SYNOPSIS

Macroecological patterns and drivers of Himalayan plant species diversity and distribution through the Ages

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Abstract. The Himalaya started with mostly immigrant flora but is today home to about 3500–4000 endemic plants that have evolved within a time span of 40–50 million years. It is, however, still unknown as to what factors have been responsible for the development of such high endemism within such a short evolutionary time. It is also unclear as to how plant diversity patterns are structured across the present-day environmental gradients in the Himalaya and whether these diversity patterns will change in the future. My results point towards a positive coincidence between endemic plant species diversification, changes in geo-physical characteristics, and climate in the Himalaya. The present-day plant species richness patterns are hump-shaped, life-form and endemic specific, and scale-dependent. Furthermore, shrublands would emerge as the most successful plant community in future climates, and there would be a need to redesign the Protected Area network due to ensuing climate change in the Himalaya.

Keywords: Climate change; Endemic; Evolution; Flora; Himalaya; Species richness pattern

Introduction

The Himalaya, located between 26° N to 41° N latitude (about 1700 km, north–south) and 70 °E to 105° E longitude (about 3200 km across), represents one of the youngest and the highest mountain chains of the world (Fig. 1, Pandit et al. 2014, Manish 2017, Pandit 2017, Manish and Pandit 2018a). The formation of this mountain chain started with the separation of the Indian plate from the Gondwanaland and subsequent collision of the Indian and the Eurasian plates in the early Cenozoic Era (Fig. 2). It was accompanied by major geo-physical events, including subsequent withdrawal and loss of Tethys Sea, formation of contiguous landmass connectivity between the neighboring biogeographic regions of Sino-Japanese in the north and Indo-Malaya in the southeast, and evolution of the modern day South West Asian monsoon system (Pandit 2017, Manish and Pandit 2018a). These events laid the ground for colonization of a nascent Himalayan ecosystem by migrating floras and faunas from all directions (Singh and Singh 1987, Pandit et al. 2014, Pandit 2017, Manish and Pandit 2018a). Starting with almost all immigrant flora, the Himalaya came to harbor about 10,000 plant species and 3500–4000 endemic species, with wide biogeographic affinities ranging from South East Asia to Sino-Japanese and Mediterranean elements (Fig. 3,

Pandit et al. 2014, Manish and Pandit 2018a). However, many unanswered questions regarding the Himalayan flora remain: (i) What was the nature of early plant migrants in the Himalaya? (ii) What were the precise time periods in which maximum migrations and endemic diversification occurred in the Himalaya? (iii) How are present-day plant diversity patterns structured across elevational gradients in the Himalaya? (iv) How will the present-day species and community distribution patterns change in response to ongoing climate and warming scenarios in the near future? (vii) Will the existing protected area boundaries be adequate in conserving species and communities under future climate change scenarios? Here, I look for answers to these specific questions and develop a geo-biological understanding for plant species diversifications and distribution during different time periods (past, present and future) since the Himalaya's formation.

Methods

To understand the evolution and diversification of endemic plants in the Himalaya during the past time periods (55–10 million years ago, mya), I prepared phylogenetic family-level supertrees and ancestral area reconstructions based on endemic species incidence data. Species data were collected through primary field surveys and online databases (Flora Himalaya
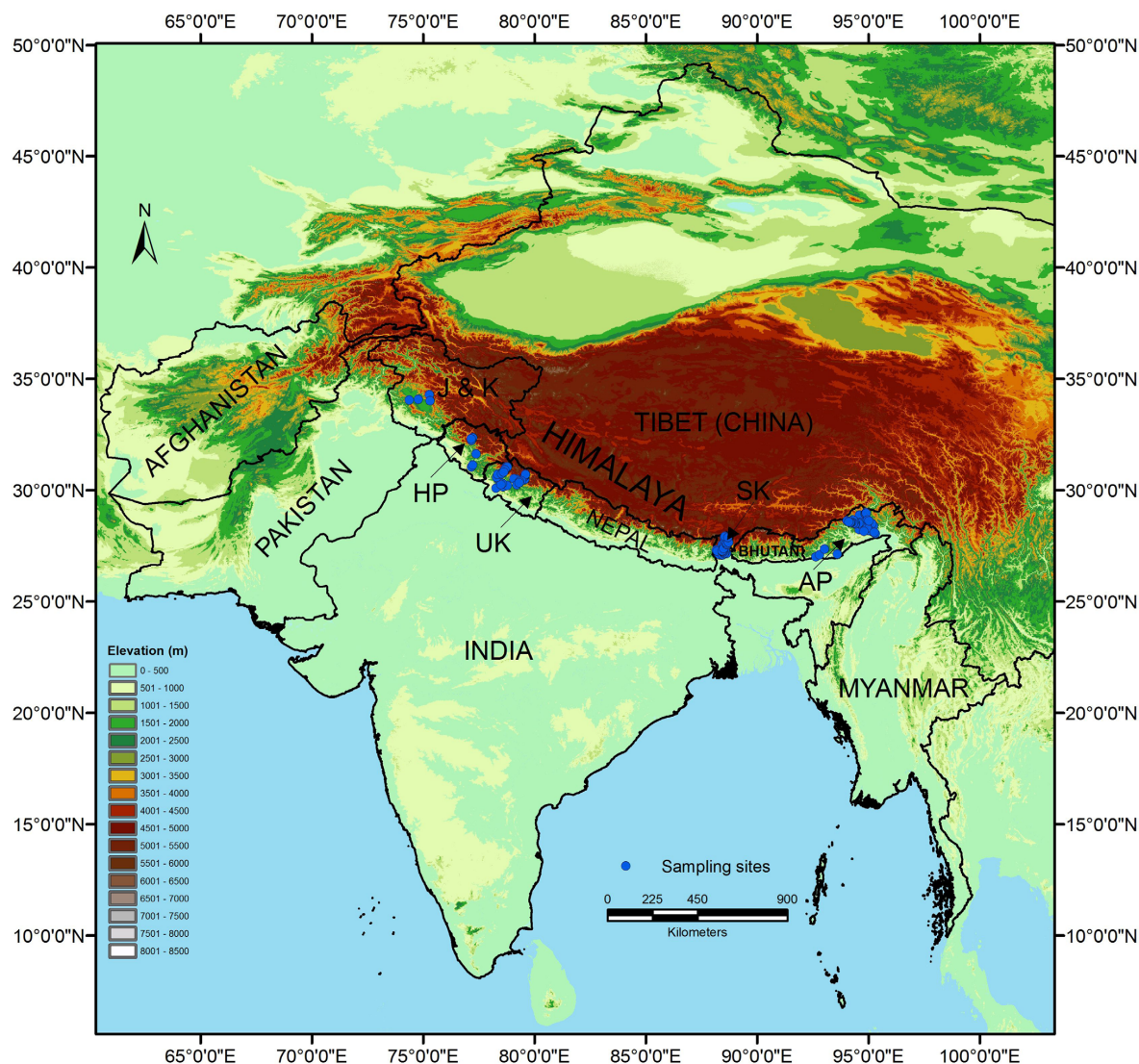
Figure 1. Spatial spread of the Himalayan mountain system across 7 nations. A total of 138 locations (blue dots) were sampled in the Indian Himalayan region using nested quadrat methods for collecting information on plant species occurrence and elevational distribution. The base map was prepared using Digital Elevation Models (DEM) in Arc GIS 9.3 software (Environmental Systems Research Institute (ESRI), Redlands, CA).

Database[1]; Global Biodiversity Information Facility Database[2]; efloras Database[3]) with information on their nomenclature, areas of occurrence, and elevational distribution ranges (see Fig. 1, Manish 2018). Based on their areas of occurrence, the endemics were classified into two categories: Eastern Himalayan endemic (EHE) and Western Himalayan endemic (WHE). Species classified as EHE were distributed exclusively across 21°–25° N latitudes (eastern Tibet, eastern Nepal, Sikkim, Bhutan, Arunachal Pradesh and northern Myanmar), while species classified as WHE were limited exclusively to 30°–40° N latitudes (western Nepal, Uttarakhand, Himachal Pradesh, Jammu and Kashmir and areas of

northern Pakistan and Afghanistan). For both EHE and WHE, separate phylogenetic family-level supertrees were prepared (resolved up to family level) using Phylomatic tool in Phylocom v.4.2 (Webb et al. 2008) and with Angiosperm Phylogeny Group III family level seed plant tree (R20120829.new) as a base (Fig. 4). The supertrees were calibrated using Branch Length Adjustment algorithm (BLADJ) in Phylocom based on angiosperm nodes contained in a dated tree of Wikström et al. (2001). The BLADJ calibrated phylogenetic trees were collapsed at the angiosperm family level nodes, and the diversification time of these nodes were noted and classified into four exclusive

1 http://www.leca.univ-savoie.fr/db/florhy/infos.html

2 GBIF, http://www.gbif.org/
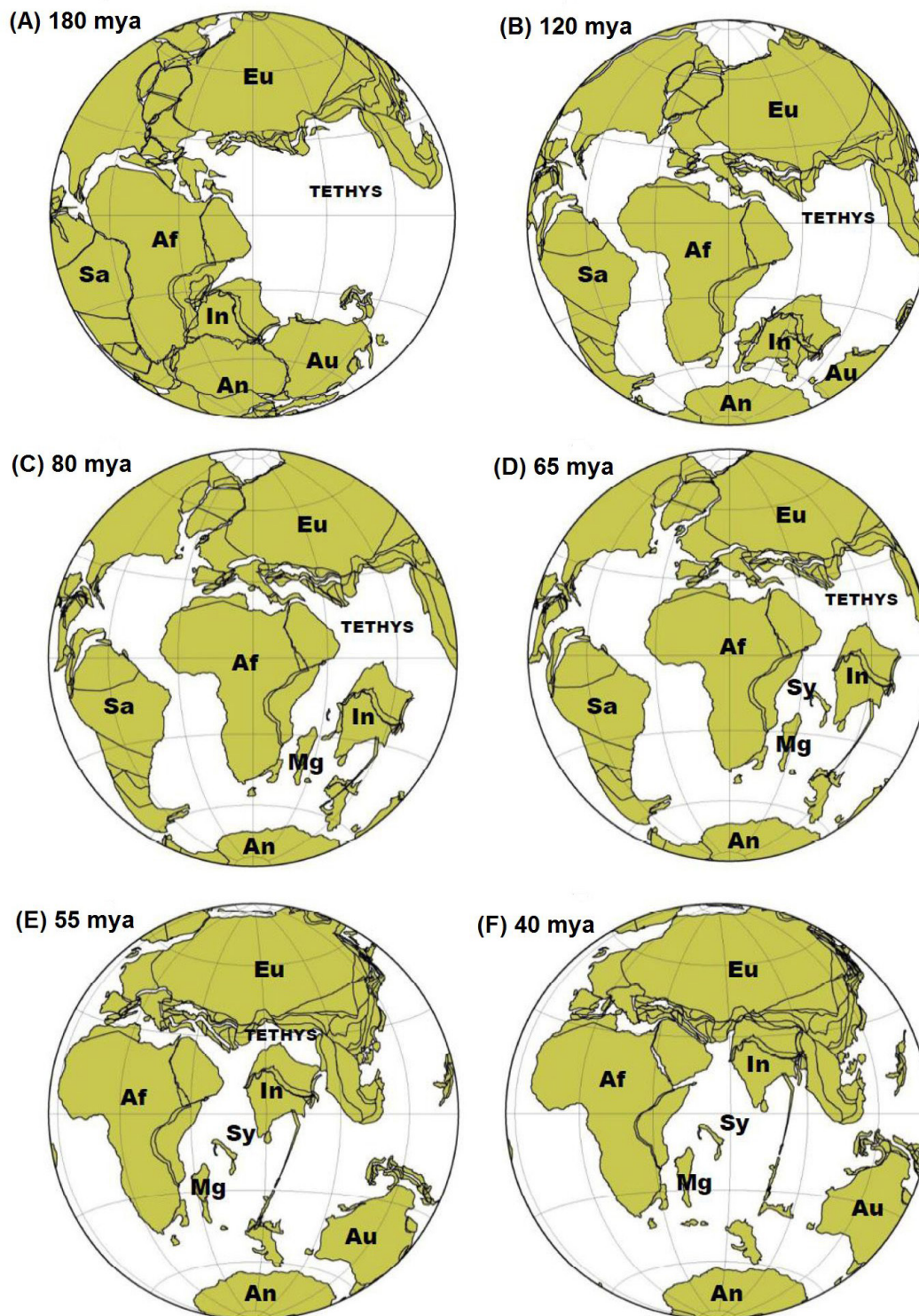
3 http://www. efloras.org/

Figure 2. Diagrammatic reconstructions of the major geological events accompanying the northward journey of the Indian plate from Gondwanaland to Eurasia. (A) 180 million years ago (mya) – arrangement of Gondwanaland showing India's position during middle Jurassic, (B) 120 mya – separation of South America from Africa in western Gondwana and the fragment containing India-Madagascar-Seychelles (IMS) separated from Antarctica and Australia in eastern Gondwana, (C) 80 mya – detachment of Madagascar block from the IMS fragment, (D) 65 mya - separation of Seychelles from the Indian plate, (E) 55 mya – onset of collision of Indian and Eurasian plates at the eastern end of Greater India, (F) 40 mya – completion of collision and birth of the Himalaya. The notations in the figure represent the following: Af – Africa, An – Antarctica, Au – Australia, Eu – Eurasia, In – India, Mg – Madagascar, Sa – South America, Sy – Seychelles. The tectonic reconstructions (as depicted in the figure) were made using open-source ODSN Plate Tectonic Reconstruction Service (http://www.odsn.de/odsn/index.html).
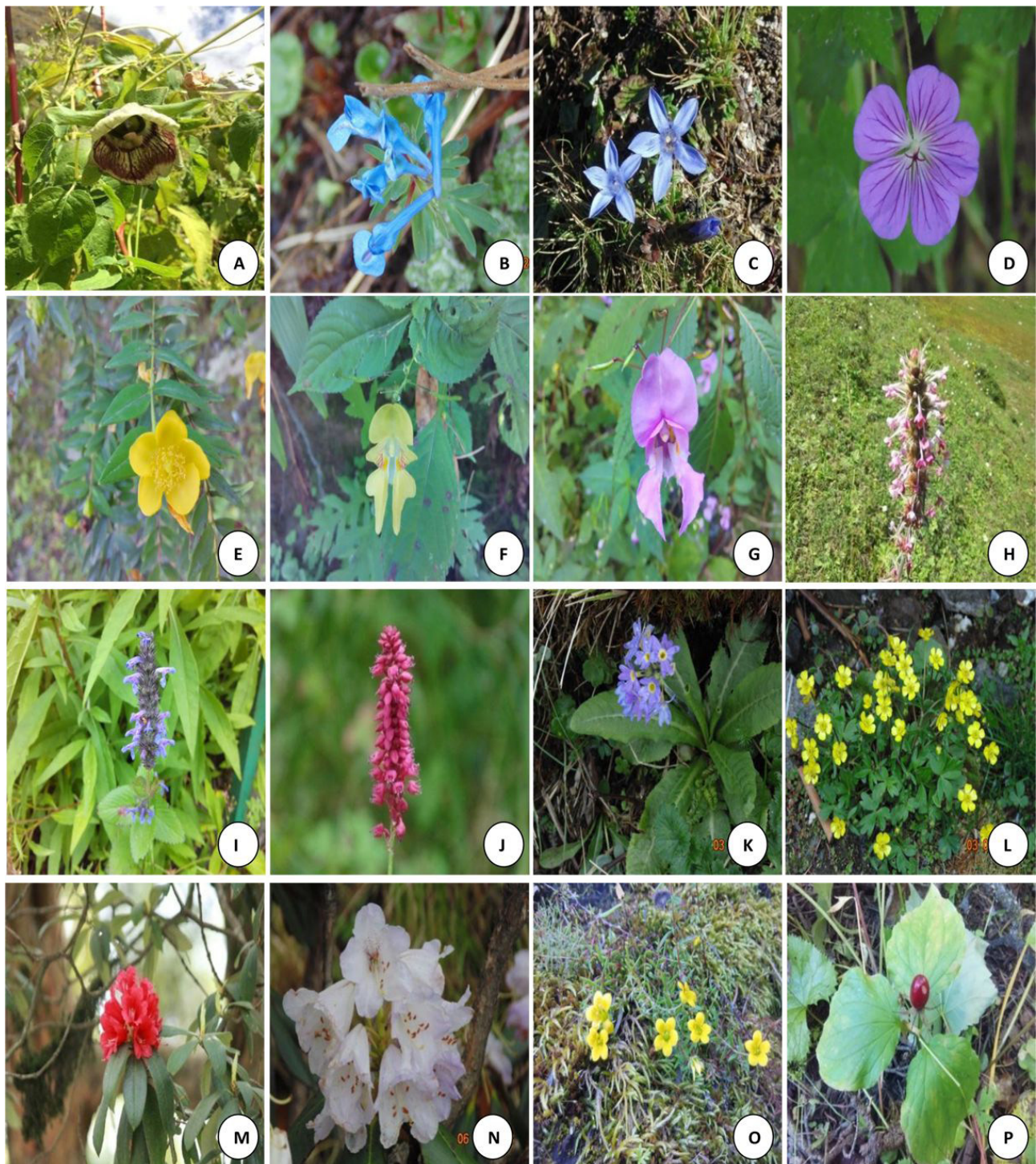
Figure 3. Some endemic plant species found in the Himalaya. (A) *Codonopsis rotundifolia* Benth. (3000–3500 m), (B) *Corydalis cashmeriana* Royle (3000–5000 m), (C) *Cyananthus microphyllus* Edgew. (3500–4500 m), (D) *Geranium wallichianum* D.Don ex (2500–3500 m), (E) *Hypericum oblongifolium* Choisy (1000–2500 m), (F) *Impatiens scabrida* DC. (2500–3500 m), (G) *Impatiens sulcata* Wall. (3000–4000 m), (H) *Morina longifolia* Wall. ex DC. (3000–4300 m), (I) *Nepeta laevigata* (D.Don) Hand.-Mazz. (2500–4000 m), (J) *Polygonum amplexicaule* D.Don (1000–3000 m), (K) *Primula denticulata* Sm. (2500–4000 m), (L) *Ranunculus adoxifolius* Hand.-Mazz. (3500–4000 m), (M) *Rhododendron arboreum* Sm. (1500–3500 m), (N) *Rhododendron campanulatum* D.Don (3000–4500 m), (O) *Saxifraga parnassifolia* D.Don (4000–5000 m), (P) *Trillidium govanianum* (Wall. ex D.Don) Kunth (2500–4000 m). In total, Himalaya harbors about 10,000 plant species with nearly 3500–4000 endemics. Photo credits: Kumar Manish.
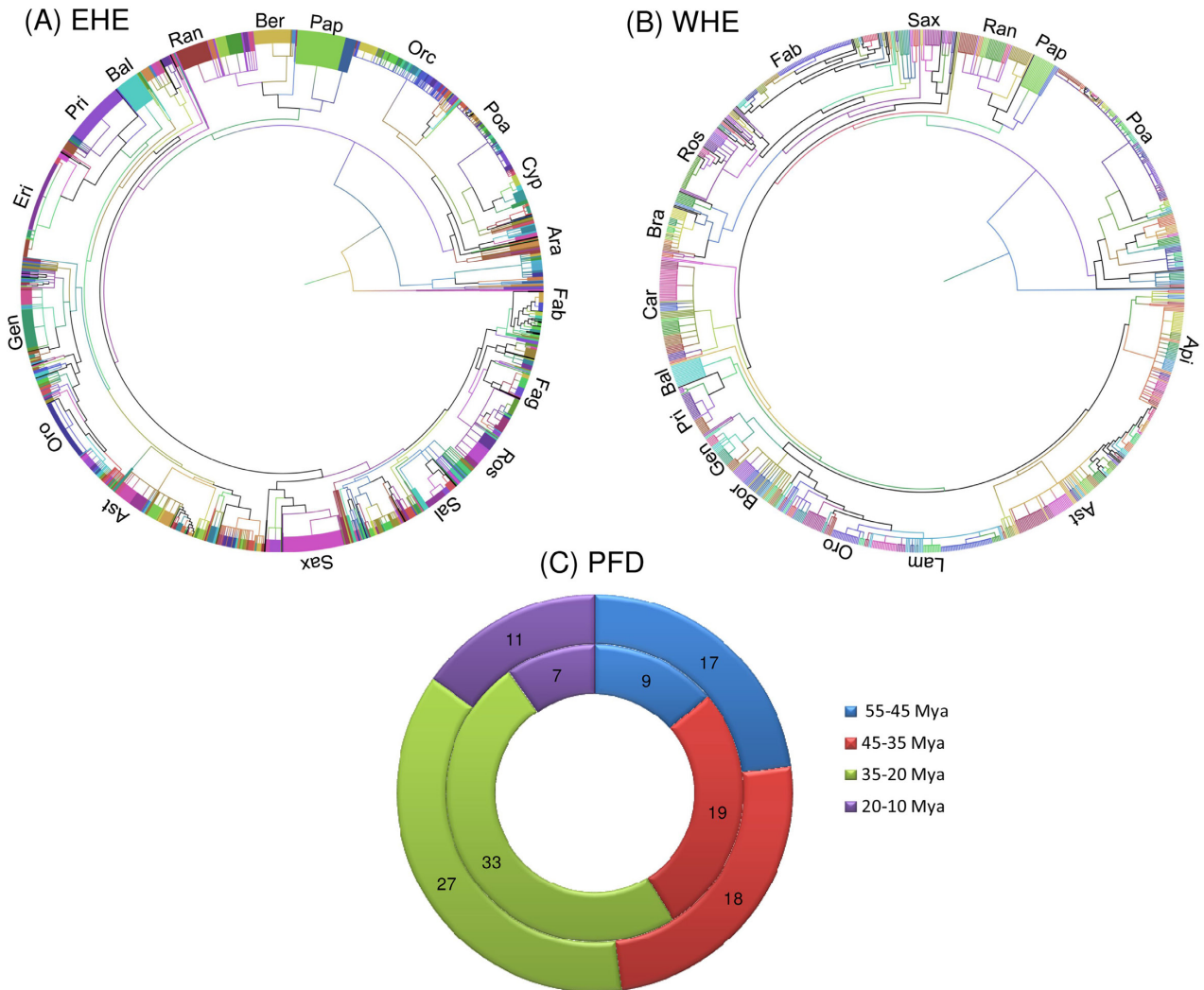
Figure 4. Family-level phylogenetic supertrees and divergence time estimates of Eastern and Western Himalayan endemic plants. (A) EHE – Eastern Himalayan endemics, (B) WHE – Western Himalayan endemics, (C) PFD – Percentage family diversifications of EHE and WHE in different time periods. The outer circle in the doughnut chart (Plot C – PFD) represents percentage family diversifications (denoted in numbers) during different time periods in the Eastern Himalayan region while the inner circle represents percentage family diversifications (denoted in numbers) during different time periods in the Western Himalayan region. The notations in different phylogenetic supertrees (Plot A and B) represents the phylogenetic position of most speciose plant families in respective Eastern and Western Himalayan regions: Api – Apiaceae, Ara – Araliaceae, Ast – Asteraceae, Bal – Balanophoraceae, Berb – Berberidaceae, Bor – Boraginaceae, Bra – Brassicaceae, Car – Caryophyllaceae, Cyp – Cyperaceae, Eri – Ericaceae, Fab – Fabaceae, Fag – Fagaceae, Gen – Gentianaceae, Lam – Lamiaceae, Orc – Orchidaceae, Oro – Orobanchaceae, Pap – Papaveraceae, Poa – Poaceae, Pri – Primulaceae, Ran – Ranunculaceae, Ros – Rosaceae, Sal – Salicaceae, Sax – Saxifragaceae.

time periods corresponding to distinct phases of geophysical changes during formation of the Himalaya: (i) 55–45 mya, collision phase, (ii) 45–35 mya, phase of early uplift of the Tibetan plateau, (iii) 35–20 mya, phase corresponding to the onset of modern day South West Asian monsoon, and (iv) 20–10 mya, phase corresponding to the further uplift of the Himalayan mountain ranges and aridification of the Central Asian region (see Favre et al. 2015). The divergence time estimates obtained from the family-level supertrees were then used to calculate percentage family diversifications and diversification rates for each exclusive

time period (55–45 mya, 45–35 mya, 35–20 mya and 20–10 mya). Furthermore, to investigate the ancestral biogeographic source area of endemic plants in the Eastern and Western Himalaya, I performed ancestral area reconstruction (ASR) analyses using Bayesian Binary Markov Chain Monte Carlo (BBM) method in RASP v.3.2 (Yu et al. 2015).

To understand how plant species are distributed across the Himalaya in the present-day scenario, I analyzed plant species richness patterns from 300 to 5300 m (tropical to alpine) along the Sikkim Himalayan elevational gradient using primary field

surveys and secondary literature (see Manish et al. 2017). Sikkim Himalaya was specifically chosen for this purpose because one can sample the entire range of ecosystems (tropical to alpine) within a short geographical distance of about 100 km. Species richness patterns were elucidated using observed, rarefaction, non-parametric and interpolation methods, accuracy assessment using scaled mean squared error (SMSE), generalized linear models (GLM), and generalized additive models (GAM) (Manish et al. 2017). GLM was further used for investigating the relationship between species richness and various environmental drivers. In this step, modelling included removal of collinearity, stepwise regression analyses to achieve least Akaike's information criterion (AIC) and the highest percentage of deviance explained (D^2), and formulation of a synthetic model where comparative performance of various environmental drivers in explaining species richness patterns along the elevational gradient was measured (Bhatt et al. 2012, Manish et al. 2017). Furthermore, I used a phylogenetic supertree approach (as described in the last paragraph) to construct separate calibrated family-level phylogenetic trees for different endemic plant life-forms (trees, shrubs, climbers and herbs) and understand the relationship between phylogenetic diversity (PD), phylogenetic structure, diversification time, and species richness along the elevational gradient in the Himalaya (see Manish and Pandit 2018b).

The last part of the study focused on understanding the likely responses of plant species and communities to future climate change scenarios in the Sikkim Himalaya. For this, individual habitat suitability projections (Species Distribution Models) were made for each endemic species using MaxEnt ver. 3.3.3k (Phillips et al. 2006) in both current and future climate scenarios based on species occurrence data collected through primary and secondary surveys in Sikkim Himalaya (see Manish et al. 2016). Current climate represented the average climate conditions for the period 1950–2000. Future climate data represented the projections for 2 time periods, 2050 (average climate conditions for 2041–2060), and 2070 (average climate conditions for 2061–2080) based on the IPCC 5th Assessment Report (Manish et al. 2016). The habitat suitability projections obtained for each species was then averaged across all species life-forms (trees, shrubs, climbers and herbs) to arrive at estimates of geographical area occupied by each life-form in current and future time periods (2050 and 2070). Furthermore, I also analyzed whether the current Protected Areas (PAs) network in Sikkim Himalaya would provide sufficient conservation in future climate change scenarios. For this, I incorporated the MaxEnt habitat suitability projections of all endemic species into spatial hierarchical systematic conservation planning software, Zonation v.4.0 (Moilanen et al. 2014). Zonation prioritized areas and regions in Sikkim Himalaya for conservation in current and future climates by ranking them according to their conservation values.

Results & Discussion

In total, 3547 endemic species belonging to 137 families were found to inhabit the Himalayan region. Of these, about 2446 species (125 families)

were found in the Eastern Himalayan region while 1101 species (75 families) were found in the Western Himalayan region. Thus, overall, the Eastern Himalaya were found to harbor approximately twice the number of endemics found in the Western Himalayan region. Analyses of diversification time patterns during the four time periods of the Himalaya's formation (55–45 mya, 45–35 mya, 35–20 mya and 20–10 mya) revealed that maximum species diversification (27% in Eastern Himalaya and 33% in Western Himalaya) occurred in the time period when modern day South West Asian monsoon originated in the Himalaya (35–20 million years ago) (Fig. 4). In particular, the monsoon system was found to have played the most dominant role in the evolution of endemic taxa in the region, particularly in the Western Himalaya. Ancestral area reconstructions revealed that the majority of the endemic plants in the Eastern Himalaya diversified from taxa which immigrated from South-East (SE) Asian (SE Asiatic Malayasian-SE Chinese) and Sino- Japanese regions, while in the Western Himalaya the majority of the endemic plants diversified from taxa which immigrated from SE Chinese, Sino- Japanese, Irano-Turanian, and Centrasiatic regions (Manish 2018).

When species richness patterns were analyzed across the present-day elevational gradient in the Himalaya, the results showed the following: (i) Humped and non-congruent richness patterns in endemics and non-endemics, which peaked at higher and lower elevations, respectively; (ii) Species richness patterns were life-form specific with different species richness maxima at different elevations; (iii) The overall species richness pattern produced by aggregation of data of various life-forms was skewed by the largest physiognomic group; (iv) Species richness patterns changed from monotonic increase in species richness with respect to elevation at smallest spatial extent (300–1500 m) to humped patterns at medium (300–3000 m) and largest spatial extents (300–5300 m); (v) Elevational species richness patterns were not explained by either Rapoport's elevational rule nor the Mid-Domain Effect; (vi) Different drivers and their combinations influenced richness patterns of various life-forms, but mean temperature emerged as the best explanatory variable with least AIC and highest D^2 values in the synthetic model (see Fig. 5, Manish et al. 2017). When endemic plant diversity patterns were analyzed in a phylogenetic and evolutionary framework using calibrated phylogenetic family-level supertrees, the results indicated that endemic plant families are not distributed randomly in the Himalaya but rather according to their ecological niches (Manish and Pandit 2018b). Both time-for-speciation effect and niche conservatism along elevational gradient were found to play a simultaneous role in determining endemic plant diversity patterns by imposing ancestral environmental and elevational constraints on species distributions in the Himalaya (Manish and Pandit 2018b). The results also revealed that mid-elevations in the Himalaya have predominantly older (more ancestral taxa), while the upper and lower elevations are dominated by more recently diverged taxa (Manish and Pandit 2018b) (Fig. 6). Thus, the hump-shaped patterns in species
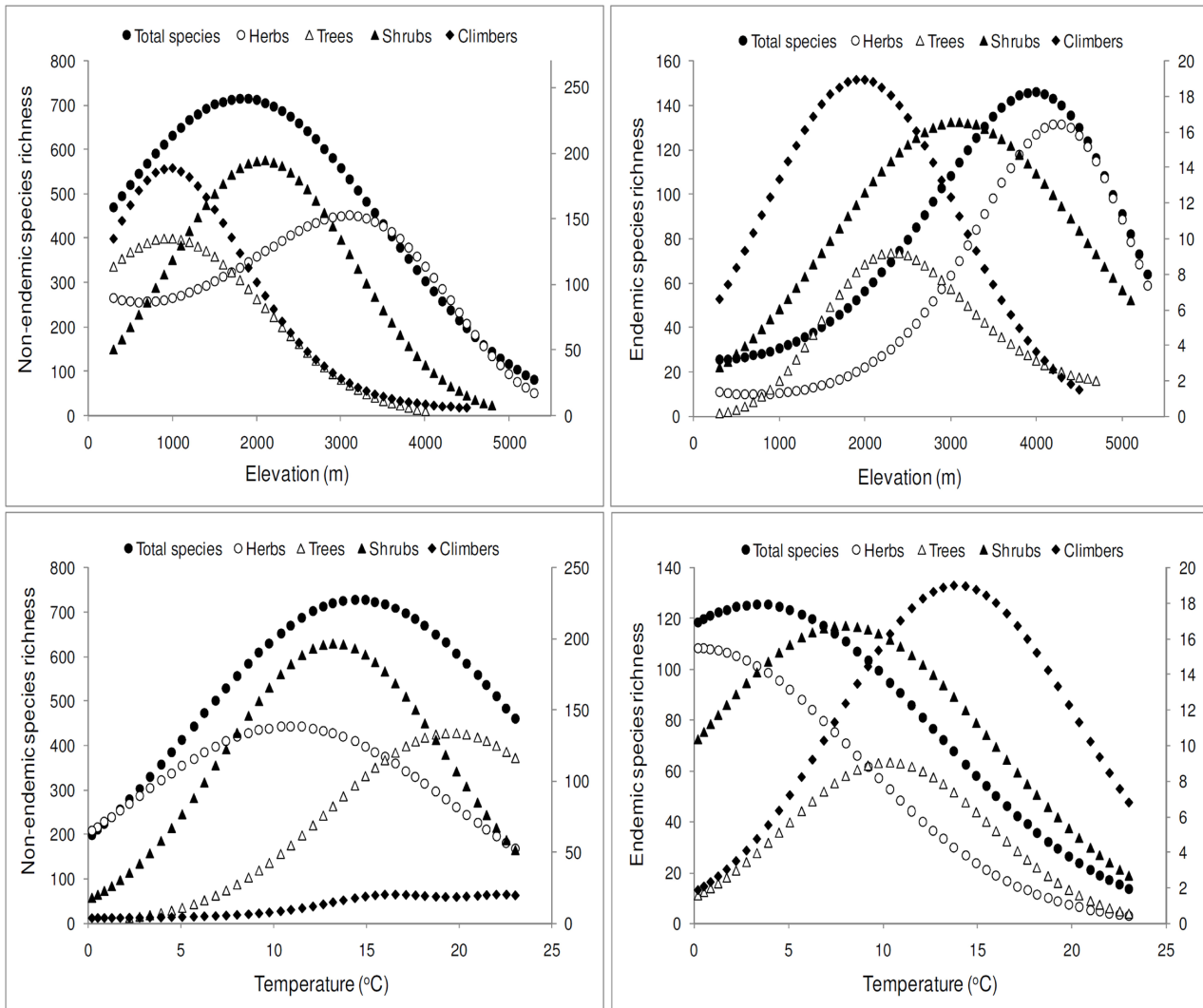
Figure 5. Variation of non-endemic and endemic plant species richness patterns for different plant life-forms along the elevational and temperature gradient in the Sikkim Himalayan region. The primary Y-axis in all the plots represents species richness for total species and herbs, while secondary Y-axis represents species richness for trees, shrubs and climbers. The fitted lines in plots represent the best-fit GLM models (Source: Modified from Manish et al. 2017).

diversity in the Sikkim Himalayan region appeared to be due to multiple endemic radiations at mid-elevations, possibly triggered by preponderance of ancestral taxa/lineages at mid-elevations. PD at family level peaked at intermediate elevations for all life-forms (Fig. 6), and there was a strong significant positive correlation between endemic species richness and family level PD along the elevational gradient (Manish and Pandit 2018b). The elevational species richness patterns and PD patterns in Sikkim Himalaya therefore were similar to each other in the case of each life-form (trees, shrubs, climbers and herbs). It was also found that endemic plant communities showed phylogenetic clustering (Net Relatedness Index (NRI) and Net Nearest Taxon Index (NTI) values > 0) at higher elevations and phylogenetic overdispersion (NRI and NTI values < 0) at mid or low elevations in the Himalaya (Manish and Pandit 2018b). It was therefore inferred that species composition and assemblage at higher elevations in

the Himalaya are determined by process of ecological filtering while at mid or low elevations, interspecific competition between species determines their presence (Manish and Pandit 2018b).

Analyses of MaxEnt species' distribution models showed that future climate conditions are likely to favor the habitat expansion of wide-range endemics such as *Primula whitei*, *Berberis sikkimensis*, and *Jaeschkea microsperma* in the Sikkim Himalaya because they possessed greater physiological tolerances (Manish et al. 2016). Comparatively, narrow-range endemics such as *Anaphalis cavei*, *Ranunculus sikkimensis*, *Saxifraga kingiana* and *Swertia hookeri* may be obliterated from their existing habitats due to their limited tolerance to fluctuating climates (Manish et al. 2016). The situation is likely to become more precarious for species which occupy the northern most reaches in the study area such as *Arenaria melandryoides*, *Astragalus acaulis*, *Chionocharis hookeri*, and *Diplarche pauciflora* because
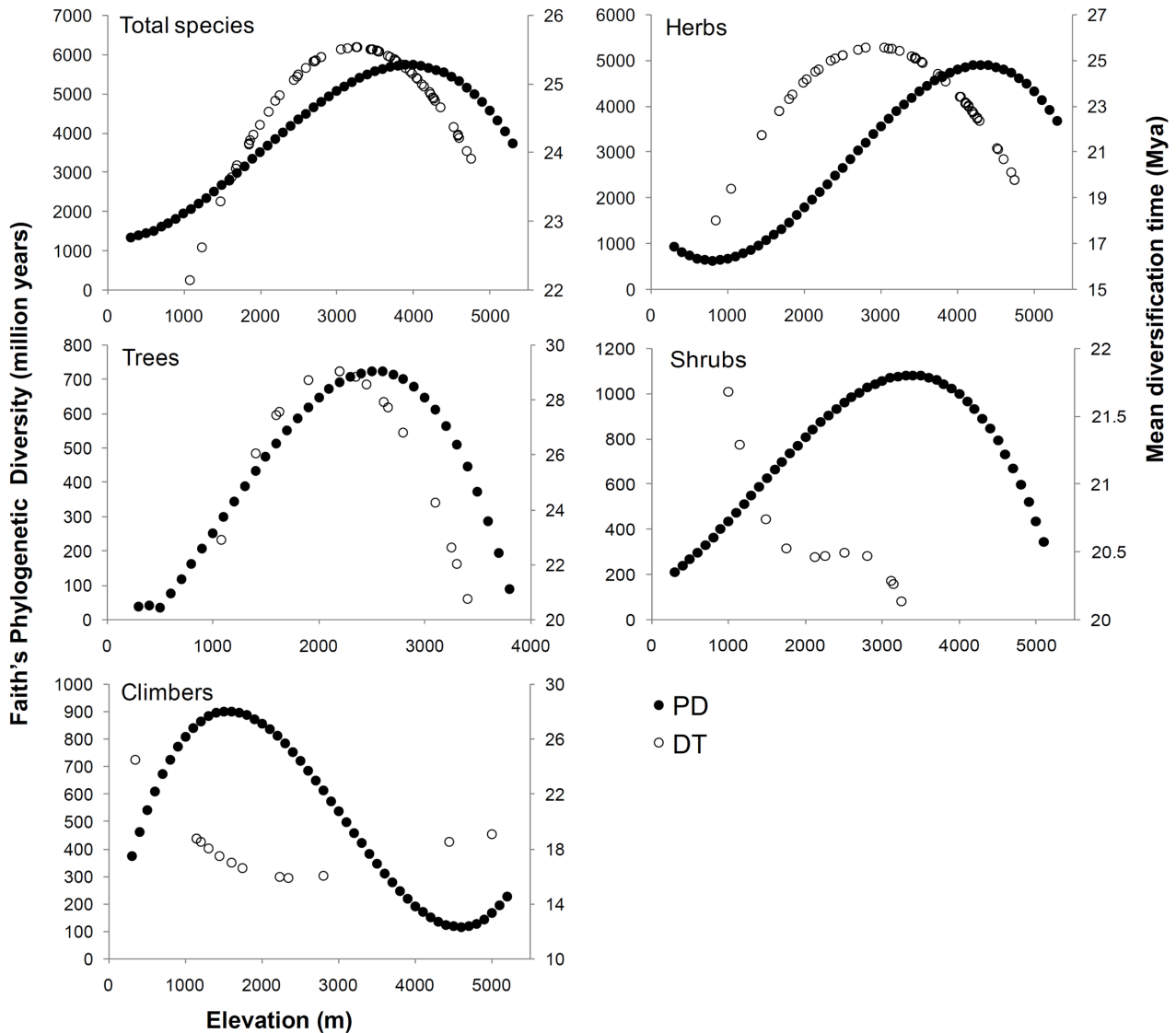

Figure 6. Patterns of phylogenetic diversity (PD) and diversification time (DT) along the Sikkim Himalayan elevational gradient for different plant life-forms. The primary Y-axis in all the plots represents phylogenetic diversity (PD), while secondary Y-axis represents mean endemic plant family diversification time (DT) in million years ago (Mya). The fitted lines in plots represent the best-fit GLM models (Source: Modified from Manish et al. 2018b).

they would have no habitable area left for migration and would likely go extinct (Telwala et al. 2013, Manish et al. 2016). In total, about 17% and 18% of endemic species would lose their potential habitats by 2050 and 2070, respectively (Manish et al. 2016). Herbaceous meadows were found to lose approximately 71–213 sq.km. of their current geographical area by 2050 and 2070. These freed-up areas would likely be occupied by shrublands in the coming future, thereby becoming the most prolific and successful community under future climate scenarios in the Himalaya (see Manish et al. 2016). The results of the Zonation prioritization analyses revealed that the areas with highest conservation priorities were located between 2000–4700 m in current climate conditions, between 2100–5200 m in 2050 and between 2100–5300 m in

2070, respectively. Furthermore, large PAs were more efficient at conserving endemic species under future climate change conditions than the small PAs. Smaller PAs in the study region showed no net increase or decrease in conservation efficiency between current and future climates. Therefore, in order to mitigate the effects of ensuing climate change in the region, a single large PA with wide geographical and elevational extents would need to be established instead of several smaller PAs. The results further showed that instead of using a single-taxon and charismatic or umbrella species approach for conservation areas delineation, it would be more prudent to adopt a multi-taxon approach for defining areas of high conservation significance. Lastly, the results indicated the need to establish 3 additional new PAs in the study region. Thus, it is both necessary
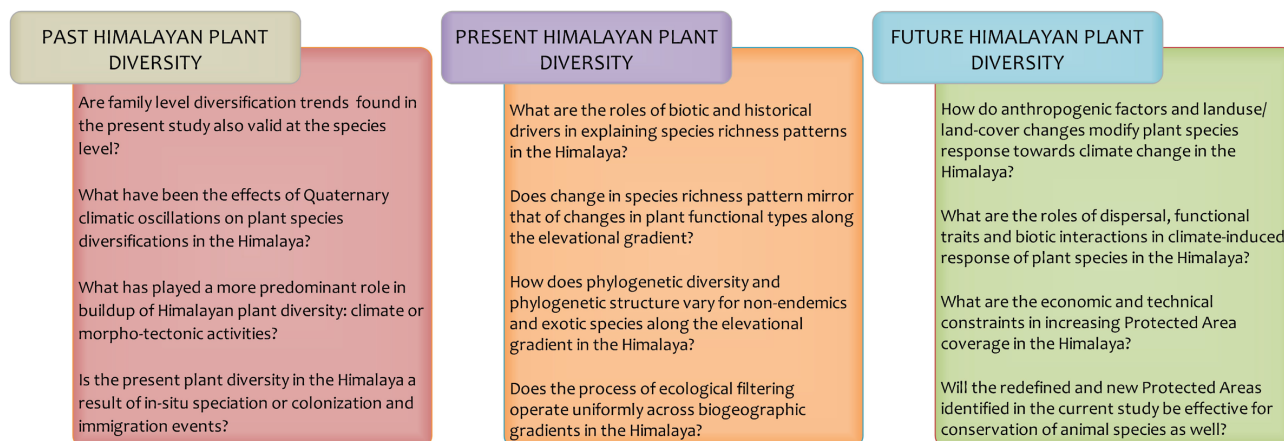
PAST HIMALAYAN PLANT DIVERSITY

Are family level diversification trends found in the present study also valid at the species level?

What have been the effects of Quaternary climatic oscillations on plant species diversifications in the Himalaya?

What has played a more predominant role in buildup of Himalayan plant diversity: climate or morpho-tectonic activities?

Is the present plant diversity in the Himalaya a result of in-situ speciation or colonization and immigration events?

PRESENT HIMALAYAN PLANT DIVERSITY

What are the roles of biotic and historical drivers in explaining species richness patterns in the Himalaya?

Does change in species richness pattern mirror that of changes in plant functional types along the elevational gradient?

How does phylogenetic diversity and phylogenetic structure vary for non-endemics and exotic species along the elevational gradient in the Himalaya?

Does the process of ecological filtering operate uniformly across biogeographic gradients in the Himalaya?

FUTURE HIMALAYAN PLANT DIVERSITY

How do anthropogenic factors and landuse/land-cover changes modify plant species response towards climate change in the Himalaya?

What are the roles of dispersal, functional traits and biotic interactions in climate-induced response of plant species in the Himalaya?

What are the economic and technical constraints in increasing Protected Area coverage in the Himalaya?

Will the redefined and new Protected Areas identified in the current study be effective for conservation of animal species as well?

Figure 7. Major gaps in the present study that need to be investigated in future studies on plant species diversity and evolution in the Himalaya.

to redesign existing PA boundaries and establish new PAs for effective conservation of plant species in future climate conditions in the Himalaya.

Conclusion

Overall, plant species have undergone rapid diversifications in the Himalaya due to continuous change in its geo-morphology and climate both at the species and assemblages level. Plant endemism is limited to the higher elevations (3500–4500 m) at present, but it is likely that the biogeographic patterns will change in the future with endemics being replaced by generalists and non-native species. A plethora of questions still needs to be answered to improve understanding of the evolution and likely fate of the hundreds and thousands of Himalayan plant species due to ensuing climate change in the region (see Fig. 7). Some of these specific questions are: (i) What role has Pleistocene glaciation and interglacial cycles played in the evolution of flora in the Himalaya? (ii) Has genome size and ploidy level played any role in the evolution of Himalayan flora? (iii) Why are non-native and invasive species predominantly limited to the Himalayan lowlands? (iv) Will non-native and invasive species dominate the future Himalayan landforms? (vii) Do changes in species physiology mirror changes in species distribution due to climate change in the Himalaya?

Acknowledgements

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