

Review article

Multifaceted plant diversity patterns across the Himalaya: Status and outlook



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ABSTRACT

Mountains serve as exceptional natural laboratories for studying biodiversity due to their heterogeneous landforms and climatic zones. The Himalaya, a global biodiversity hotspot, hosts rich endemic flora, supports vital ecosystem functions, and offers a unique window into multifaceted plant diversity patterns. This review synthesizes research on Himalayan plant diversity, including species, phylogenetic, functional, and genetic dimensions, highlighting knowledge gaps and solutions. Research on Himalayan plant diversity has developed significantly. However, gaps remain, especially in studies on phylogenetic and functional diversity. The region's vegetation ranges from tropical rainforests to alpine ecosystems, with species richness typically following a hump-shaped distribution along elevation gradients. The eastern Himalaya exhibits higher plant diversity than the central and western regions. Low-elevation communities were found to be more functionally diverse, whereas high-elevation communities displayed greater ecological specialization. Communities at mid-elevations tend to show greater phylogenetic diversity than those at higher and lower elevations. The eastern and western flanks of the Himalaya retain high levels of genetic diversity and serve as glacial refugia, whereas the central region acts as a hybrid zone for closely related species. Himalayan plant diversity is shaped by historical, climatic, ecological and anthropogenic factors across space and time. However, this rich biodiversity is increasingly threatened by environmental change and growing anthropogenic pressures. Unfortunately, research efforts are constrained by spatial biases and the lack of transnational initiatives and

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collaborative studies, which could significantly benefit from interdisciplinary approaches, and other coordinated actions. These efforts are vital to safeguarding the Himalayan natural heritage.

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1. Introduction

The Himalaya, spanning China, India, Bhutan, Nepal, and Pakistan, is globally renowned for its exceptional biodiversity (Wambulwa et al., 2021; Liu et al., 2022). As one of the youngest mountain ranges in the world, the Himalaya began to form approximately 60 million years ago (Ma) during the early Cenozoic Era, following the onset of the collision between the Indian and the Eurasian amalgam of continental tectonic plates (Ding et al., 2022). This collision, and associated geodynamic processes, initially resulted in a slow rise of the Himalaya until the late Middle Miocene (around 25–15 Ma) when the range rose from approximately 2 km to approaching 5 km (Gébelin et al., 2013; Ding et al., 2017, 2022). Today, the Himalaya can be divided into five distinct parts, from south to north: the Siwalik (Outer or Sub-) Himalaya, Lesser (Middle) Himalaya, Greater (Higher) Himalaya, Tethyan Himalaya, and the Trans-Himalaya, which lies to the north of the Indus Yarlung Tsangpo Suture Zone (Fig. 1B) (Mukherjee, 2015; Searle and Treloar, 2019). The Siwalik Himalaya, consisting primarily of Miocene sandstone and mudstone deposits, is the youngest part of the range. In contrast, the Lesser and Greater Himalaya are mostly composed of Proterozoic–Cambrian metamorphic rocks, including schist, gneiss and granites. The Tethys Himalaya, formed from Paleozoic and Mesozoic sedimentary rocks, and the Trans-Himalaya, mostly made up of granitic and volcanic rocks.

Geographically, the Himalaya can be divided into three longitudinal regions: the Western, Central, and Eastern Himalaya (Fig. 1C) (Wambulwa et al., 2021; Liu et al., 2022). Stretching 2381 km from west to east and 1018 km from north to south, the range covers an area of 6.62×10^5 km², with a mean elevation of 3326 m, ranging from 88 m to 8848 m at its highest peak, Mount Qomolangma (Figs. 1D and 2I) (Liu et al., 2022). Functioning as a formidable natural barrier, the Himalaya plays a crucial role in shaping regional climates by blocking cold Siberian winds and influencing monsoon precipitation patterns over a very large region. Together with the Tibetan Plateau and adjacent mountain ranges, collectively known as the “Third Pole” (Qiu, 2008; Liu et al., 2018, 2022), the region holds the world’s third-largest ice and snow deposit. It has earned the nickname the “Water Tower of Asia” as it is the source of numerous major river systems, including the Ganges, Brahmaputra, and Indus, along with their extensive tributaries. These rivers are of immense ecological, social, and economic significance, sustaining millions of people downstream (Xu et al., 2009).

Orogenic events during the Himalaya formation triggered significant physiographic and environmental transformations, and profoundly influenced the emerging ecosystems (Favre et al., 2015; Spicer, 2017; Zhu et al., 2022; Spicer et al., 2025). These changes promoted geographical isolation, vegetation shifts, vicariance (mixing and separation), and the evolutionary divergence of plant species (Pandit et al., 2014; Manish and Pandit, 2018; Qian et al., 2019; Khan et al., 2023; Spicer et al., 2025). The transformation of the marine Tethys into terrestrial ecosystems further integrated the Indian subcontinent into neighbouring floristic regions, such as the Sino-Japanese region in the east, the Caucasian regions in the west, and the Indo-Malayan region in the southeast (Wambulwa et al.,

2021). Orbitally driven fluctuations in temperature also play a role in speciation in a topographically complex region like the Himalaya. Cyclical changes in temperature repeatedly drive taxa up and down slopes allowing repeated opportunities for genetic separation and drift followed by hybridization. This generates a ‘speciation pump’ (Spicer et al., 2020) that likely contributed to the diversity of the Himalayan biota (Spicer et al., 2025).

Fossil evidence from the western foothills highlights strong links to modern Indo-Malayan flora (Prasad, 1993). Likewise, a comparison of Paleogene and Neogene flora from southwestern China and the northeast India suggests that the Chinese flora merged into the Himalaya via the Tibetan corridor (Mehrotra et al., 2005). Despite geographical proximity, the Himalaya, Hengduan Mountains, and the Tibetan Plateau exhibit distinct floral characteristics and diversity patterns (Xing and Ree, 2017; Yu et al., 2020; Liu et al., 2022). Notably, the Himalaya likely inherited a diverse biota from the adjacent more ancient Gangdese mountain system. Migration to the Himalaya likely also took place from the Hengduan Mountains that still host the world’s oldest temperate alpine biome (Xing and Ree, 2017; Ding et al., 2020) and with its extreme relief seems to have particularly benefitted from the speciation pump as evidenced by glimpses of reticulate evolution (Qin et al., 2023).

Climate variations, complex geology, diverse geography, evolutionary history, and human influence have led to different vegetation types and distributions across the Western, Central, and Eastern Himalaya (Fig. 2) (Srinivasan et al., 2014; Huang et al., 2024). As a result, grasslands cover the most area, followed by non-vegetated land, evergreen needle-leaved forest, and deciduous broad-leaved forest, while the smallest area is covered by wetland, followed by shrubland and deciduous needle-leaved forest (Fig. 2A). In particular, the Eastern Himalaya, with a range of warm and moist climates characterised by heavy rainfall (3800–4000 mm), supports rich sub-tropical and tropical forests (Manish and Pandit, 2018; Sun and Zhou, 2002). In contrast, the western area receives less rainfall (75–150 mm; Manish and Pandit, 2018) is much more arid and is dominated by temperate, sub-alpine, and alpine vegetation (Måren et al., 2015; Khan et al., 2025). This rainfall disparity shapes a strong west to east bioclimatic gradient, while the central Himalaya experiences intermediate conditions (Fig. 1D).

Along the elevational gradients, vegetation may be divided into seven types based on rainfall and temperature (Chang, 1981; Singh and Singh, 1987; QXPCSE, 1988), with grasslands covering the largest area, and shrublands the smallest (Fig. 2A). Photographs from various regions, including the Western, Central, Eastern, and Tethyan Himalaya (Fig. 3D–I), visually capture the diverse vegetation patterns and landscapes. There is a clear zonation of forest types in the Western Himalaya from *Pinus roxburghii* forests in the sub-tropical zone, broadleaf (*Quercus semecarpifolia*) and coniferous forests (*Cedrus deodara*, *Cupressus torulosa*) in the temperate zone (Gairola et al., 2008), and *Betula utilis* and *Abies pindrow* forests in the alpine zone (Gairola et al., 2008). The central region comprises *Tectona grandis* in the sub-tropical zone (Singh and Singh, 1987), and *Pinus wallichiana*, *Quercus leucotrichophora*, and *Acer acuminatum* dominate the temperate zone (Ahmad, 2022;

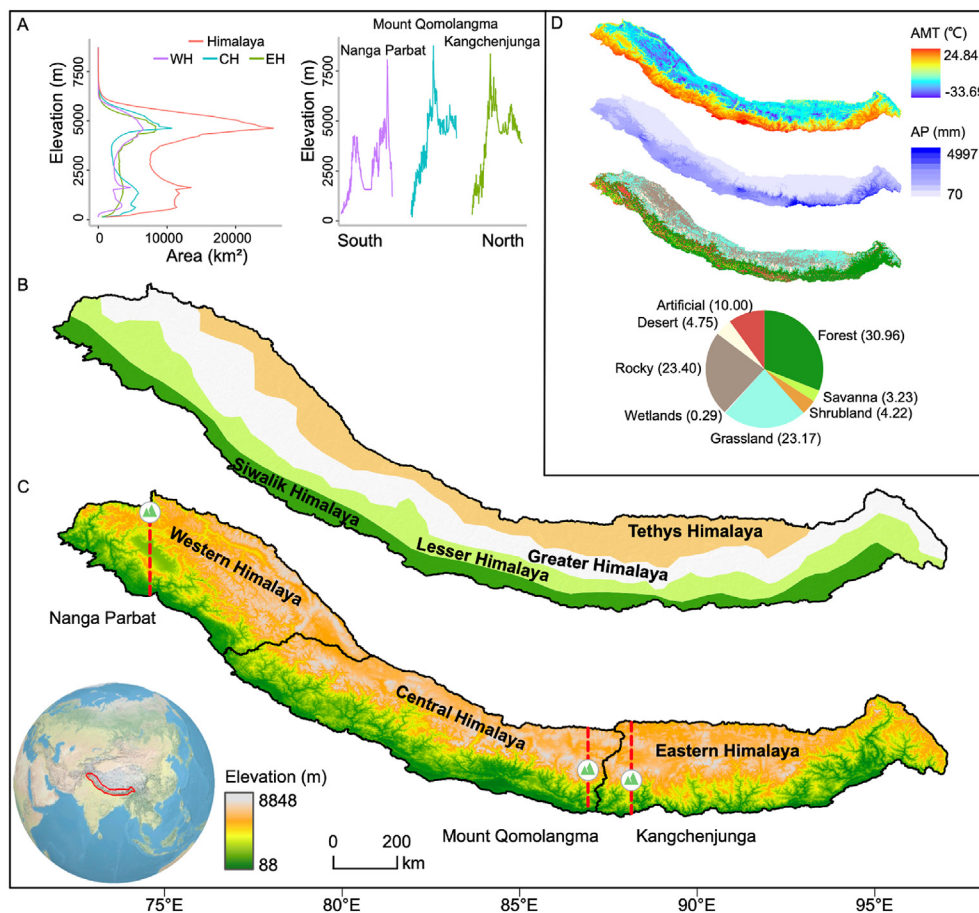


Fig. 1. Geographical, geological, and environmental characteristics of the Himalaya. A, C) Topographical map of the Himalaya, divided into Western, Central, and Eastern Himalaya according to Liu et al. (2022) and Wambulwa et al. (2021). Green mountain labels indicate the highest mountain peaks of each sub-region (Nanga Parbat, Qomolangma, and Kangchenjunga, going from west to east). The three red dashed lines depict the profile position (corresponding to those in the upper line charts of A). The left-lower corner inset indicates the global location of the Himalaya. The upper line charts (A) depict the total land areas along elevations (100 m interval) and the elevation change of longitudinal profiles of three peaks in the Western, Central, and Eastern Himalaya. B) The geological divisions of the Himalaya, arranged from south to north, comprise the Siwalik (Outer) Himalaya, Lesser (Middle) Himalaya, Greater (Higher) Himalaya, and Tethys Himalaya. The Trans-Himalaya, situated north of the Himalaya, is not shown here. This map is inspired from Searle and Treloar (2019) and Mukherjee (2015). D) The two upper maps show the annual mean temperature (AMT) and mean annual precipitation (AP) across the Himalaya; the climatic data were downloaded from WorldClim2 (Fick and Hijmans, 2017). The lower map displays the land cover of the Himalaya, and the pie chart shows the relative proportion of each land cover type. [For A and C, we used 30 m resolution elevation data from the Terra Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) and Global Digital Elevation Model (GDEM) Version 3, while D is based on the landcover data from Jung et al. (2020). We employed the R package terra (Hijmans and Bivand, 2022) to calculate the area changes for six categories of vegetation and one category of non-vegetation surface cover at 100 m elevational intervals. The resulting line in A and pie chart of D were generated using the R package ggplot2].

Singh et al., 2020). By contrast, in the Eastern Himalaya, *Shorea robusta*, *Ficus* spp., and bamboo species dominate sub-tropical and tropical forests (Singh and Singh, 1987; Ashton and Zhu, 2020), *Acer* spp., *Alnus nepalensis* typify temperate broadleaf and mixed forests, and *Abies spectabilis*, *Juniperus tibetica*, *Rhododendron* spp., are prevalent in sub-alpine and alpine zones (Zhang, 1978; Singh and Singh, 1987; Sun and Zhou, 2002).

To develop prior work on evolutionary and ecological contexts for the Himalayan flora, a comprehensive literature search was conducted on January 15th, 2025, using the query strings provided in Table S1 within the Web of Science database. This search identified a total of 2100 publications that address species, phylogenetic, functional, and genetic diversity in the Himalaya. These sources include research articles, reviews, thesis, reports, and books (see Table S2). Most publications focus on species diversity, followed by genetic diversity, with a noticeable increase after year 2001 (Fig. 3A and C). Geographically, plant diversity studies have been predominantly conducted from within India and China (Fig. 3B). India leads with 653 articles on species diversity, 385 on genetic diversity, 24 on functional diversity, and 5 on phylogenetic

diversity, while China has produced 356 articles on species, 244 on genetic, 13 on functional traits/diversity, and 20 on phylogenetic diversity (Table S2). Despite the growing body of research and previous efforts to synthesize this information (e.g., Wambulwa et al., 2021), significant knowledge gaps remain, particularly in our understanding of the Himalaya's functional, phylogenetic and genetic diversity.

We have five important research questions: 1) How have Himalayan landforms and climates influenced plant diversity, and what processes shape current diversity patterns? 2) What are the patterns of species, phylogenetic, functional, and genetic diversity across elevation, and what are the main drivers of these patterns? 3) How do temperature and aridity affect functional traits and physiological adaptations of high-elevation plants? 4) How does environmental change impact on plant diversity? And, lastly, 5) What are the current challenges and future directions of multi-disciplinary research, and how can such approaches enhance understanding of Himalayan biodiversity hotspots and guide conservation priorities?

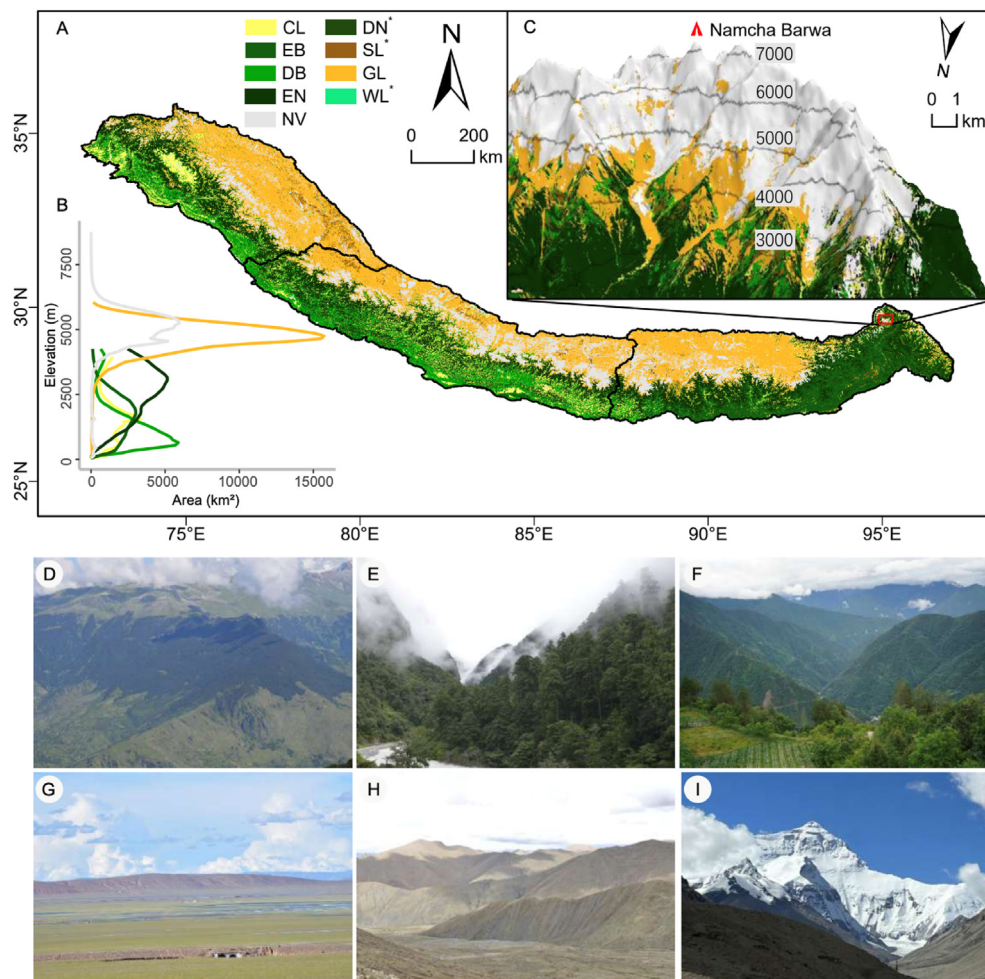


Fig. 2. Major vegetation types distributed across the Himalaya. A) Horizontal distribution of major vegetation types across the Himalaya. These include cropland (CL), evergreen broadleaved forest (EB), deciduous broadleaved forest (DB), evergreen needle leaved forest (EN), deciduous needle leaved forest (DN), shrub land (SL), grassland (GL), wetlands (WL), and non-vegetation (NV). Vegetation types marked with an asterisk (*) represent areas too small to be displayed in the line chart. B) Vegetation area distribution with elevation. The line chart shows the area occupied by each vegetation type at 100 m elevation intervals. Data were derived from the Global Digital Elevation Model (GDEM) version 3 and 30 m resolution vegetation data from GLC_FCS30 (Zhang et al., 2021). C) Vertical vegetation zonation along elevation on the northern slope of mount Namcha Barwa (7782 m) in the Eastern Himalaya. Contour lines generated using GDEM data are shown at 1000 m interval from 3000 m to 7000 m. The maps and visualizations were created using ArcGIS Pro v.2.9.2 (ESRI, Redlands, CA, USA). D) Landscape views across the Western Himalaya; E) Scenic landscapes of the Central Himalaya; F) Vegetation-rich landscapes of the Eastern Himalaya; and G) Tethyan Himalaya with its distinct grassland vegetation. H) Landscape to the north of Qomolangma (Tethys Himalaya) and I) View of the high-elevation northern slope of Qomolangma. Photo credits: D, Mustaqeem Ahmad; E–I, Jie Liu. All the pictures were taken during the growing season of each landscape.

In this review, we explore multifaceted aspects of plant biodiversity, including species diversity, phylogenetic diversity, functional diversity, and genetic diversity, across both temporal and spatial scales. Additionally, we identify critical research gaps and emphasize the importance of robust data collection and analysis to inform conservation prioritization. For clarity, the following terminologies have been used: **species diversity** refers to the number of different species in a given area; **functional diversity** encompasses the diversity of species traits within ecosystems or communities (Villéger et al., 2008); **phylogenetic diversity** captures the evolutionary history represented by the organisms in a particular area (Faith, 1992; Cadotte and Davies, 2016); **genetic diversity** represents the range of genetic variation within a species.

2. Patterns of species diversity in the Himalaya

The Himalaya hosts remarkable plant diversity, with approximately 10,000 plant species, including 3160 species across 71 genera that are endemic to the region (Rana et al., 2019). Wani et al. (2024) reported an even higher count, documenting 11,743 plant

species across the Indian Himalayan region, distributed across 2320 genera in 244 families. In contrast, our primary analysis based on online occurrence databases indicates a total of 12,023 species, spanning 2286 genera and 253 families across the Himalaya (Fig. 4A), which is relatively high compared to previous studies. This discrepancy is likely attributable to differences in data sources, filtering criteria, and taxonomic resolution. Additionally, some studies, such as Wani et al. (2024), have included Nagaland and parts of West Bengal as part of the Himalayan flora, whereas these regions were not included in our delineation of the Himalayan range (Fig. 1C) (Liu et al., 2022), potentially contributing to inconsistencies in species diversity estimates. Therefore, the precise number of plant species in the Himalaya remains an open question, warranting further investigation through standardized, regionally inclusive studies.

At high elevations, where glaciers and rocky terrains dominate, only cold-adapted species can survive. Among these, cushion plants show exceptional adaptability, thriving above 6100 m in extreme environmental conditions. A striking example is the occurrence of *Saussurea gnaphalodes* and *Lepidostemon everestianus* at 6400 m on

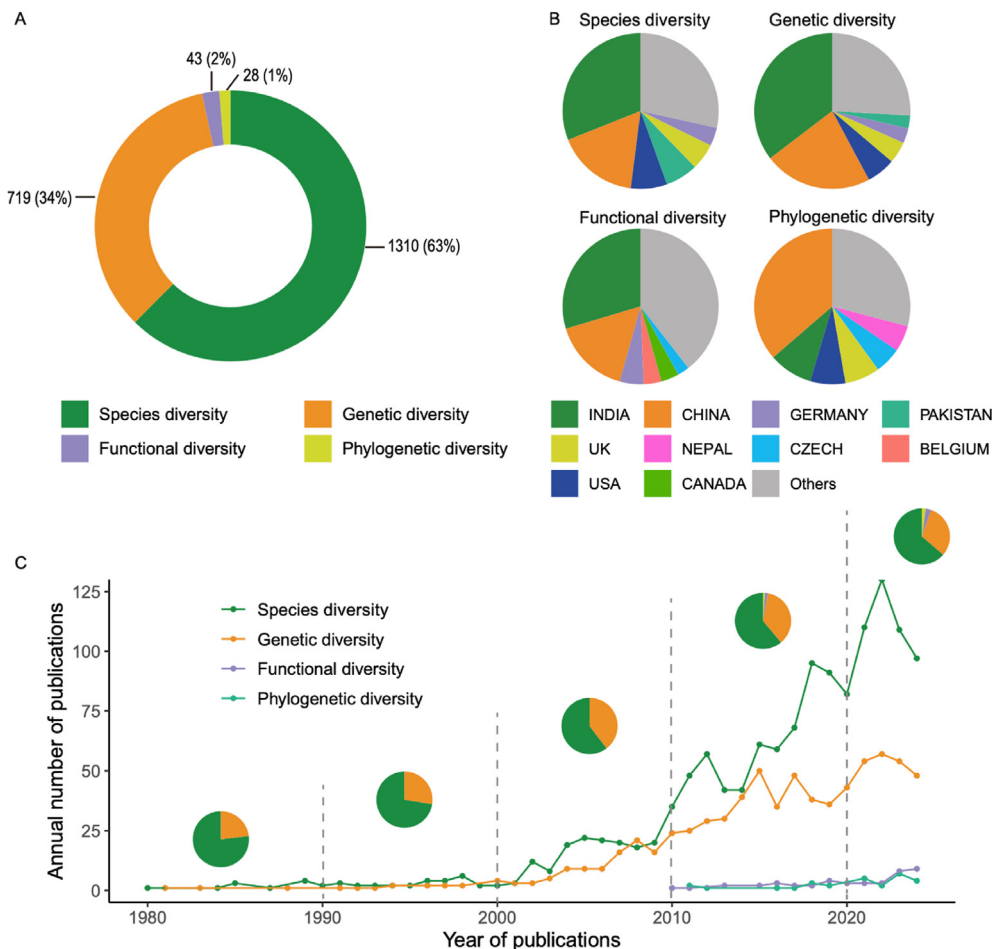


Fig. 3. Current research contributions in the Himalaya. A) Relative proportion of each diversity measure. B) Country-wise percentage contribution to diversity studies. C) Temporal trends in plant diversity publications from 1980 to 2024 in the Himalaya. Data source: The analysis is based on an advanced search in the core database of Web of Science, which covers literature from 1900 to 2024. However, relevant articles on the selected diversity topics were only available starting from 1980 onwards. Consequently, the timespan presented in Fig. 3 is limited to 1980–2024.

the slopes of Mount Qomolangma (Everest), setting the record for the highest-elevational plant occurrence records (Dentant, 2018). Other iconic plant species, such as *Rheum tibeticum*, *Rheum nobile*, *Saussurea gossipiphora*, *Cassiope fastigiata*, *Gentiana vernayi*, *Urtica hperborea*, *Meconopsis horridula*, *Eriophyton wallichii*, and *Roscoea tumjensis*, are also found at higher elevations in the Himalaya (Fig. 4B–K).

The published literature indicates that the Eastern Himalaya (e.g., Bhutan, with approximately 5452 species) harbors roughly three times more species than the northwestern Himalaya (e.g., Jammu and Kashmir, with approximately 1649 species), a pattern that broadly aligns with our findings (Fig. 4A). Our primary results show that the western region contains 3672 species, the central region 7228 species, and the Eastern Himalaya 8138 species (Fig. 4A). The species richness map clearly highlights that the eastern region supports greater plant diversity compared to the central and western regions (Fig. 4A). Tree diversity declines five-fold from the east (Bhutan; Kluge et al., 2017) to the northwest (Jammu and Kashmir), while shrubs and herbs display a threefold reduction (Rana et al., 2019). Similarly, Behera and Roy (2019) noted that herbaceous species richness varies with changing longitudes of the Himalaya, but the full extent of plant diversity patterns remains unclear.

Despite this, there are still unexplored regions that harbor new species. Since the publication of Sir J. D. Hooker's *Flora of British*

India" (Hooker, 1872–1897), thousands of new flowering plant species have been discovered, with new records and discoveries continuing to emerge regularly. For example, the floristic composition of over 5000 sacred groves in the Indian Himalayan regions is still poorly understood and under-documented (Singh and Pusalkar, 2020), and many authors focus only on the Indian Himalaya, which differs from our Himalaya (as region delineated in Fig. 1). Such census data confined by political boundaries have always frustrated researchers aiming to understand the full picture of Himalayan flora, which is more closely linked to the region's physical landscape and climatic conditions. Similarly, the Eastern Himalaya and the steep, high-elevation areas across the whole range remain underexplored (Fig. 4A), resulting in an incomplete understanding of the region's plant diversity. The statistics of plant diversity will likely change significantly once explorations across all regions are completed and species are fully documented.

Species diversity patterns across different elevations vary due to climatic conditions, resource availability, and species adaptability (McCain and Grytnes, 2010; Khan et al., 2013; Ahmad et al., 2020). Generally, species richness follows a hump-shaped pattern along elevation, peaking at mid-elevations. This phenomenon, known as the 'mid-domain effect' (Colwell et al., 2004; Hawkins et al., 2005), arises from the overlap of species from lower and higher elevations, coupled with favorable environmental conditions for many species with intermediate requirements at mid-elevations (Fig. 5A)

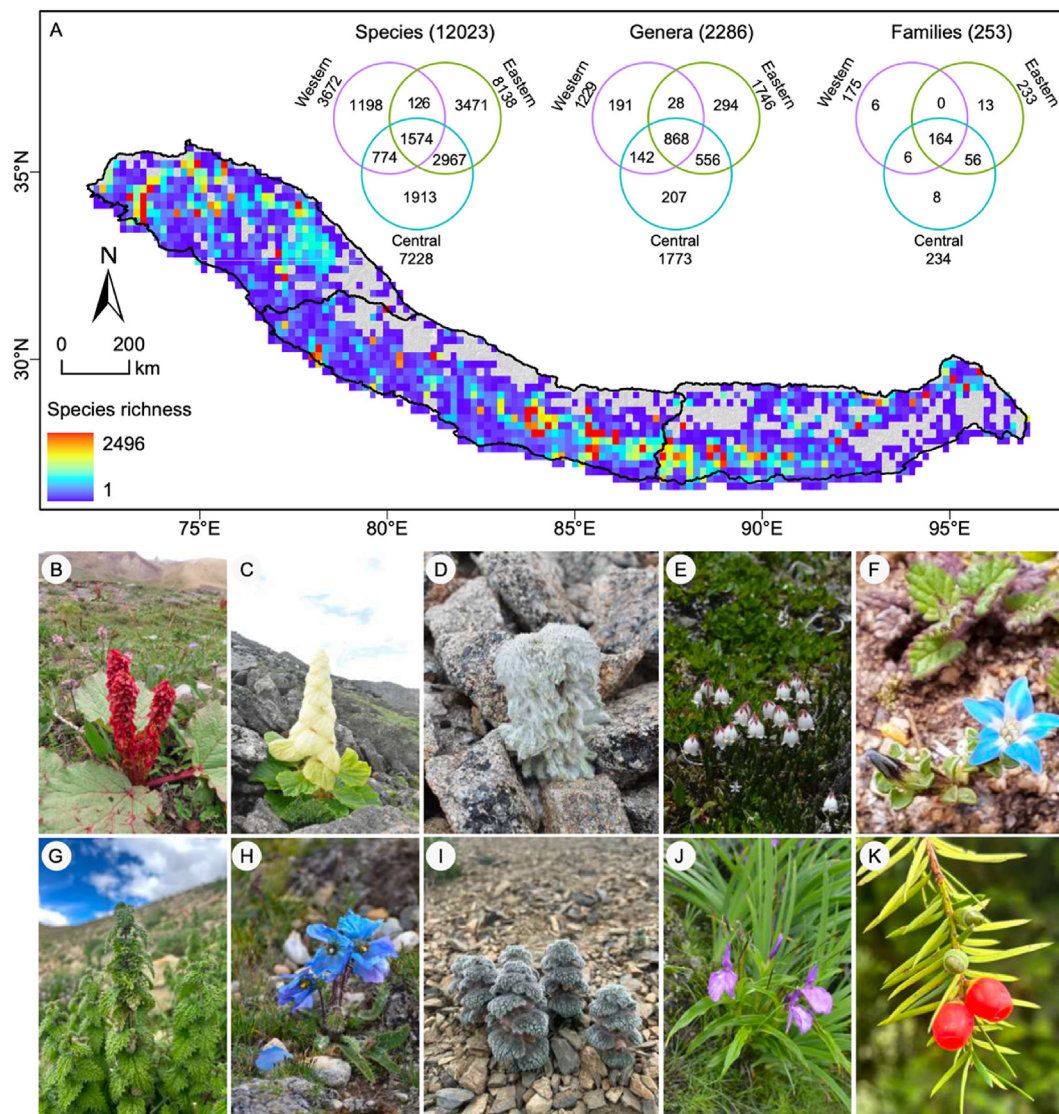


Fig. 4. Species richness map of the Himalaya, along with iconic Himalayan plant species. A) The map illustrates species richness for vascular plant species across the Himalaya, including a breakdown of totals for each region represented in a Venn diagram. The Venn diagram highlights the shared and unique species, genus and family numbers within each region. Color gradients on the map indicate species richness intensity, while grey shaded areas represent regions for which no data was available. The species occurrence data were obtained from four sources: the National Plant Specimen Resource Center of China (NPSRC, <https://www.cvh.ac.cn/>), the Global Biodiversity Information Facility (GBIF, <https://doi.org/10.15468/dl.fmds4>), the Flora of Nepal (FON, <https://www.floraofnepal.org/data/mapping>), and the India Biodiversity Portal (IBP, <https://indiabiodiversity.org/>). These data were accessed on January 15th, 2025, without extensive filtering. Figs. B to K represent some iconic Himalayan plant species. B) *Rheum tibeticum*, C) *Rheum nobile*, D) *Saussurea tridactyla*, E) *Cassiope fastigiata*, F) *Gentiana vernayi*, G) *Urtica hperborea*, H) *Meconopsis horridula*, I) *Eriophyton wallichii*, J) *Roscoeia tumjensis*, K) *Taxus contorta*. Photo credits: B–K by Jie Liu, except F by Debabrata Maity.

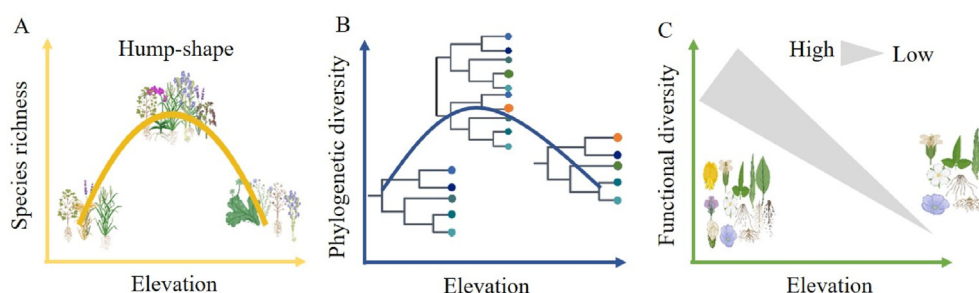


Fig. 5. Schematic illustration of plant diversity patterns along elevational gradients in the Himalaya. A) Illustrates a hump-shaped pattern of species richness along elevational gradients, B) Depicts a similar hump-shaped pattern of phylogenetic diversity, with mid-elevations harboring the greatest evolutionary diversity driven by overlapping lineages and optimal ecological conditions and, C) Shows a declining trend of functional diversity with increasing elevation. The broader part of the shaded triangular area of functional diversity indicates functional divergence (i.e., greater functional diversity), the narrower part represents functional convergence (i.e., lower functional diversity) in plant functional traits. Notably, these patterns may not apply uniformly to all plant groups or mountain regions.

(Ahmad et al., 2020). Notably, species diversity decreases with increasing elevation as colder, harsher conditions, and resource limitations dominate alpine zones (McCain and Grytnes, 2010; Luo et al., 2019a, 2019b). In contrast, lower elevations also exhibit reduced species diversity, largely due to human activities like agriculture, urbanization, and overgrazing (Ahmad et al., 2023b). In the Central and Western Himalaya, endemic species display evident increased along elevational gradients (Vetaas and Grytnes, 2002; Khan et al., 2014; Wani et al., 2024). For pteridophytes, Qian et al. (2022) identified temperature and precipitation as key drivers of richness along elevational gradients, with precipitation having a slightly stronger influence. Extreme low temperatures at high elevations and seasonal precipitation variations at lower elevations are the most critical factors of pteridophyte diversity, while Ahmad et al. (2020) observed herbaceous species exhibit decreased β -diversity, and its turnover component, moving from low to high regions.

Apart from longitude, factors like latitude, and elevation, local factors such as aspect and slope, microclimates, and edaphic factor also play a major role in shaping the environment at the regional and local scales. These variations also relate to the roles of climate, climate change and geographical barriers in shaping plant species diversity patterns in the Himalaya. However, researchers have not adequately studied key drivers, like interactions among temperature, rainfall, soil properties, and microclimatic variability, while also overlooking factors like habitat fragmentation, both natural and due to human activity, which limits insights into species-specific adaptability and distribution. Temporal dynamics, which are crucial for understanding biodiversity trends, remain underexplored. Additionally, the lack of collaborative, multidisciplinary approaches and compatible long-term monitoring program hampers the study of complex drivers of plant diversity.

3. Patterns of phylogenetic diversity in the Himalaya

Unlike traditional estimates of biodiversity that focus only on species richness, phylogenetic diversity reflects the evolutionary distances separating species, usually in terms of lengths of a phylogenetic tree (Miller et al., 2018). Mountain ecosystems often host unique species that represent special branches of the evolutionary tree, important for phylogenetic diversity and endemism. The Himalaya, with its vast elevational gradient and east to west extent, provides diverse environmental conditions that have driven speciation and adaptation among plant lineages (Singh and Singh, 1987; Pandit et al., 2014; Wambulwa et al., 2021). Historical biogeographic events, including mountain uplift, past climatic fluctuations, and Quaternary glacial oscillation, have played a significant role in shaping the distribution and evolution of plant lineages in the region (Favre et al., 2015; Liu et al., 2017; Ding et al., 2020).

Shooner et al. (2018) proposed that glacial relicts—part of once more diverse clades with convergent traits suitable for climate at the Last Glacial Maximum—might have influenced community assemblages in the Eastern Himalaya. Additionally, studies from the Western Himalaya observed phylogenetic overdispersion (net relatedness index, NRI) at lower elevations and clustering at higher elevations on both northern and southern-facing aspects (Rana et al., 2019). Similarly, communities in the Eastern Himalaya exhibit greater phylogenetic overdispersion (Manish and Pandit, 2018), although this dispersion appears to diminish progressively from east to west. The overdispersion at lower elevations is likely driven by wide environmental gradients and habitat heterogeneity (such as climate, geographic scales, biotic factors, presence of river valleys, etc.), that support diverse niches. These gradients create diverse microhabitats, enabling species with varied ecological

requirements to occupy distinct niches, thereby reducing competition. In contrast, at higher elevations, environmental harshness imposes strong selective pressure, favoring a limited number of highly specialized or cold-adapted species. This results in phylogenetic clustering, as observed in the Tibetan Plateau, where clustering increases with elevation (Yan et al., 2013). However, in the Eastern Himalaya, clustering tendencies are more subtle (Shooner et al., 2018), revealing nuanced patterns that vary across elevations. Additionally, a zig-zag pattern was observed in angiosperm assemblages along an elevational gradient in the Eastern and Central Himalaya, with the causes of this pattern attributed to the interplay of geophysical and eco-evolutionary processes (Qian et al., 2019; Li et al., 2022; Qian and Grau, 2025). In the Central Himalaya, Liang et al. (2023) reported left-skewed hump-shaped patterns of phylogenetic diversity, suggesting less relatedness at mid-elevations, attribution it to intense inter-species competition at lower elevations and environmental filtering at higher elevations. Alternatively, this pattern may be an artifact of the elevation range sampled, which only included areas above 1800 m.

Rana et al. (2019) observed that across longitudes and elevations in the Himalaya, middle elevations (1500–2800 m) exhibit greater phylogenetic dispersion among trees, shrubs, and herbs compared with higher and lower elevations. This trend is particularly pronounced in the Eastern Himalaya, where phylogenetic overdispersion peaks at mid-elevations: around 1700 m for trees, 2700 m for shrubs, and 2800 m for herbs. This pattern likely arises from dispersal and diversification dynamics. The mixing of distinct flora from both higher and lower elevations should theoretically increase phylogenetic dispersion, as illustrated in Fig. 5B. Thakur (2019) emphasized the significance of considering both species richness and phylogenetic composition in the western Himalaya for understanding community dynamics, rather than studying species richness alone. Shooner et al. (2018) similarly found that tree communities in the eastern region display phylogenetic clustering at lower elevations, transitioning to overdispersion at higher elevations, consistent with findings from Rana et al. (2019) across various Himalayan regions. These patterns suggest the influence of common underlying mechanisms, such as intense paleoclimate oscillations in shaping phylogenetic clustering.

Phylogenetic diversity indices offer valuable insights into ecosystem functioning and stability. Higher phylogenetic diversity is linked to greater functional diversity, thereby enhancing ecosystem productivity and resistance to disturbances (Cadotte et al., 2012). Manish (2021) highlighted the roles of ecological filtering and competition in structuring exotic and native plant communities in the Eastern Himalaya. These findings underscore the complexity of interactions shaping phylogenetic diversity in the eastern region, further underscoring the complexity of interactions shaping phylogenetic diversity in the Himalayan region. Overall the spatial patterns of phylogenetic diversity in the Himalaya are shaped by a combination of geological, climatic (including climate dynamics), ecological, historical, and anthropogenic factors. Addressing these patterns requires the use of advanced analytical models and comprehensive datasets to drive deeper into the mechanisms influencing phylogenetic diversity and their implications for biodiversity conservation.

4. Plant functional trait strategies and functional diversity in the Himalaya

4.1. Plant functional trait strategies

Plant functional traits are crucial for plant fitness and survival in mountain environments, since they represent adaptive strategies tailored to regional conditions and environmental harshness

(Fig. 6) (Körner, 2003; Laughlin, 2023). These traits are also vital for ecosystem process and functioning (e.g., productivity; Sigdel et al., 2023), and exploring trait variations within plant communities helps in understanding the ecosystem responses to climate change (Ahmad et al., 2023a). Habitat heterogeneity in mountainous regions also influences plant distribution, species interactions, speciation, and trait variation (Sigdel et al., 2023). While global studies on plant functional traits have expanded (e.g., Read et al., 2014; Vanneste et al., 2019; Laughlin, 2023), such research in the Himalaya remains limited. The few existing studies have largely focused on leaf traits among woody species or species-specific patterns within vegetation/elevational community (Basnett and Devy, 2021; Maharjan et al., 2021; Sigdel et al., 2023; Table 1). For instance, most researchers have reported that leaf number, mass, area, specific leaf area, and specific flower area values decreased with increasing abiotic stress—particularly temperature and aridity—at higher elevations (Western Himalaya—Ahmad et al., 2023a; Islam et al., 2024; Central—Maharjan et al., 2021; Eastern Himalaya—Basnett and Devy, 2021; Fig. 6 and Table 1).

The duration of the growing season across elevation gradients seems to be a crucial factor influencing functional traits. Basnett et al. (2019) found early phenological events strongly linked to daylength and temperature, show a strong phylogenetic signal. Building on these findings, Basnett and Devy (2021) demonstrated

that longer leaf life span correlated with greater leaf thickness and size, while shorter-lived leaves displayed reduced thickness and size, and these traits showed a pronounced phylogenetic signal among *Rhododendron* species (Fig. 6). Additionally, species that initiate early leaf growth are better adapted to protect tissues from frost conditions, as seen in Western Himalayan temperate trees that are sensitive to frost, temperature and moisture (Singh et al., 2023a), while Ahmad et al. (2021) observed that total flowering duration of flowering plant communities increased with elevation. Despite progress, quantitative phenological data on tree species, shrubs and herbs at spatial and temporal scales are still lacking. Key gaps include limited knowledge of intra- and interspecific trait variability, trade-offs, and interactions with biotic and abiotic factors across elevations and landscape. Addressing these gaps requires a holistic approach that incorporates the whole-plant trait spectrum, including leaf, root, shoot, flower and seed traits, in order to understand the mechanisms in play and functions that drive plant strategies and adaptations.

4.2. Functional diversity patterns across the Himalaya

Functional diversity indices reflect the dispersion of species in trait space and their roles within an ecosystem, showing how different species contribute to different ecological processes

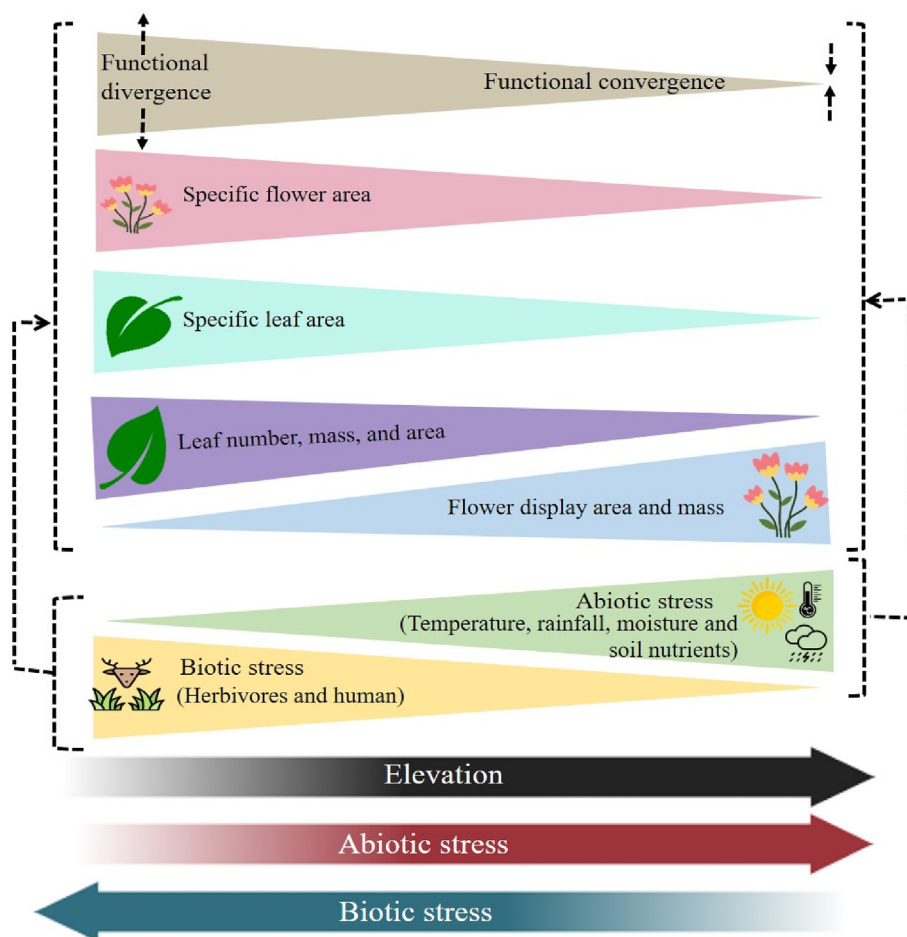


Fig. 6. Schematic illustration summarizing the variations in plant organ functional traits (e.g., leaf and flower traits) along environmental gradients (biotic and abiotic) in the Himalaya. At high elevations, plants face significant abiotic stress due to harsh environmental conditions, and reduced plant–plant competition. These factors drive habitat or environmental filtering, leading to trait convergence. In contrast, low elevations, characterized by a warmer climate, diverse climatic gradients, abundant resources, and intense species competition, promote trait divergence (and broader trait distributions), thereby facilitating functional niche partitioning. Notably, these patterns may not be consistent across all plant groups or mountain systems.

Table 1
A summary of functional traits and diversity studies in the Himalaya and their associated references.

Traits	Broad aspect behind study	References
Leaf traits	Functional composition and structure	Gratzner et al. (2004); Shah et al. (2019); Thakur and Chawla (2019); Thakur (2019); Rawat et al. (2020); Basnett and Devy (2021); Rawat et al. (2021); Sigdel et al. (2023); Singh et al. (2023a); Islam et al. (2024); Sharma et al. (2024)
Whole plant traits (height and life forms)	Ecosystem functioning, and processes	Klimes (2003); Shah et al. (2019); Thakur (2019); Maharjan et al. (2021); Ahmad (2022); Sigdel et al. (2023); Singh et al. (2023a)
Stem and leaf physiology	Biochemical processes and functions	Krishna et al. (2021); Rawat et al. (2021); Singh et al. (2023a); Islam et al. (2024); Mehta and Chawla (2024)
Floral traits	Flowering events and visualization cost and community assembly	Shrestha et al. (2014); Basnett et al. (2019); Ahmad et al. (2021); Ahmad (2022); Ahmad et al. (2023a,b); Singh et al. (2023b)
Vegetative phenology	Temporal processes and functions	Basnett et al. (2019); Singh et al. (2023b)
Root traits	Trade-off and root functions and process	Rawat et al. (2020)

(Petchey and Gaston, 2006; Ahmad et al., 2023a). Both abiotic (climate and land use) and biotic drivers (herbivores and human activities etc.) have direct or indirect effects on the functional diversity over an elevational gradient (Ahmad, 2022; Ma et al., 2024). Understanding these indices can provide valuable insights into elevational patterns in plant community functions, processes, and assemblages. In this sub-section, we examine how functional diversity changes from west to east across elevations in the Himalaya, thereby exploring potential mechanisms for these variations.

Thakur and Chawla (2019) reported that at higher elevations, functional diversity indicated reduced niche differentiation, complementarity, and abundance of functionally specialized species. This suggests that functionally similar species (functional convergence) were more likely to co-occur at higher elevations, possibly due to harsher climatic conditions, reduced competition, and the greater prevalence of positive species interactions observed (Callaway et al., 2002). These patterns align with the hypothesis proposed by Cornwell and Ackerly (2009) that regions experiencing strong environmental filtering tend to exhibit lower FD (Figs. 5C and 6), leading to stronger competitive interactions among species. Similarly, Luo et al. (2019a) proposed that species in natural forests differ in their assembly processes allowing them to occupy various stratum spaces (local environment filtered), thereby enhancing ecosystem function in the Hengduan Mountains, adjacent to the Himalaya.

Ahmad et al. (2023a) found strong convergence in floral traits at higher elevations compared to lower elevations, indicating greater functional diversity at lower elevations (Figs. 5C and 6). This underscores the critical role of phenological and morphological floral traits in shaping plant community structures, particularly in high-elevation areas. These findings demonstrate the need to consider various traits representing diverse ecological functions in plant research (Ahmad et al., 2023a; Laughlin, 2023). However, most studies estimated functional diversity on the basis of a few specific traits (such as leaf or floral), overlooking a multi-trait-based approach that can better represent diverse ecological processes and functions (Cadotte, 2017). Furthermore, spatial and temporal variations, including microhabitat and seasonal differences, remain underexplored, even though such knowledge is crucial for predicting how species and ecosystem functions might adapt to future environmental changes. Although functional diversity generally decreases with increasing elevation and latitude, studies in sub-tropical regions of China suggest that functional diversity increases with increasing longitude (Huang et al., 2021; Zhao et al., 2022). Similarly, Ma et al. (2024) examined the tree species community assembly process and found that most traits displayed convergent patterns across the entire elevational gradient of Gaoligong Mountains in the Hengduan Mountains. However, in the Himalaya biotic interactions are often ignored. Furthermore, comparative studies on functional diversity differentiation across the Himalaya

east-west gradient are currently lacking. To fill these gaps, over-arching, multi-scale studies are needed to advance knowledge of functional diversity in the region.

5. Patterns of genetic diversity in the Himalaya

Genetic diversity is essential for understanding the evolutionary history of species and assessing their resilience to future risks, including climate change and human disturbance (Jump et al., 2009; Pauls et al., 2013; Frankham et al., 2017). The Himalaya, celebrated for its high diversity and numerous endemic species, exhibits significant intraspecific genetic variation across its diverse ecosystems, mirroring the high level of interspecific diversity. This variation is shaped by the region's uplift and erosional dissection history, topography, and wide range of climatic conditions (Favre et al., 2015; Wambulwa et al., 2021; Spicer et al., 2025). Such genetic diversity is crucial for species' adaptability and resilience in the face of environmental changes and anthropogenic pressures.

Most genetic diversity studies in the Himalaya have focused on the germplasm evaluation of cultivated crops or economically significant plants, often with limited geographic and genomic sampling (e.g., Nag et al., 2015; Roy et al., 2016). Conversely, only a few studies have focused on wild plants with comprehensive sampling (Cun and Wang, 2010; Liu et al., 2013; Yan et al., 2024; Wambulwa et al., 2025). These studies reveal that genetic diversity in the Himalaya is often higher at lower elevations due to greater heterogeneity and more stable environmental conditions (Jugran et al., 2013), while higher elevations display reduced genetic diversity due to harsher climatic conditions with geographical isolation. However, these studies reveal contrasting patterns of genetic diversity between lower and higher elevations across different species. Longitudinally, for species distributed in the Lesser Himalaya (approximately 1500–4500 m), genetic diversity exhibits significant variation, shaped by a complex interplay of environmental gradients, historical processes, and geographical isolation. Genetic diversity is generally higher in the Eastern and Western Himalaya compared to the Central region as revealed in *Taxus* (Liu et al., 2013) and *Juglans* (Yan et al., 2024; Ye et al., 2024). Such a pattern pin-points the two flanks of the Himalaya (e.g., Yarlung Tsangpo vally in the Eastern Himalaya) as glacial refugia. Moreover, populations of some species recolonized the Central Himalaya after glaciation (Cun and Wang, 2010; Liu et al., 2013), which potentially created hybrid zone and introgression between populations due to secondary contact between closely related species (Poudel et al., 2014; Yan et al., 2024). Across the Greater Himalaya, the higher Central Himalaya exhibits high and unique genetic diversity, serving as a refugium for species such as *Juniperus tibetica* (Opgenoorth et al., 2010) and *Primula tibetica* (Ren et al., 2017). Geoclimatic factors have also been assumed to have driven population differentiation in the Central and Eastern Himalaya (Xu et al., 2010; Luo et al.,

2016a; Qiong et al., 2017; Ren et al., 2017), where higher levels of unique genetic diversity and greater genetic differentiation have been observed. For example, the ridges of the Himalaya act as physical barriers to gene flow between the northern and southern populations of *Hippophae tibetana* in the Qomolangma region (Qiong et al., 2017). In contrast, the western region displays evolutionarily significant, high genetic differentiation among populations, as observed in *Dactylorhiza hatagirea* (Sharma et al., 2022). These patterns are attributed to selection pressures, habitat fragmentation, and population isolation.

One limitation of current studies on genetic diversity in the Himalaya is incomplete sampling across the entire range. Additionally, many medicinally and economically important plant species are at serious risk of extinction and significant genetic erosion (Wambulwa et al., 2025), yet detailed genetic information on these species remains scarce. Furthermore, there are only a few studies that use robust population genomic approaches (Ren et al., 2017; Zhao et al., 2021; Wang et al., 2024) and these still suffer limited or biased sampling. These studies have primarily focused on specific Himalayan ranges, providing valuable insights into localized genetic diversity patterns. However, such isolated findings fail to capture a generalized genetic diversity pattern across the entire Himalaya, a region characterized by diverse climates and complex geography (Fig. 1), and further fail to capture spatial and temporal dimensions of genetic adaptation and divergence. Analyzing species genetic diversity patterns across varying elevations, geographical regions, and landscapes presents significant challenges due to the interplay of complex environmental factors, historical events and geopolitical disputes. To address these gaps, cross-national joint collaborations that integrate broader and more detailed landscape-level data, while focusing on the population genomic studies of endangered and economic or endemic species, will pave the way forward. This approach will enable a more holistic understanding of genetic diversity patterns and support the development of informed and effective conservation strategies.

6. Impacts of environmental change on plant diversity

Impacts of climate change and human interferences profoundly alter vegetation, species, functional, phylogenetic, and genetic diversity, intensifying stress on plant species in mountain ecosystems. Climate change induces shift in temperature and precipitation, influencing traits such as leaf size, root structure, reproductive timing, etc (Peppe et al., 2011; Ma et al., 2020; Ahmad et al., 2021). Concurrently, human activities like deforestation, urbanization, land use changes, and pollution exacerbate these changes by degrading and fragmenting habitats, introducing invasive species, and altering nutrient cycles (Peppe et al., 2011; Liu et al., 2018). For instance, deforestation and habitat fragmentation can reduce genetic diversity and alter hydrology, making plant populations more vulnerable to climate-induced changes, while pollution alters soil and water chemistry, affecting nutrient uptake and growth (Elbasiouny et al., 2022). These compound pressures can lead to maladaptation, reduced resilience, and shifts in species and functional composition, and reduced genetic diversity, ultimately threatening ecosystem integrity, stability and biodiversity (Pauls et al., 2013; Brauer et al., 2023).

In the Himalaya, global warming leads montane species to undergo range shift as they adapt to the changing climate. The rate of warming and environmental constraints strongly influence these distributional shifts (Dubey et al., 2003). Despite some ecological niche modelling studies suggesting that some species might shift to lower elevations (Bhatta et al., 2018; Liu et al., 2025), evidence remains inconclusive. Conversely, most climate models project an

upward shift of elevation-related climatic parameters (Wambulwa et al., 2025), consistent with empirical studies in the Western Himalaya (Hamid et al., 2020), the Central Himalaya (Gaire et al., 2014; Liu et al., 2025), and the Eastern Himalaya (Telwala et al., 2013). Dolezal et al. (2021) reported significant warming trends in the Himalaya, which are expected to persist, impacting vegetation and species distribution in Ladakh. Similarly, Hamid et al. (2020) observed species distribution shift in the Kashmir Himalaya (Western Himalaya). Moreover, highland species are anticipated to experience faster range shifts compared to lowland species due to increased precipitation and higher warming rates at higher elevations (Maharjan et al., 2023). These dynamics are likely lead to result in shrinking distribution ranges for high-elevation species, although comprehensive large-scale studies in the Himalaya are lacking (Hamid et al., 2020; Maharjan et al., 2023). Conversely, warm-adapted lowland species with wide ecological amplitude are predicted to maintain their lower limits while spreading upslope (Maharjan et al., 2023). In addition, human disturbances, such as logging, construction, and recreational activities, are also impacting plant species, driving changes in their distribution and abundance, and causing soil erosion and habitat fragmentation (Malik et al., 2016). Things will worsen if climate change and human exploitation occur simultaneously (Liu et al., 2025). Despite numerous studies on climate modelling, we still lack a general understanding of species changes under future climate change. A comprehensive modelling approach, combined with a monitoring network covering the entire flora, will be the best way forward (see Section 7 below).

Plant functional traits are crucial for understanding and predicting how species might respond to climate change and anthropogenic pressure. Traits associated with acquisitive strategies, such as faster growth rates, are generally assumed to facilitate significant range shifts. However, Sharma et al. (2024) conducted a transplant experiment in the Western Himalaya and reported a negative association between these traits and range shifts. In contrast, in the warmer and wetter conditions of the Nepal, studies show that species with the widest conduits (water-conducting vessels in plants) are expected to thrive, becoming more competitive and expanding their distribution under changing climate (Maharjan et al., 2023). Previous studies have shown that regeneration, growth patterns, and distribution range of woody plants, are closely linked to their functional traits and are heavily influenced by climate change (Sigdel et al., 2023). These responses are highly site- and species-specific, with some species benefiting from a warming climate and others facing challenges such as moisture stress. Although studies across broad bioclimatic gradients highlight the complexity of plant responses to climate, research specifically focused on plant traits and their responses to climate change in the Himalaya remains limited.

Climate change and anthropogenic pressure also significantly impact genetic and phylogenetic diversity, posing serious threats to the resilience and adaptability of plant species. These factors often lead to reduced gene flow between isolated populations, increasing the likelihood of inbreeding (Frankham et al., 2017). Reduced genetic diversity makes populations more vulnerable to environmental stressors such as disease and pests (Breed et al., 2019). Moreover, the loss of unique genetic variants adapted to specific microclimates further diminishes the gene pool, undermining the ability of plant species to adapt to ongoing and future climate changes (Jump et al., 2009; Pauls et al., 2013). Despite the critical importance of these issues, studies on the impact of climate change and human activities on plant genetic diversity remain scarce. However, two recent exceptions provide valuable insights. Yan et al. (2024) found that the genetic landscape of walnut (*Juglans regia* and *J. sigillata*) has been reshaped by human interventions.

Additionally, Wambulwa et al. (2025) projected that future climate scenarios could lead to a substantial loss up to 15.49% of genetic diversity due to species range shifts. These findings underscore the urgent need for further research in the Himalaya to explore the combined effects of climate change and anthropogenic disturbance on plant genetic and phylogenetic diversity.

7. Current challenges and future perspectives

7.1. Current challenges

Most studies on species richness across spatial and temporal scales in the Himalaya predominantly rely on pre-existing data on species occurrences from herbarium specimens, virtual databases, or monographic records (Wambulwa et al., 2021). These retrospective approaches are inherently limited by sampling biases, as they often lack standardized protocols for data collection. Given these limitations, we advocate for methodologies that incorporate current primary data derived from direct field observations connected to long term monitoring of elevational gradient change. Notable examples include permanent transects established in the Gaoligong Mountains (GMT; Luo et al., 2023, 2024; Ma et al., 2024), Yulong Mountains (YMT; e.g., Luo et al., 2016b; 2019b) and Dhauladhar Mountains (Ahmad et al., 2020). Some of the key limitations of the existing studies in the region are highlighted below.

- There is a gap in understanding the drivers of different facets of plant biodiversity as well as interdisciplinary approaches at the whole taxon level, in biodiversity priority areas of the Himalaya. The knowledge gap encompasses various factors, including the complex interplay of environmental, ecological, and human-induced influences on biodiversity across different scales. Understanding these drivers involves unravelling the relationships between climate, habitat diversity, species interactions, and human activities.
- There is incomplete knowledge of plant functional traits in the Himalaya, particularly regarding how different species contribute to ecosystem functions. This gap stems from the vast number of species traits and the complexity of their interactions. Moreover, data on the functional composition—encompassing leaf, root, and reproductive traits (whole plant traits)—are limited both within and between regions across the west-to-east Himalayan gradient. Such information is crucial for understanding key ecological processes, including community assembly, trait trade-offs, species fitness, and dynamics under climate change.
- Phylogenetic relatedness is poorly resolved, and detailed phylogenetic relationships for Himalayan plants are unknown, which inhibits our understanding of evolutionary processes. This lack of detailed phylogenetic information limits insights into the complex evolutionary history of the Himalayan endemic flora, which has been shaped by geological events, climatic shifts, and their inter-relationships, remains largely unresolved.
- Evaluating genetic diversity in the Himalaya is hindered by the region's rugged terrain and geopolitical complexities, which limits access to diverse ecosystems. These challenges are further exacerbated by climate change, which alters habitats and species' survival strategies. Additionally, insufficient research efforts on wild plant species further constrains the ability to conduct comprehensive, large-scale genetic analyses.
- A major drawback is the lack of robust national and international collaboration, particularly in regard to interdisciplinary efforts that integrate taxonomy, genomics, bioinformatics, and ecology. Such integrated approaches are essential to build a comprehensive understanding of plant diversity across

spatiotemporal scales and the tree of life. Moreover, existing citizen science and local engagement initiatives, while promising, suffer from several drawbacks that limit their impact and sustainability. Socio-economic challenges, such as limited access to technology and education, restrict broader community participation.

7.2. Recommendations

While the applicability of this review for conservation and management practices may vary for different regions of the Himalaya, several key recommendations are outlined below:

- Establish long-term monitoring across environmental gradients: Developing a network of permanent monitoring transects is essential for the Himalaya.
- Utilize advanced remote sensing and AI: Leverage state-of-the-art remote sensing technologies integrated with artificial intelligence to determine and catalogue plant species in inaccessible areas, to enhance our understanding of overall plant diversity.
- Employ High-Throughput Phenotyping Platforms and Next-Generation Sequencing: Utilize high-throughput phenotyping technologies to quickly assess functional traits across a wide range of species, improving insights into ecosystem functioning and resilience. Additionally, NGS technologies can be used to generate complete phylogenomic and population genomic data, providing deeper insights into species evolution and adaptation in the Himalaya.
- Foster interdisciplinary collaborations across the geo-political borders: Promote transboundary collaborations integrating diverse fields of ecology, genomics, bioinformatics, and environmental science to develop a holistic understanding of plant diversity.
- Data collection and sharing: Emphasize the adoption of standardized protocols and the development of open-access platforms to facilitate efficient data collection and sharing, to encourage national as well as international collaboration and informed decision-making for biodiversity conservation.
- Citizen science and social engagement: Actively involve local communities and citizen scientists in biodiversity monitoring efforts to discover unknown species and gather data on plant distributions and phenology, which can contribute to initiating targeted conservation actions.

By implementing these recommendations through innovative techniques and collaborative efforts, future research can greatly advance our understanding and conservation of plant diversity in the Himalayan biodiversity hotspot. Comprehensive studies spanning multiple trophic levels and taxa in the Himalaya will leverage advanced methodologies, including omics technologies, to unravel intricate ecological dynamics. Long-term monitoring programs should be established to track community responses to climate changes, while predictive modelling efforts can inform conservation strategies. Moreover, research into eco-evolutionary dynamics and processes will illuminate how these processes shape ecological relationships, community assembly, and ecosystem functions. This integrated approach holds the promise of deepening our understanding of Himalayan biodiversity and strengthening conservation efforts in this globally significant biodiversity hotspot.

8. Conclusions

This review goes beyond examining simple species diversity encompassing the phylogenetic, functional and genetic diversity,

and champions a holistic vision of how environment intricately influences the composition and distribution of plant life in the Himalaya. By highlighting the nuanced relationship between environment and species diversity, this review aims to encourage a deeper understanding of Himalayan plant diversity and offers insights into broader ecological principles governing diversity across diverse landscapes facing varying degrees of climatic and anthropogenic pressures.

We acknowledge that the biodiversity of the Himalaya is intricately shaped by historical, climatic, ecological and anthropogenic factors. Speciation, extinction, and dispersal processes, driven by geological events and climate fluctuations, have contributed to the distinct vegetation types across elevations and regions. The Eastern Himalaya harbors significant endemic plant diversity, thriving in diverse habitats ranging from tropical forest to alpine meadows. Conversely, the northern and western Himalaya exhibit lower species richness, likely due to more pronounced climatic fluctuations over time, such as marked drying. Despite harboring high biodiversity, the Himalaya are also undoubtedly one of the most threatened mountain ecosystems in the world. Anthropogenic pressures, such as hydropower and infrastructure development, urbanization, agriculture, tourism, deforestation, invasive species spread, and hunting pose significant threats to the native biodiversity and ecosystem functions (Liu et al., 2018). Furthermore, global warming and related environmental changes pose serious challenges to Himalayan biodiversity with the region experiencing warming at a rate three times faster than the global average (Shrestha et al., 1999; Liu and Chen, 2000). This review highlights the critical roles of phylogenetic as well as functional and genetic diversity in shaping the plant diversity patterns, distribution and adaptation strategies, particularly in mountain system.

Our review also highlights key trends and research gaps critical for advancing understanding and conservation efforts in the Himalaya biodiversity hotspot. It is worth noting that the significant positive relationships found among species, phylogenetic, functional, and genetic diversity indicate higher diversity levels enhance the ecosystem resilience. However, deriving inferences from existing data and literature risks introducing biases, challenging the generality of plant clustering patterns across the Himalaya. Addressing these gaps requires robust data collection, interdisciplinary research, and effective conservation practices, supported by adequate funding, international collaboration, and stakeholder engagement. Such efforts are pivotal to significantly enhancing the preservation of the Himalayan natural heritage while ensuring sustainable development throughout the region. These measures are essential for filling existing knowledge gaps and fortifying conservation frameworks in this globally significant hotspot.

CRediT authorship contribution statement

Mustaqeem Ahmad: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Conceptualization. **Ya-Huang Luo:** Writing – review & editing, Visualization, Validation, Investigation, Funding acquisition. **Sonia Rathee:** Writing – review & editing, Validation, Investigation. **Robert A. Spicer:** Writing – review & editing. **Jian Zhang:** Writing – review & editing, Validation, Investigation. **Moses C. Wambulwa:** Writing – review & editing, Validation, Investigation. **Guang-Fu Zhu:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Marc W. Cadotte:** Writing – review & editing. **Zeng-Yuan Wu:** Writing – review & editing. **Shujaul Mulk Khan:** Writing – review & editing, Validation, Investigation. **Debabrata Maity:** Writing – review & editing. **De-Zhu Li:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization. **Jie Liu:** Writing – review & editing, Writing –

original draft, Visualization, Supervision, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Author's statement

All authors have read the final draft and agree to the publication, ensuring that all individuals deserving authorship have been appropriately acknowledged in the authorship contribution statement.

Data availability statement

The data presented in this study are included within the article. Additional datasets used for visualizations are available from the corresponding author upon reasonable request.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pld.2025.04.003>.

References

- Ahmad, M., 2022. Species Composition and Floral Trait Diversity along an Altitudinal Gradient in the Western Himalaya. Panjab University, Chandigarh, India. Ph.D. thesis. <https://hdl.handle.net/10603/373396>.
- Ahmad, M., Uniyal, S.K., Batish, D.R., et al., 2020. Patterns of plant communities along vertical gradient in Dhauladhar mountains in Lesser Himalaya in North-Western India. *Sci. Total Environ.* 716, 136919. <https://doi.org/10.1016/j.scitotenv.2020.136919>.
- Ahmad, M., Uniyal, S.K., Batish, D.R., et al., 2021. Flower phenological events and duration pattern is influenced by temperature and elevation in Dhauladhar mountain range of Lesser Himalaya. *Ecol. Indic.* 129, 107902. <https://doi.org/10.1016/j.ecolind.2021.107902>.
- Ahmad, M., Rosbakh, S., Bucher, S.F., et al., 2023a. The role of floral traits in community assembly processes at high elevations in the Himalaya. *J. Ecol.* 111, 1107–1119.
- Ahmad, M., Uniyal, S.K., Sharma, P., et al., 2023b. Enhanced plasticity and reproductive fitness of floral and seed traits facilitate non-native species spread in mountain ecosystems. *J. Environ. Manag.* 348, 119222. <https://doi.org/10.1016/j.jenvman.2023.119222>.
- Ashton, P., Zhu, H., 2020. The tropical-subtropical evergreen forest transition in East Asia: an exploration. *Plant Divers.* 42, 255–280. <https://doi.org/10.1016/j.pld.2020.04.001>.
- Basnett, S., Devy, S.M., 2021. Phenology determines leaf functional traits across *Rhododendron* species in the Sikkim Himalaya. *Alpine Bot.* 131, 63–72. <https://doi.org/10.1007/s00035-020-00244-5>.

- Basnett, S., Nagaraju, S.K., Ravikanth, G., et al., 2019. Influence of phylogeny and abiotic factors varies across early and late reproductive phenology of Himalayan *Rhododendrons*. *Ecosphere* 10, e02581. <https://doi.org/10.1002/ecs2.2581>.
- Behra, M.D., Roy, P.S., 2019. Pattern of distribution of angiosperm plant richness along latitudinal and longitudinal gradients of India. *Biodivers. Conserv.* 28, 2035–2048. <https://doi.org/10.1007/s10531-019-01772-1>.
- Bhatta, K.P., Grytnes, J.A., Vetaas, O.R., 2018. Downhill shift of alpine plant assemblages under contemporary climate and land-use changes. *Ecosphere* 9, e02084. <https://doi.org/10.1002/ecs2.2084>.
- Brauer, C.J., Sandoval-Castillo, J., Gates, K., et al., 2023. Natural hybridization reduces vulnerability to climate change. *Nat. Clim. Change* 13, 282–289. <https://doi.org/10.1038/s41558-022-01585-1>.
- Breed, M.F., Harrison, P.A., Blyth, C., et al., 2019. The potential of genomics for restoring ecosystems and biodiversity. *Nat. Rev. Genet.* 20, 615–628. <https://doi.org/10.1038/s41576-019-0152-0>.
- Cadotte, M.W., 2017. Functional traits explain ecosystem function through opposing mechanisms. *Ecol. Lett.* 20, 989–996. <https://doi.org/10.1111/ele.12796>.
- Cadotte, M.W., Davies, T.J., 2016. *Phylogenies in Ecology: a Guide to Concepts and Methods*. Princeton University Press, Princeton, New Jersey, US.
- Cadotte, M.W., Dinnage, R., Tilman, D., 2012. Phylogenetic diversity promotes ecosystem stability. *Ecology* 93, S223–S233. <https://doi.org/10.1890/11-0426.1>.
- Callaway, R.M., Brooker, R.W., Choler, P., et al., 2002. Positive interactions among alpine plants increase with stress. *Nature* 417, 844–848. <https://doi.org/10.1038/nature00812>.
- Chang, D., 1981. The vegetation zonation of the Tibetan Plateau. *Mt. Res. Dev.* 1, 29–48.
- Colwell, R.K., Rahbek, C., Gotelli, N.J., 2004. The mid-domain effect and species richness patterns: what have we learned so far? *Am. Nat.* 163, E1–E23. <https://doi.org/10.1086/382056>.
- Cornwell, W.K., Ackerly, D.D., 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecol. Monogr.* 79, 109–126. <https://doi.org/10.1890/07-1134.1>.
- Cun, Y.Z., Wang, X.Q., 2010. Plant recolonization in the Himalaya from the south-eastern Qinghai-Tibetan Plateau: geographical isolation contributed to high population differentiation. *Mol. Phylogenet. Evol.* 56, 972–982. <https://doi.org/10.1016/j.ympev.2010.05.007>.
- Dentant, C., 2018. The highest vascular plants on Earth. *Alpine Bot.* 128, 97–106. <https://doi.org/10.1007/s00035-018-0208-3>.
- Ding, L., Spicer, R.A., Yang, J., et al., 2017. Quantifying the rise of the Himalaya orogen and implications for the South Asian monsoon. *Geology* 45, 215–218. <https://doi.org/10.1130/G38583>.
- Ding, W.N., Ree, R.H., Spicer, R.A., et al., 2020. Ancient orogenic and monsoon-driven assembly of the world's richest temperate alpine flora. *Science* 369, 578–581. <https://doi.org/10.1126/science.abb4484>.
- Ding, L., Kapp, P., Cai, F., et al., 2022. Timing and mechanisms of Tibetan Plateau uplift. *Nat. Rev. Earth Environ.* 3, 652–667. <https://doi.org/10.1038/s43017-022-00318-4>.
- Dolezal, J., Jandova, V., Macek, M., et al., 2021. Climate warming drives Himalayan alpine plant growth and recruitment dynamics. *J. Ecol.* 109, 179–190. <https://doi.org/10.1111/1365-2745.13459>.
- Dubey, B., Yadav, R., Singh, J.S., et al., 2003. Upward shift of Himalayan pine in Western Himalaya, India. *Curr. Sci.* 85, 1135–1136.
- Elbasiouny, H., El-Ramady, H., Elbehiry, F., et al., 2022. Plant nutrition under climate change and soil carbon sequestration. *Sustainability* 14, 914. <https://doi.org/10.3390/su14020914>.
- Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10. [https://doi.org/10.1016/0006-3207\(92\)91201-3](https://doi.org/10.1016/0006-3207(92)91201-3).
- Favre, A., Packert, M., Pauls, S.U., et al., 2015. The role of the uplift of the Qinghai-Tibetan Plateau for the evolution of Tibetan biotas. *Biol. Rev.* 90, 236–253. <https://doi.org/10.1111/brv.12107>.
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315. <https://doi.org/10.1002/joc.5086>.
- Frankham, R., Ballou, J.D., Ralls, K., et al., 2017. *Genetic Management of Fragmented Animal and Plant Populations*. Oxford University Press, Oxford, England, UK.
- Gaire, N.P., Koirala, M., Bhuju, D.R., et al., 2014. Treeline dynamics with climate change at Central Nepal Himalaya. *Clim. Past* 9, 1277–1290. <https://doi.org/10.5194/cp-10-1277-2014>.
- Gairola, S., Rawal, R.S., Todaria, N.P., 2008. Forest vegetation patterns along an altitudinal gradient in sub-alpine zone of west Himalaya, India. *Afr. J. Plant Sci.* 2, 42–48. <https://www.academicjournals.org/AJPS>.
- Gébelin, A., Mulch, A., Teyssier, C., et al., 2013. The miocene elevation of Mount Everest. *Geology* 41, 799–802. <https://doi.org/10.1130/G34331.1>.
- Gratzner, G., Rai, P.B., Darabant, A., et al., 2004. Leaf characteristics and growth response to light of understory *Rhododendron hodgsonii* in the Bhutan Himalaya. *Ekológia* 23, 283–297.
- Hamid, M., Khuroo, A.A., Malik, A.H., et al., 2020. Early evidence of shifts in alpine summit vegetation: a case study from Kashmir Himalaya. *Front. Plant Sci.* 11, 421. <https://doi.org/10.3389/fpls.2020.00421>.
- Hawkins, B.A., Diniz-Filho, J.A.F., Weis, A.E., 2005. The mid-domain effect and diversity gradients: is there anything to learn? *Am. Nat.* 166, E140–E143. <https://doi.org/10.1086/491686>.
- Hijmans, R.J., Bivand, R., 2022. *Terra: Spatial Data Analysis*. <https://doi.org/10.32614/CRAN.package.terra>. R package version 1.7, 1.
- Huang, C., Xu, Y., Zang, R., 2021. Variation patterns of functional trait moments along geographical gradients and their environmental determinants in the subtropical evergreen broadleaved forests. *Front. Plant Sci.* 12, 686965. <https://doi.org/10.3389/fpls.2021.686965>.
- Huang, X., Yin, Y., Feng, L., et al., 2024. A 10 m resolution land cover map of the Tibetan Plateau with detailed vegetation types. *Earth Syst. Sci. Data* 16, 3307–3332. <https://doi.org/10.5194/essd-16-3307-2024>.
- Islam, T., Hamid, M., Nawchoo, I.A., et al., 2024. Leaf functional traits vary among growth forms and vegetation zones in the Himalaya. *Sci. Total Environ.* 906, 167274. <https://doi.org/10.1016/j.scitotenv.2023.167274>.
- Jugran, A.K., Bhatt, I.D., Rawal, R.S., et al., 2013. Patterns of morphological and genetic diversity of *Valeriana jatamansi* Jones in different habitats and altitudinal range of West Himalaya, India. *Flora* 208, 13–21. <https://doi.org/10.1016/j.flora.2012.12.003>.
- Jump, A.S., Marchant, R., Peñuelas, J., 2009. Environmental change and the option value of genetic diversity. *Trends Plant Sci.* 14, 51–58. <https://doi.org/10.1016/j.tplants.2008.10.002>.
- Jung, M., Dahal, P.R., Butchart, S.H., et al., 2020. A global map of terrestrial habitat types. *Sci. Data* 7, 256. <https://doi.org/10.1038/s41597-020-00599-8>.
- Khan, M.A., Mahato, S., Spicer, R.A., et al., 2023. Siwalik plant megafossil diversity in the Eastern Himalayas: A review. *Plant Divers.* 45, 243–264.
- Khan, M.S., Khan, S.M., Abdullah, et al., 2025. Ecological assessment of *Iris hookeriana* across subalpine and alpine regions of the Hindu-Himalayas. *Front. For. Glob. Change* 8, 1539025. <https://doi.org/10.3389/ffgc.2025.1539025>.
- Khan, S.M., Page, S.E., Ahmad, H., et al., 2013. Sustainable utilization and conservation of plant biodiversity in montane ecosystems: the western Himalayas as a case study. *Ann. Bot.* 112, 479–501. <https://doi.org/10.1093/aob/mct125>.
- Khan, S.M., Page, S.E., Ahmad, H., et al., 2014. Ethno-ecological importance of plant biodiversity in mountain ecosystems with special emphasis on indicator species of a Himalayan Valley in the northern Pakistan. *Ecol. Indic.* 37, 175–185. <https://doi.org/10.1016/j.ecolind.2013.09.012>.
- Klimeš, L., 2003. Life-forms and clonality of vascular plants along an altitudinal gradient in E Ladakh (NW Himalayas). *Basic Appl. Ecol.* 4, 317–328. <https://doi.org/10.1078/1439-1791-00163>.
- Kluge, J., Worm, S., Lange, S., et al., 2017. Elevational seed plants richness patterns in Bhutan, Eastern Himalaya. *J. Biogeogr.* 44, 1711–1722. <https://doi.org/10.1002/ecs2.2945>.
- Körner, C., 2003. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Springer, Berlin.
- Krishna, M., Winternitz, J., Garkoti, S.C., et al., 2021. Functional leaf traits indicate phylogenetic signals in forests across an elevational gradient in the central Himalaya. *J. Plant Res.* 134, 753–764. <https://doi.org/10.1007/s10265-021-01289-1>.
- Laughlin, D.C., 2023. *Plant Strategies: The demographic Consequences of Functional Traits in Changing Environments*. Oxford University Press, Oxford, UK.
- Li, L., Xu, X., Qian, H., et al., 2022. Elevational patterns of phylogenetic structure of angiosperms in a biodiversity hotspot in eastern Himalaya. *Divers. Distrib.* 28, 2534–2548. <https://doi.org/10.1111/ddi.13513>.
- Liang, J., Ding, Z., Lie, G., et al., 2023. Patterns and drivers of phylogenetic diversity of seed plants along an elevational gradient in the central Himalaya. *Glob. Ecol. Conserv.* 47, e02661. <https://doi.org/10.1016/j.gecco.2023.e02661>.
- Liu, X., Chen, B., 2000. Climatic warming in the Tibetan Plateau during recent decades. *Int. J. Climatol.* 20, 1729–1742. [https://doi.org/10.1002/1097-0088\(20001130\)20:14<1729::AID-JOC556>3.0.CO;2-Y](https://doi.org/10.1002/1097-0088(20001130)20:14<1729::AID-JOC556>3.0.CO;2-Y).
- Liu, J., Möller, M., Provan, J., et al., 2013. Geological and ecological factors drive cryptic speciation of yews in a biodiversity hotspot. *New Phytol.* 199, 1093–1108. <https://doi.org/10.1111/nph.12336>.
- Liu, J., Luo, Y.H., Li, D.Z., et al., 2017. Evolution and maintenance mechanisms of plant diversity in the Qinghai-Tibet Plateau and adjacent regions: retrospect and prospect. *Biodivers. Sci.* 25, 163–174.
- Liu, J., Milne, R.I., Cadotte, M.W., et al., 2018. Protect Third Pole's fragile ecosystem. *Science* 362, 1368. <https://doi.org/10.1126/science.aaw0443>. –1368.
- Liu, J., Milne, R.I., Zhu, G.F., et al., 2022. Name and scale matters: clarifying the geography of Tibetan Plateau and adjacent mountain regions. *Global Planet. Change* 215, 103893. <https://doi.org/10.1016/j.gloplacha.2022.103893>.
- Liu, F.L., Mambo, W.W., Liu, J., et al., 2025. Spatiotemporal range dynamics and conservation optimization for endangered medicinal plants in the Himalaya. *Glob. Ecol. Conserv.* 57, e03390.
- Luo, D., Yue, J.P., Sun, W.G., et al., 2016a. Evolutionary history of the subnival flora of the Himalaya-Hengduan Mountains: first insights from comparative phylogeography of four perennial herbs. *J. Biogeogr.* 43, 31–43. <https://doi.org/10.1111/jbi.12610>.
- Luo, Y., Liu, J., Tan, S., et al., 2016b. Trait variation and functional diversity maintenance of understory herbaceous species coexisting along an elevational gradient in Yulong Mountain, Southwest China. *Plant Divers.* 38, 303–311. <https://doi.org/10.1016/j.pld.2016.11.002>.
- Luo, Y.H., Cadotte, M.W., Burgess, K.S., et al., 2019a. Forest community assembly is driven by different strata-dependent mechanisms along an elevational gradient. *J. Biogeogr.* 46, 2174–2187. <https://doi.org/10.1111/jbi.13669>.
- Luo, Y.H., Cadotte, M.W., Burgess, K.S., et al., 2019b. Greater than the sum of the parts: how the species composition in different forest strata influence ecosystem function. *Ecol. Lett.* 22, 1449–1461. <https://doi.org/10.1111/ele.13330>.

- Luo, Y.H., Ma, L.L., Seibold, S., et al., 2023. The diversity of mycorrhiza-associated fungi and trees shapes subtropical mountain forest ecosystem functioning. *J. Biogeogr.* 50, 715–729. <https://doi.org/10.1111/jbi.14563>.
- Luo, Y.H., Ma, L.L., Cadotte, M.W., et al., 2024. Testing the ectomycorrhizal dominance hypothesis for ecosystem multifunctionality in a subtropical mountain forest. *New Phytol.* 243, 2401–2415. <https://doi.org/10.1111/nph.20003>.
- Ma, Z., Chang, S.X., Bork, E.W., et al., 2020. Climate change and defoliation interact to affect root length across northern temperate grasslands. *Funct. Ecol.* 34, 2611–2621. <https://doi.org/10.1111/1365-2435.13669>.
- Ma, L.L., Seibold, S., Cadotte, M.W., et al., 2024. Niche convergence and biogeographic history shape elevational tree community assembly in a subtropical mountain forest. *Sci. Total Environ.* 935, 173343. <https://doi.org/10.1016/j.scitotenv.2024.173343>.
- Maharjan, S.K., Sterck, F.J., Dhakal, B.P., et al., 2021. Functional traits shape tree species distribution in the Himalaya. *J. Ecol.* 109, 3818–3834. <https://doi.org/10.1111/1365-2745.13759>.
- Maharjan, S.K., Sterck, F.J., Raes, et al., 2023. Climate change induced elevational range shifts of Himalayan tree species. *Biotropica* 55, 53–69. <https://doi.org/10.1111/btp.13159>.
- Malik, Z.A., Pandey, R., Bhatt, A.B., 2016. Anthropogenic disturbances and their impact on vegetation in Western Himalaya, India. *J. Mt. Sci.* 13, 69–82. <https://doi.org/10.1007/s11629-015-3533-7>.
- Manish, K., 2021. Species richness, phylogenetic diversity and phylogenetic structure patterns of exotic and native plants along an elevational gradient in the Himalaya. *Ecol. Process* 10, 1–13. <https://doi.org/10.1186/s13717-021-00335-z>.
- Manish, K., Pandit, M.K., 2018. Geophysical upheavals and evolutionary diversification of plant species in the Himalaya. *PeerJ* 6, e5919. <https://doi.org/10.7717/peerj.5919>.
- Måren, I.E., Karki, S., Prajapati, C., et al., 2015. Facing north or south: does slope aspect impact forest stand characteristics and soil properties in a semiarid trans-Himalayan valley? *J. Arid Environ.* 121, 112–123. <https://doi.org/10.1016/j.jaridenv.2015.06.004>.
- McCain, C.M., Grytnes, J.A., 2010. Elevational gradients in species richness. In: *Encyclopedia of Life Sciences (ELS)*. John Wiley & Sons, Ltd., Hoboken, pp. 1–10. <https://doi.org/10.1002/9780470015902.a002548>.
- Mehrotra, R.C., Liu, X.Q., Li, C.S., et al., 2005. Comparison of the Tertiary flora of southwest China and northeast India and its significance in the antiquity of the modern Himalayan flora. *Rev. Palaeobot. Palynol.* 135, 145–163. <https://doi.org/10.1016/j.revpalbo.2005.03.004>.
- Mehta, N., Chawla, A., 2024. Eco-physiological trait variation in widely occurring species of Western Himalaya along elevational gradients reveals their high adaptive potential in stressful conditions. *Photosynth. Res.* 159, 29–59. <https://doi.org/10.1007/s11120-023-01071-5>.
- Miller, J.T., Jolley-Rogers, G., Mishler, B.D., et al., 2018. Phylogenetic diversity is a better measure of biodiversity than taxon counting. *J. Syst. Evol.* 56, 663–667. <https://doi.org/10.1111/jse.12436>.
- Mukherjee, S., 2015. A review on out-of-sequence deformation in the Himalaya. In: Mukherjee, S., et al. (Eds.), *Tectonics of the Himalaya*. Geological Society of London. <https://doi.org/10.1144/SP1412.1113>.
- Nag, A., Ahuja, P.S., Sharma, R.K., 2015. Genetic diversity of high-elevation populations of an endangered medicinal plant. *AoB Plants* 7, plu076. <https://doi.org/10.1093/aobpla/plu076>.
- Opgenoorth, L., Vendramin, G.G., Mao, K.S., et al., 2010. Tree endurance on the Tibetan Plateau marks the world's highest known tree line of the Last Glacial Maximum. *New Phytol.* 185, 332–342. <https://doi.org/10.1111/j.1469-8137.2009.03007.x>.
- Pandit, M.K., Manish, K., Koh, L.P., 2014. Dancing on the roof of the world: ecological transformation of the Himalayan landscape. *BioScience* 64, 980–992. <https://doi.org/10.1093/biosci/biu152>.
- Pauls, S.U., Nowak, C., Bálint, M., et al., 2013. The impact of global climate change on genetic diversity within populations and species. *Mol. Ecol.* 22, 925–946. <https://doi.org/10.1111/mec.12152>.
- Peppe, D.J., Royer, D.L., Cariglino, B., et al., 2011. Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. *New Phytol.* 190, 724–739. <https://doi.org/10.1111/j.1469-8137.2010.03615.x>.
- Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. *Ecol. Lett.* 9, 741–758. <https://doi.org/10.1111/j.1461-0248.2006.00924.x>.
- Poudel, R.C., Möller, M., Liu, J., et al., 2014. Low genetic diversity and high inbreeding of the endangered yews in Central Himalaya: implications for conservation of their highly fragmented populations. *Divers. Distrib.* 20, 1270–1284. <https://doi.org/10.1111/ddi.12237>.
- Prasad, M., 1993. Siwalik (Middle Miocene) woods from the Kalagarh area in the Himalayan foot hills and their bearing on palaeoclimate and phytogeography. *Rev. Palaeobot. Palynol.* 76, 49–82. [https://doi.org/10.1016/0034-6667\(93\)90080-E](https://doi.org/10.1016/0034-6667(93)90080-E).
- Qian, H., Grau, O., 2025. Geographic patterns and ecological causes of phylogenetic structure in mosses along an elevational gradient in the central Himalaya. *Plant Divers.* 47, 98–105. <https://doi.org/10.1016/j.pld.2024.07.005>.
- Qian, H., Sandel, B., Deng, T., et al., 2019. Geophysical, evolutionary and ecological processes interact to drive phylogenetic dispersion in angiosperm assemblages along the longest elevational gradient in the world. *Bot. J. Linn. Soc.* 190, 333–344. <https://doi.org/10.1093/botlinnean/boz030>.
- Qian, H., Kessler, M., Vetaas, O.R., 2022. Pteridophyte species richness in the central Himalaya is limited by cold climate extremes at high elevations and rainfall seasonality at low elevations. *Ecol. Evol.* 12, e8958. <https://doi.org/10.1002/ecs3.8958>.
- Qin, S.Y., Zuo, Z.-Y., Guo, C., et al., 2023. Phylogenomic insights into the origin and evolutionary history of evergreen broadleaved forests in East Asia under Cenozoic climate change. *Mol. Ecol.* 32, 2850–2868. <https://doi.org/10.1111/mec.16904>.
- Qiong, L., Zhang, W., Wang, H., et al., 2017. Testing the effect of the Himalayan mountains as a physical barrier to gene flow in *Hippophae tibetana* Schlect. (Elaeagnaceae). *PLoS ONE* 12, e0172948. <https://doi.org/10.1371/journal.pone.0172948>.
- Qiu, J., 2008. The third Pole. *Nature* 454, 393–396. <https://doi.org/10.1038/454393a>.
- QXPCE (The Qinghai-Xizang Plateau Comprehensive Scientific Expedition of Chinese Academy of Sciences), 1988. *The Series of the Scientific Expedition to the Qinghai-Xizang Plateau: Vegetation of Xizang (Tibet)*. Science Press, Beijing, China.
- Rana, S.K., Price, T.D., Qian, H., 2019. Plant species richness across the Himalaya driven by evolutionary history and current climate. *Ecosphere* 10, e02945. <https://doi.org/10.1002/ecs2.2945>.
- Rawat, M., Arunachalam, K., Arunachalam, A., et al., 2020. Relative contribution of plant traits and soil properties to the functioning of a temperate forest ecosystem in the Indian Himalaya. *Catena* 194, 104671. <https://doi.org/10.1016/j.catena.2020.104671>.
- Rawat, M., Arunachalam, K., Arunachalam, A., et al., 2021. Assessment of leaf morphological, physiological, chemical and stoichiometry functional traits for understanding the functioning of Himalayan temperate forest ecosystem. *Sci. Rep.* 11, 23807. <https://doi.org/10.1038/s41598-021-03235-6>.
- Read, Q.D., Moorhead, L.C., Swenson, N.G., et al., 2014. Convergent effects of elevation on functional leaf traits within and among species. *Funct. Ecol.* 28, 37–45. <https://doi.org/10.1111/1365-2435.12162>.
- Ren, G., Mateo, R.G., Liu, J., et al., 2017. Genetic consequences of Quaternary climatic oscillations in the Himalayas: *Primula tibetica* as a case study based on restriction site-associated DNA sequencing. *New Phytol.* 213, 1500–1512. <https://doi.org/10.1111/nph.14221>.
- Roy, S., Marnid, B.C., Mawkhlieng, B., et al., 2016. Genetic diversity and structure in hill rice (*Oryza sativa* L.) landraces from the North-Eastern Himalayas of India. *BMC Genetics* 17, 107. <https://doi.org/10.1007/s00438-021-01844-4>.
- Searle, M.P., Treloar, P.J., 2019. Introduction to Himalayan tectonics: a modern synthesis. In: Searle, M.P., Treloar, P.J. (Eds.), *Himalayan Tectonics: A Modern Synthesis*. Geological Society of London, London, UK. <https://doi.org/10.1144/SP483-2019-20>.
- Shah, S.S., Shrestha, K.K., Scheidegger, C., 2019. Variation in plant functional traits along altitudinal gradient and land use types in Sagarmatha National Park and buffer zone, Nepal. *Am. J. Plant Sci.* 10, 595–614. <https://doi.org/10.4236/ajps.2019.104043>.
- Sharma, S., Chhabra, M., Singh, S.K., et al., 2022. Genetic diversity and population structure of critically endangered *Dactylorhiza hatagirea* (D. Don) Soo from North-Western Himalayas and implications for conservation. *Sci. Rep.* 12, 11699. <https://doi.org/10.1038/s41598-022-15742-1>.
- Sharma, M.K., Hopak, N.E., Chawla, A., 2024. Alpine plant species converge towards adopting elevation-specific resource-acquisition strategy in response to experimental early snow-melting. *Sci. Total Environ.* 907, 167906. <https://doi.org/10.1016/j.scitotenv.2023.167906>.
- Shoener, S., Davies, T.J., Saikia, P., et al., 2018. Phylogenetic diversity patterns in Himalayan forests reveal evidence for environmental filtering of distinct lineages. *Ecosphere* 9, e02157. <https://doi.org/10.1002/ecs2.2157>.
- Shrestha, A.B., Wake, C.P., Mayewski, P.A., et al., 1999. Maximum temperature trends in the Himalaya and its vicinity: an analysis based on temperature records from Nepal for the period 1971–94. *J. Clim.* 12, 2775–2786. [https://doi.org/10.1175/1520-0442\(1999\)012<2775:MTTITH>2.0.CO;2](https://doi.org/10.1175/1520-0442(1999)012<2775:MTTITH>2.0.CO;2).
- Shrestha, M., Dyer, A.G., Bhattarai, P., et al., 2014. Flower colour and phylogeny along an altitudinal gradient in the Himalayas of Nepal. *J. Ecol.* 102, 126–135. <https://doi.org/10.1111/1365-2745.12185>.
- Sigdel, S.R., Liang, E., Rokaya, M.B., et al., 2023. Functional traits of a plant species fingerprint ecosystem productivity along broad elevational gradients in the Himalaya. *Funct. Ecol.* 37, 383–394. <https://doi.org/10.1111/1365-2435.14226>.
- Singh, D.K., Pusalkar, P.K., 2020. Floristic diversity of the Indian Himalaya. In: Dar, G.H., Khuroo, A.A. (Eds.), *Biodiversity of the Himalaya: Jammu and Kashmir State*. Springer Nature, Singapore, pp. 93–126. https://doi.org/10.1007/978-981-32-9174-4_5.
- Singh, J.S., Singh, S.P., 1987. Forest vegetation of the Himalaya. *Bot. Rev.* 53, 80–192.
- Singh, S.P., Gumber, S., Singh, R.D., et al., 2020. How many tree species are in the Himalayan treelines and how are they distributed? *Trop. Ecol.* 61, 317–327. <https://doi.org/10.1007/s42965-020-00093-7>.
- Singh, R., Rawat, M., Pandey, R., 2023a. Quantifying leaf-trait co-variation and strategies for ecosystem functioning of *Quercus leucotrichophora* (Ban Oak) forest in Himalaya. *Ecol. Indic.* 150, 110212. <https://doi.org/10.1016/j.ecolind.2023.110212>.
- Singh, R., Rawat, M., Chand, T., et al., 2023b. Phenological variations in relation to climatic variables of moist temperate forest tree species of western Himalaya, India. *Heliyon* 9, e16563. <https://doi.org/10.1016/j.heliyon.2023.e16563>.
- Spicer, R.A., 2017. Tibet, the Himalaya, Asian monsoons and biodiversity—In what ways are they related? *Plant Divers.* 39, 233–244. <https://doi.org/10.1016/j.pld.2017.09.001>.

- Spicer, R.A., Farnsworth, A., Su, T., 2020. Cenozoic topography, monsoons and biodiversity conservation within the Tibetan Region: an evolving story. *Plant Divers.* 4, 229–254. <https://doi.org/10.1016/j.pld.2020.06.011>.
- Spicer, R.A., Farnsworth, A., Su, T., et al., 2025. The progressive Co-evolutionary development of the Pan-Tibetan Highlands, the Asian monsoon system and Asian biodiversity. Geological Society, London, Special Publications 549. <https://doi.org/10.1144/sp549-2023-180>. SP549-2023–2180.
- Srinivasan, U., Tamma, K., Ramakrishnan, U., 2014. Past climate and species ecology drive nested species richness patterns along an east-west axis in the Himalaya. *Global Ecol. Biogeogr.* 23, 52–60. <https://doi.org/10.1111/geb.12082>.
- Sun, H., Zhou, Z.K., 2002. *Seed Plants of the Big Bend Gorge of Yalu Tsangpo in SE Tibet, E Himalayas*. Yunnan Science and Technology Press, Kunming, China.
- Telwala, Y., Brook, B.W., Manish, K., et al., 2013. Climate-induced elevational range shifts and increase in plant species richness in a Himalayan biodiversity epicentre. *PLoS ONE* 8, e57103. <https://doi.org/10.1371/journal.pone.0057103>.
- Thakur, D., 2019. *Functional Ecology of High-Altitude Vegetation of Western Himalaya*. Ph.D. dissertation, CSIR-IHBT, Palampur, India.
- Thakur, D., Chawla, A., 2019. Functional diversity along elevational gradients in the high-altitude vegetation of the western Himalaya. *Biodivers. Conserv.* 28, 1977–1996. <https://doi.org/10.1007/s10531-019-01728-5>.
- Vanneste, T., Valdés, A., Verheyen, K., et al., 2019. Functional trait variation of forest understorey plant communities across Europe. *Basic Appl. Ecol.* 34, 1–14. <https://doi.org/10.1016/j.baae.2018.09.004>.
- Vetaas, O.R., Grytnes, J.A., 2002. Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecol. Biogeogr.* 11, 291–301. <https://doi.org/10.1046/j.1466-822X.2002.00297.x>.
- Villéger, S., Mason, N.W., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301. <https://doi.org/10.1890/07-1206>.
- Wambulwa, M.C., Milne, R., Wu, Z.Y., et al., 2021. Spatiotemporal maintenance of flora in the Himalaya biodiversity hotspot: current knowledge and future perspectives. *Ecol. Evol.* 11, 10794–10812. <https://doi.org/10.1002/ece3.7906>.
- Wambulwa, M.C., Zhu, G.-F., Luo, Y.-H., et al., 2025. Incorporating genetic diversity to optimize the plant conservation network in the third Pole. *Glob. Change Biol.* 31, e70122. <https://doi.org/10.1111/gcb.70122>.
- Wang, Y.L., Li, L., Paudel, B.R., et al., 2024. Genomic insights into high-altitude adaptation: a comparative analysis of *Roscoea alpina* and *R. purpurea* in the Himalayas. *Int. J. Mol. Sci.* 25, e2265. <https://doi.org/10.3390/ijms25042265>.
- Wani, S.A., Khuroo, A.A., Zaffar, N., et al., 2024. Data synthesis for biodiversity science: a database on plant diversity of the Indian Himalayan Region. *Biodivers. Conserv.* 33, 3377–3397. <https://doi.org/10.1007/s10531-024-02784-2>.
- Xing, Y., Ree, R.H., 2017. Uplift-driven diversification in the Hengduan Mountains, a temperate biodiversity hotspot. *Proc. Natl. Acad. Sci. U.S.A.* 114, E3444–E3451. <https://doi.org/10.1073/pnas.1616063114>.
- Xu, J., Grumbine, R.E., Shrestha, A., et al., 2009. The melting Himalaya: cascading effects of climate change on water, biodiversity, and livelihoods. *Conserv. Biol.* 23, 520–530. <https://doi.org/10.1111/j.1523-1739.2009.01237.x>.
- Xu, T., Abbott, R.J., Milne, R.L., et al., 2010. Phylogeography and allopatric divergence of cypress species (*Cupressus* L.) in the Qinghai-Tibetan Plateau and adjacent regions. *BMC Evol. Biol.* 10, 1–10. <https://doi.org/10.1186/1471-2148-10-194>.
- Yan, Y., Yang, X., Tang, Z., 2013. Patterns of species diversity and phylogenetic structure of vascular plants on the Qinghai Tibetan Plateau. *Ecol. Evol.* 3, 4584–4595. <https://doi.org/10.1002/ece3.847>.
- Yan, L.J., Fan, P.Z., Wambulwa, M.C., et al., 2024. Human-associated genetic landscape of walnuts in the Himalaya: implications for conservation and utilization. *Divers. Distrib.* 30, e13809. <https://doi.org/10.1111/ddi.13809>.
- Ye, L.J., Shavvon, R.S., Qi, H.L., et al., 2024. Population genetic insights into the conservation of common walnut (*Juglans regia*) in Central Asia. *Plant Divers.* 46, 600–610.
- Yu, H., Miao, S., Xie, G., et al., 2020. Contrasting floristic diversity of the Hengduan mountains, the Himalayas and the Qinghai-Tibet Plateau sensu stricto in China. *Front. Ecol. Evol.* 8, 136. <https://doi.org/10.3389/fevo.2020.00136>.
- Zhang, X.S., 1978. The plateau zonality of vegetation in Xizang. *Acta Bot. Sin.* 20, 140–149.
- Zhang, X., Liu, L., Chen, X., et al., 2021. GLC_FCS30: global land-cover product with fine classification system at 30 m using time-series Landsat imagery. *Earth Syst. Sci. Data* 13, 2753–2776. <https://doi.org/10.5194/essd-13-2753-2021>.
- Zhao, J.L., Paudel, B.R., Yu, X.Q., et al., 2021. Speciation along the elevation gradient: divergence of *Roscoea* species within the south slope of the Himalayas. *Mol. Phylogenet. Evol.* 164, 107292. <https://doi.org/10.1016/j.ympev.2021.107292>.
- Zhao, F., Yang, T., Luo, C., et al., 2022. Comparing elevational patterns of taxonomic, phylogenetic, and functional diversity of woody plants reveal the asymmetry of community assembly mechanisms on a mountain in the Hengduan Mountains Region. *Front. Ecol. Evol.* 10, 869258. <https://doi.org/10.3389/fevo.2022.869258>.
- Zhu, W., Ding, L., Ji, Y., et al., 2022. Subduction evolution controlled Himalayan orogenesis: implications from 3-D subduction modeling. *Appl. Sci.* 12, 7413. <https://doi.org/10.3390/app12157413>.