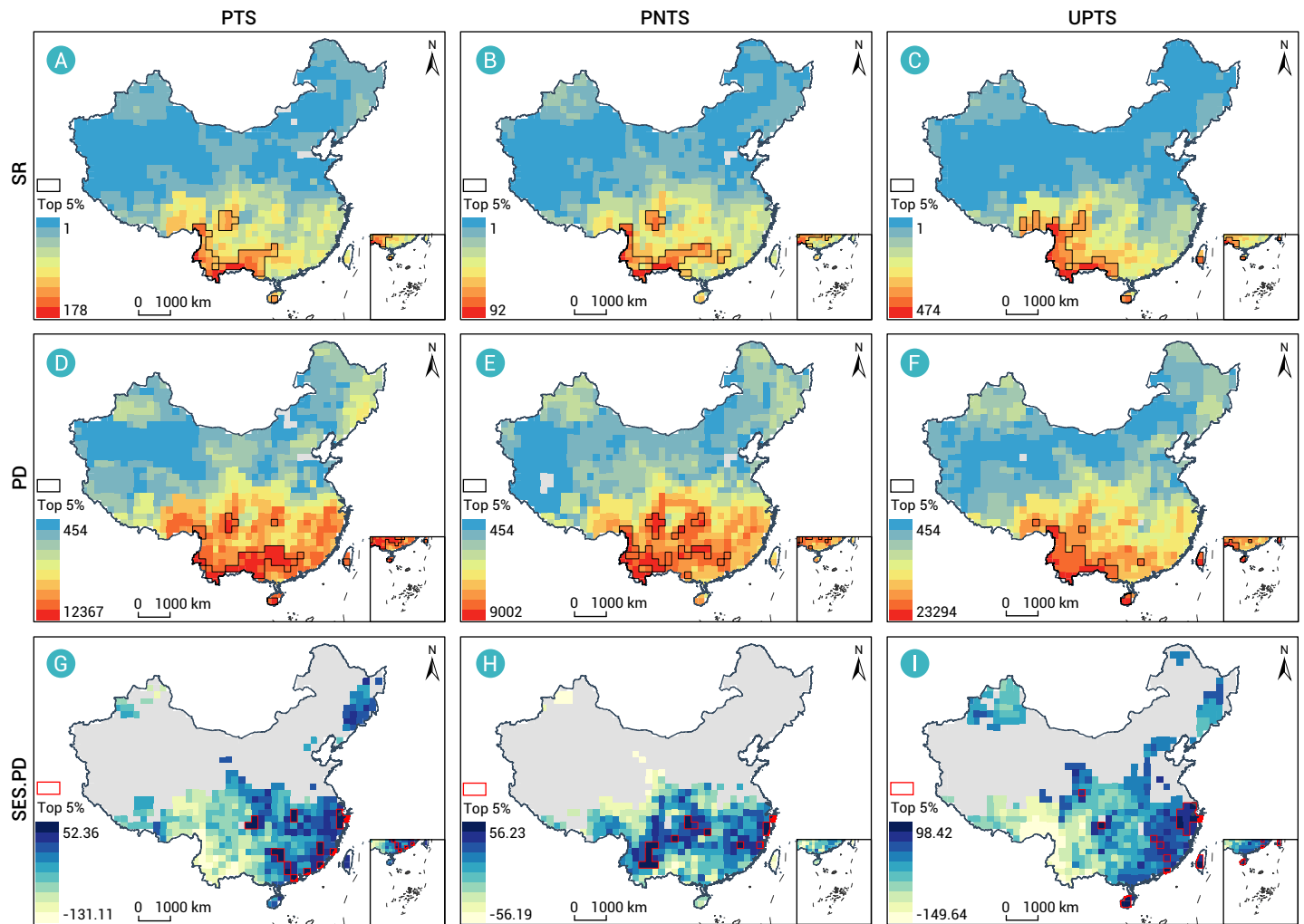


Figure 3. Spatial patterns of diversity for China's Key Vascular Plants Spatial patterns for protected threatened species (PTS), protected non-threatened species (PNTS), and unprotected threatened species (UPTS): (A–C) species richness (SR), (D–F) phylogenetic diversity (PD), and (G–I) standardized effect size of PD (SES.PD). The black (A–F) and red (G–I) outlines highlight the top 5% of the grid cells (hotspots). The gray cells indicate the absence of species in the corresponding category. Review drawing number for maps: GS(2019)1823.

confirmed the strongest phylogenetic signal ($D = 0.007$, $p_0 = 0.501$, $p_1 < 0.001$) in UPTS (Figure S5), approaching a Brownian-motion model ($D = 0$).

Our compiled data revealed insufficient coverage of threatened species in the Legal Protection List, with 3,241 (~82.1%) threatened species lacking legal protection (i.e., UPTS). This unprotected group includes 427 Critically Endangered, 1,046 Endangered, 1,750 Vulnerable species, and 18 species classified as Extinct, Extinct in the Wild, or Regionally Extinct (Table S2). Notably, over half of these UPTS are endemic, with their proportion increasing progressively with threat levels (Table S2). In addition, we identified 446 vascular plant species not currently listed as threatened on China's Red List (i.e., PNTS). While 30 species are Data Deficient, 79 are Least Concern, and 71 are Near Threatened, the majority (266 species) are Not Evaluated by the IUCN (Table S3). This means that at least 66.4% of PNTS require additional data and formal assessment to determine their true extinction risk.

Among major phylogenetic clades, monocots contained the highest numbers of PTS and PNTS, whereas superasterids harbored the highest number of UPTS (Table S4). Relative proportions of PTS, PNTS, and UPTS varied substantially across clades. Lycophytes and gymnosperms had notably higher proportions (95.3% and 69.0%, respectively) of PTS-PNTS compared to UPTS, whereas UPTS accounted for over 50% in other major clades (Table S4). At the family level, UPTS dominated in most families (~83.6%), particularly Orchidaceae, Fabaceae, Ericaceae, Gesneriaceae, and Lauraceae (Figure 1B). Interestingly, coverage by the Legal Protection List varied dramatically across highly diverse families: PTS and PNTS predominated in Liliaceae, Lycopodiaceae, and Cycadaceae, whereas UPTS

overwhelmingly dominated in Ericaceae, Gesneriaceae, and Lauraceae (Figure 1B).

Current status and future changes of species range sizes

Our analysis of current species ranges indicated that most of China's Key Vascular Plant species have limited geographic ranges, with a median range size of 70,000 km², and approximately 91.4% of species having ranges no larger than 500,000 km² (Figure 2A). Among the three categories, the ranges of PTS and PNTS were significantly larger than those of UPTS (medians: PTS = 120,000 km², PNTS = 90,000 km², UPTS = 60,000 km²; $p < 0.001$) (Figure 2B). Analyses based specifically on endemic species yielded similar results, with endemic UPTS also having significantly smaller ranges (medians: PTS = 100,000 km², PNTS = 140,000 km², UPTS = 60,000 km²; $p < 0.001$) (Figure S4).

We projected changes in the future ranges of PTS and UPTS by the 2070s. Despite similar overall trends across climate scenarios, range dynamics differed markedly by legal protection status (Figures 2C–F). Range contractions significantly outpaced expansions for all species. However, UPTS exhibited a consistently higher proportion of range contraction compared to PTS (Figure 2C). Specifically, under SSP1-2.6 and SSP5-8.5 scenarios, 69.3% and 70.4% of UPTS were predicted to experience range contractions, compared to only 61.0% and 61.3% in PTS. Moreover, endemic species, herbaceous plants, and pteridophytes were disproportionately affected, showing higher rates of contraction than their non-endemic, woody, and seed plant counterparts (Figures 2D–F). In addition, sensitivity analysis using point-occurrence

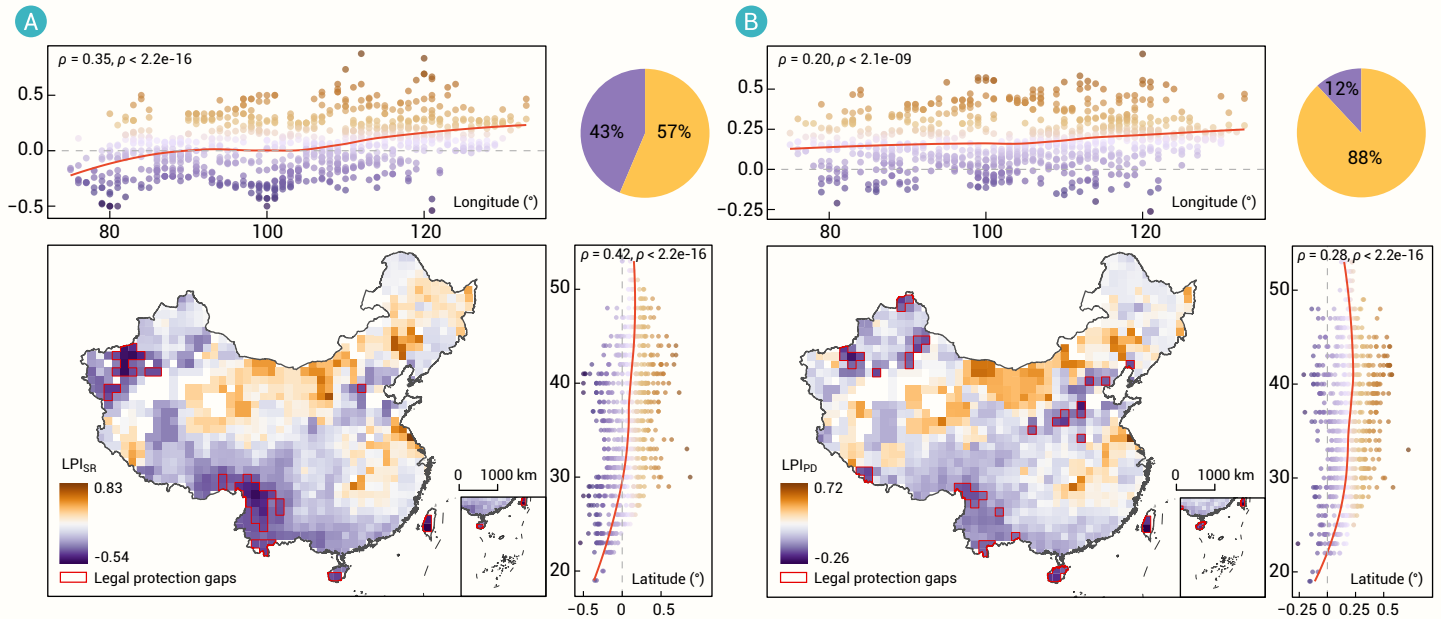


Figure 4. Spatial patterns of legal protection effectiveness Spatial patterns of legal protection effectiveness based on richness-based (LPI_{SR} , A) and phylogeny-based (LPI_{PD} , B) metrics. Red outlines indicate legal protection gaps. Scatter plots above and to the right of each map show the longitudinal and latitudinal trends in LPI_{SR} and LPI_{PD} , respectively. The pie charts in the upper right show the proportions of grid cells with LPI_{SR} and LPI_{PD} values greater than 0 (yellow) and less than or equal to 0 (purple), respectively. Spearman correlation coefficients (ρ) and corresponding p -values indicate the strength and significance of spatial trends. Review drawing number for maps: GS(2019)1823.

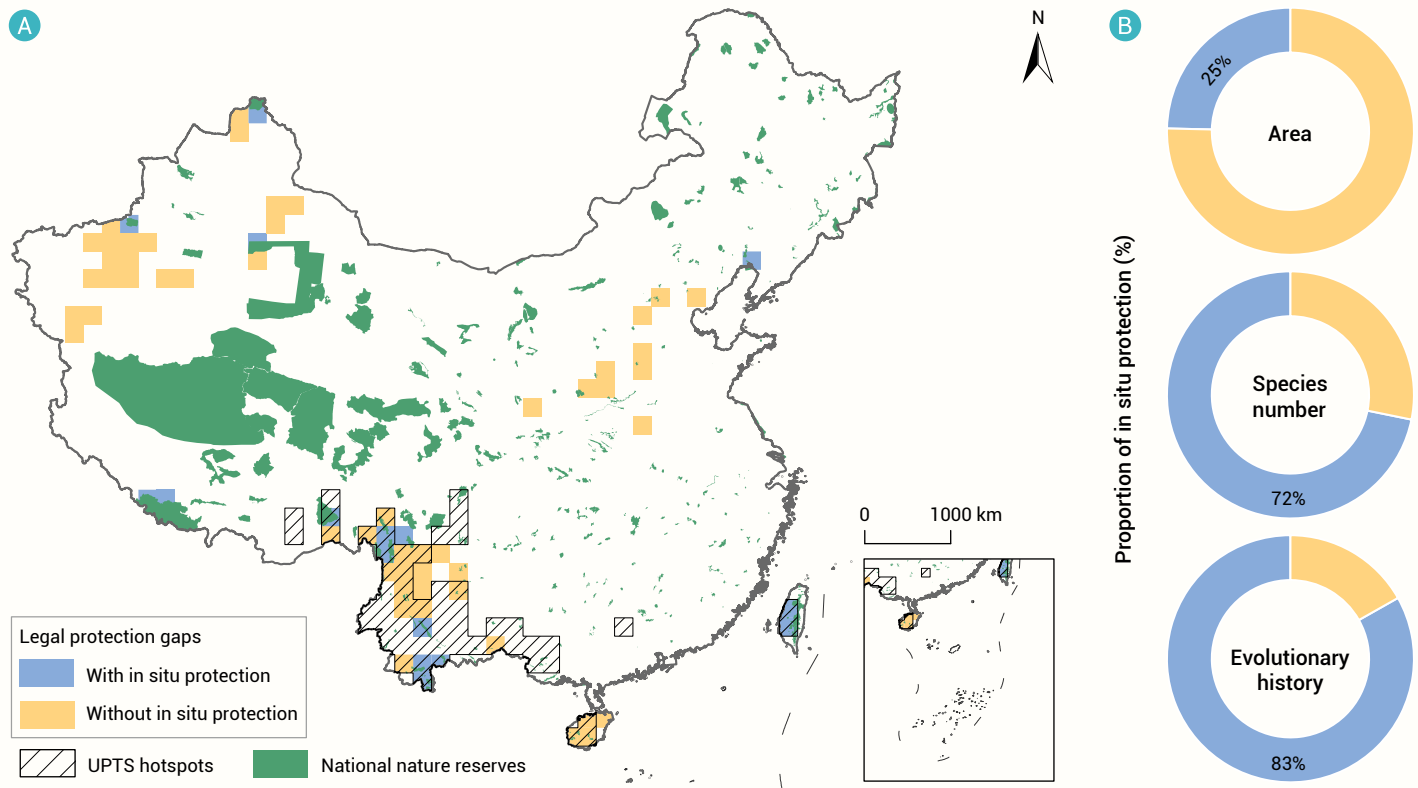


Figure 5. Geographic patterns of legal protection gaps compared to *in situ* conservation by nature reserves (A) Geographic distribution of legal protection gaps and national nature reserves. Grid cells are colored based on *in situ* protection: blue indicates $\geq 10\%$ coverage by national nature reserves and yellow indicates insufficient coverage. Hatched grid cells indicate the combined hotspots of unprotected threatened species (UPTS) richness and phylogenetic diversity. (B) *In situ* conservation status of legal protection gaps. Donut charts show the proportions of land area, number of UPTS, and their evolutionary history that are protected (blue) versus unprotected (yellow) by national nature reserves. Review drawing number for maps: GS(2019)1823.

records showed that, despite minor differences between two SDM approaches, both approaches projected a slightly higher proportion of range contractions for UPTS than for PTS under future climate scenarios (Table S1), supporting greater climate-change vulnerability in UPTS.

By integrating current legal protection status, threat level, endemism, and

projected responses to climate change, we identified 208 species warranting prioritized consideration in future updates of the Legal Protection List (Table S5). These species, spanning 134 genera and 69 families, are Critically Endangered, endemic to China, and projected to suffer further range contractions under climate change. Their high vulnerability necessitates urgent

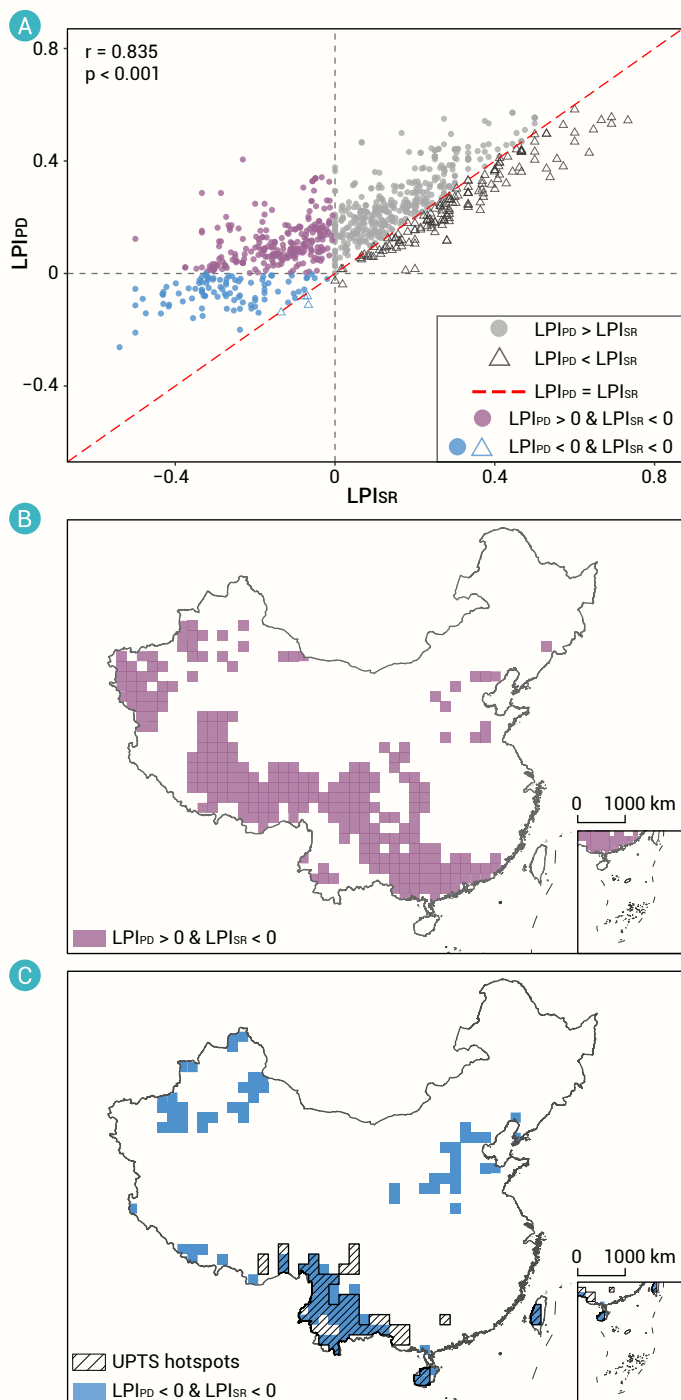


Figure 6. Comparison between richness-based and phylogeny-based legal protection effectiveness (A) Relationship between richness- and phylogeny-based Legal Protection Index (LPI_{SR} and LPI_{PD}) across grid cells in China. Purple represents cells with high phylogenetic diversity protection (LPI_{PD} > 0) but low species richness protection (LPI_{SR} < 0), while blue indicates cells where both are poorly protected (LPI_{PD} < 0 and LPI_{SR} < 0). (B-C) Spatial pattern of cells highlighted in purple (B) and blue (C) points in (A). Hatched cells indicate the hotspots of unprotected threatened species (UPTS). Review drawing number for maps: GS(2019)1823.

conservation action to prevent biodiversity loss.

Spatial patterns of legal protection effectiveness and gaps

Spatial patterns of species richness (SR) and phylogenetic diversity (PD) among PTS, PNTS, and UPTS were generally congruent, with the highest diversity concentrated in southern China, particularly southwestern regions, Hainan, and Taiwan (Figures 3A-F). However, SR and PD hotspots (top 5% grid cells) showed category-specific patterns: PTS and PNTS hotspots were

dispersed across southern China, whereas UPTS hotspots were more concentrated in southwestern regions. Analysis of the standardized effect size of PD (SES.PD) revealed higher values in eastern China, especially Zhejiang, Fujian, and Guangdong for PTS and UPTS (Figures 3G & I), while hotspots of PNTS did not exhibit a clear east-west differentiation and were more dispersed (Figure 3H).

The effectiveness of legal protection showed pronounced spatial heterogeneity, generally increasing from west to east and south to north (Figures 4 & S6). Regions such as northeastern China, Inner Mongolia, Ningxia, Gansu, Qinghai, and parts of eastern and central China exhibited high effectiveness, with more than half of threatened species legally protected (LPI_{SR} > 0) in 494 grid cells. Conversely, northern China, Xinjiang, southwestern China, southern China, Hainan, and Taiwan showed poorer legal protection, with no more than half of threatened species protected (LPI_{SR} ≤ 0) in 380 grid cells (Figure 4A). While the spatial patterns for richness- and phylogeny-based protection effectiveness (LPI_{PD}) were similar, the latter had more grid cells ($n = 772$) exhibiting better effectiveness (i.e., LPI_{PD} > 0) (Figure 4B).

Legal protection gaps, identified from both LPI_{SR} and LPI_{PD} values, were primarily concentrated in the mountainous regions of northern and southwestern China, as well as Hainan and Taiwan (Figures 4 & 5A). Notably, the gaps in southern China exhibited substantial spatial overlap with taxonomic and phylogenetic diversity hotspots of UPTS (Figure 5A). Spatial intersection with China's national nature reserves revealed that although *in situ* conservation covers only 25% of the total gap area, the protected grid cells contain 72% of UPTS recorded in these gap regions (Figure 5B). The proportion rose to 83% when considering evolutionary history (i.e., phylogenetic diversity; Figure 5B). However, critical dual protection gaps persist in diversity hotspots, primarily in Yunnan and Hainan, where legal protection and *in situ* conservation remain insufficient (Figure 5A). More broadly, across China, 1,195 threatened species remain neither legally protected nor conserved in nature reserves, accounting for 36.9% of UPTS.

Correlation analyses revealed a significant positive relationship between LPI_{SR} and LPI_{PD} ($r = 0.835$, $p < 0.001$) (Figure 6A). When comparing richness-based and phylogeny-based LPI, 721 grid cells (~82.5%) showed higher LPI_{PD} than LPI_{SR}, including 246 cells with positive LPI_{PD} and negative LPI_{SR} values, mostly located in western and southern China (Figure 6B). Nevertheless, 100 grid cells had negative values for both LPI_{PD} and LPI_{SR}, concentrated in Yunnan, Hainan, Taiwan, and scattered mountainous regions in northern China (Figure 6C). Both LPI_{SR} and LPI_{PD} showed moderate negative correlations ($r = -0.54$, $p = 0.0016$ and $r = -0.44$, $p = 0.0011$, respectively) with species richness of China's Key Vascular Plants (Figure 7). Moreover, grid cells with lower LPI_{SR} and LPI_{PD} values often had higher PD and lower SES.PD.

DISCUSSION

Uneven distribution of legal protection status across the tree of life

The significant phylogenetic clustering observed among UPTS, PTS, and PNTS aligns with previous findings indicating non-random extinction risk patterns across the tree of life.^{39,57,58} According to the phylogenetic niche conservatism hypothesis, closely related species typically share traits linked to extinction risk (e.g., life form, range size, and habitat preference),^{59,60} suggesting heightened vulnerability for phylogenetically clustered groups. Our results indicated stronger phylogenetic clustering among UPTS, suggesting elevated extinction risks that may be compounded by insufficient legal protection currently afforded to threatened species.

Specifically, legal protection coverage is highly unevenly distributed across major branches of the tree of life (Figure 1). Pteridophytes and gymnosperms exhibit higher protection levels compared to angiosperms, largely due to the adoption of taxonomic similarity criteria of the Legal Protection List,¹² which includes entire taxa (e.g., families, genera) when threatened species are abundant and morphologically similar (e.g., *Huperzia* and *Cycas*).⁶¹ Within angiosperms, higher coverage in families such as Orchidaceae, Fabaceae, Liliaceae, and Poaceae is mainly driven by their economic value, particularly as medicinal, ornamental, or crop wild relatives.^{12,62,63} In contrast, Gesneriaceae, keystone taxa in vulnerable karst habitats,⁶⁴ and Ranunculaceae, vital in northern temperate grassland/meadow ecosystems, receive notably less

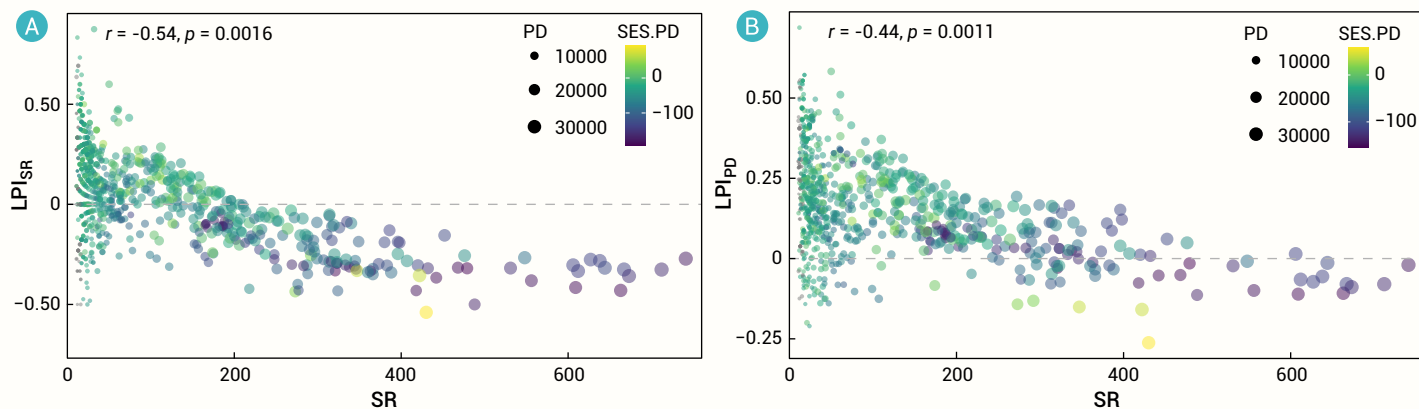


Figure 7. Relationships between Legal Protection Index and biodiversity metrics across grid cells in China Scatter plots show the relationships between species richness (SR) of China's Key Vascular Plants and Legal Protection Index (LPI): richness-based (LPI_{SR} , A) and phylogeny-based (LPI_{PD} , B) metrics. Each dot represents a grid cell, with dot size proportional to PD and color indicating the SES.PD.

protection despite their ecological significance.^{65,66} Furthermore, we found inadequate legal protection coverage for woody plant families such as Ericaceae, Lauraceae, and Fagaceae. Despite their limited recognized economic profile or biases stemming from systematic classification and aesthetic preferences, these woody species play crucial roles in alpine shrublands and subtropical-tropical forests.^{67,68} Insufficient protection for these families threatens forest community stability and ecological balance.

Protected non-threatened species (PNTS) also warrant serious attention and further investigation. First, roughly one-third of PNTS do not currently meet formal threat criteria but are already subject to intensive use or exploitation, or have been listed at the genus level under the taxonomic similarity criterion.¹² These lineages may require refinement and possible delisting as more comprehensive data become available. Second, about two-thirds of PNTS are classified as Data Deficient or Not Evaluated in the Red List, indicating the urgent need for formal assessment.

Inconsistent impacts of climate change on threatened vascular plants

Our results show that a higher proportion of UPTS is projected to experience range contractions compared to PTS (Figure 2C & Table S1). This pattern is likely attributable to the more restricted geographic ranges of UPTS (Figure 2B), which are often associated with smaller populations, higher environmental specialization, and limited dispersal capacity.^{69,70} These traits leave them less able to track shifting climatic niches, increasing their extinction risk.⁷¹⁻⁷³ A recent study further suggests that the number of threatened woody endemic plants in China will continue to rise,²⁵ implying that the Legal Protection List may increasingly fail to cover threatened taxa adequately. Pteridophytes are particularly vulnerable, showing a disproportionately high rate of projected range contractions. Their unique biological characteristics, including complex reproductive stages and a moisture-dependent life cycle,^{74,75} impose strict habitat requirements, rendering them exceptionally sensitive to climate change.

Our county-level projections indicate a higher proportion of threatened vascular plants will experience range contractions than estimates derived from point-occurrence records, including our sensitivity analysis and previous study based on georeferenced point records,¹⁸ suggesting a more severe biodiversity crisis. This discrepancy may stem from differences in sampling and distribution data coverage. First, our county-level distribution dataset is more comprehensive, including nearly all known threatened vascular plants in China (3,942 species), which roughly doubles the sample size of earlier study and almost triples that of our sensitivity analysis.¹⁸ Second, while coordinate-based occurrence data are valuable, county-level records often provide higher completeness and accurate identification for large-scale studies in China.^{13,48} Moreover, we utilized a modeling framework in Mikrubi specifically designed for county-level distribution data,⁴⁹ unlike the maximum entropy algorithm in MaxEnt for coordinate data.^{18,76} The influence of data resolution and model selection on projection highlights a critical need for further comparative studies to refine future forecasts.

Spatial bias in legal protection effectiveness and conservation implications

Our analyses reveal pronounced spatial disparities in the effectiveness of the Legal Protection List (Figure 4). We find higher protection levels in northern and east-central China, in terms of both species richness ($LPI_{SR} > 0$) and phylogenetic diversity ($LPI_{PD} > 0$). This pattern may reflect the relatively lower threatened species richness and a historical focus on flagship taxa such as *Cynomorium songaricum*, *Glycyrrhiza uralensis*, and *Phellodendron amurense*.⁷⁷ In contrast, we identify southwestern China, Hainan, Taiwan, Xinjiang, and scattered mountainous areas in northern China as severe protection gaps for both threatened species richness and phylogenetic diversity ($LPI_{SR} < 0$ and $LPI_{PD} < 0$). Alarming, these same gap regions are centers of diversity for key families such as Ericaceae, Gesneriaceae, and Lauraceae,⁸ which are disproportionately represented among UPTS (Figure 1B). The spatial mismatch indicates the areas with the highest and most unique biodiversity are the least legally protected, concentrating extinction risk. While previous studies focusing on national key protected wild plants have flagged southern China, particularly Yunnan, Guangxi, Xizang, and Sichuan, as conservation priority,^{13,17,19} our results demonstrate that current legal efforts are insufficient given the region's extraordinary concentration of threatened and phylogenetically distinct plants. Future revisions of the Legal Protection List must prioritize these underprotected biodiversity centers.

While the spatial patterns of richness- and phylogeny-based LPI (LPI_{SR} and LPI_{PD}) are broadly similar (Figure 4), their extent differs significantly (Figure 6A). Specifically, the Legal Protection List is more effective at capturing evolutionary history than species richness across most regions of China. This is largely driven by grid cells in western and southern China, where LPI_{PD} exceeds LPI_{SR} , particularly in areas where $LPI_{PD} > 0$ and $LPI_{SR} < 0$. These regions host a high richness of threatened species with low standardized phylogenetic diversity (SES.PD), indicating they are dominated by phylogenetically clustered distributions of closely related taxa such as *Rhododendron*, *Bulbophyllum*, *Aspidistra*, and *Lithocarpus*. Consequently, while many species remain unprotected, the amount of unique evolutionary history at risk is comparatively low. Nevertheless, the phylogenetic clustering of UPTS poses a distinct threat: the concentrated extinction of an entire lineage could lead to the irreversible loss of unique evolutionary lineages and their associated traits,⁷⁸ even if the overall loss of phylogenetic diversity appears limited.

Moreover, the effectiveness of legal protection is lowest in regions identified as hotspots of both species richness and phylogenetic diversity, regardless of richness- or phylogeny-based assessments. An encouraging finding is that most UPTS and their evolutionary history within legal protection gaps are effectively covered by China's network of nature reserves. This spatial complementarity between legal frameworks and *in situ* conservation offers a form of layered protection, buffering against the limitations of either approach alone. The extensive coverage is likely attributable to the high habitat representativeness and environmental heterogeneity captured by China's protected area system.^{79,80} Nevertheless, critical exceptions remain. Areas with dual protection gaps for both legal and *in situ* conservation (such as

parts of Yunnan and Hainan) and the 1,195 threatened vascular plants lacking both legal protection and nature reserve coverage represent the highest priorities for future conservation action. Specifically, the genera *Aspidistra*, *Primulina*, and *Begonia* contain the largest numbers of such species. Most of them have extremely narrow ranges and are adapted to specialized habitat conditions (e.g., karst landscapes), so the lack of effective protection may expose them to high extinction risk and result in substantial biodiversity loss.

Although our assessment focuses on species protected at the national level, we acknowledge that many provinces and municipalities have their own lists of locally protected species and that additional information exists in conservation reports, scientific studies, and project-based initiatives. Incorporating these diverse sources would undoubtedly provide a more comprehensive picture of conservation efforts across China. Our study therefore represents a first national-scale baseline, and future work integrating local protection measures and project-level conservation actions will be essential for developing more fine-grained and regionally informed assessments.

CONCLUSION

In this study, we integrated the Red List and the Legal Protection List, using large-scale phylogeny and geographic data, to assess the legal protection biases and gaps for threatened vascular plants in China. We find that unprotected threatened species (UPTS) are more phylogenetically clustered, have narrower distributions, and face greater future range contractions than the protected threatened species (PTS), indicating a higher extinction risk. We identify specific species and regions requiring priority conservation actions. While hotspots of threatened species richness and phylogenetic diversity are concentrated in southwestern China, Hainan, and Taiwan, these regions also exhibit the most severe legal protection gaps. Fortunately, China's well-established protected area system provides *in situ* conservation for 72% of UPTS and 83% of their evolutionary history within these gaps, offering a crucial foundation for targeted legal protection. Our findings provide critical scientific guidance to support China's efforts in meeting the targets of the Kunming-Montreal Global Biodiversity Framework and inform timely conservation actions to prevent multidimensional biodiversity loss.

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AUTHOR CONTRIBUTIONS

Z.C., L.L., Y.F., and Y.L. conceived, designed and refined the study. Y.F., J.L. and Y.L. compiled the data. Y.F. performed data analysis with assistance from J.L., Y.L., L.Z. and Y.Y. Y.F. and Z.C. wrote the paper with edits from all authors. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

ETHICAL STATEMENT AND PATIENT CONSENT

Not applicable.

DATA AND CODE AVAILABILITY

Our data comprise a detailed list of China's Key Vascular Plants, phylogenetic trees, species distribution data, and raw outputs from species distribution models. All datasets and scripts are publicly available on ScienceDB (<https://doi.org/10.57760/sciencedb.29888>).

SUPPLEMENTAL INFORMATION

It can be found online at <https://doi.org/10.59717/j.xinn-life.2026.100205>

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