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Original Article

Origin and diversification of endemic seed plants in Central (Nepal) and Eastern (Bhutan) Himalaya

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ABSTRACT

Mountains are rich in endemic species diversity due to various factors, including steep elevational and climatic gradients and high habitat heterogeneity. While the causal factors behind high species endemism have been well worked out with respect to habitat characteristics and climate, the evolutionary mechanisms have received little attention. In this study, we attempt to decipher the evolutionary patterns of diversification of endemic plants in Nepal (Central Himalaya) and Bhutan (Eastern Himalaya) using species-presence records, phylogenetic supertrees, and ancestral area reconstruction methods. We found that the Nepal Himalaya was richer than Bhutan Himalaya with respect to endemic plant species. Maximum diversification of endemic plants in Nepal Himalaya occurred 35-20 million years ago (Mya), and in Bhutan Himalaya, it occurred during 55-45 Mya. Ancestral area reconstructions revealed that the maximum number of endemics in both Nepal and Bhutan Himalaya have diversified from taxa that migrated from Southeast Asiatic Malaysian and Southeast Chinese regions. We conclude that the plant species endemism in the Himalaya is closely linked with the phase-wise gradual uplift of mountains, long-term climate variation, species migration and floristic composition of the neighboring landscapes.

Introduction

The Himalaya spanning seven countries (Afghanistan, Pakistan, India, China, Nepal, Bhutan and Myanmar) comprise one of the youngest and highest mountain chains in the world (Grierson and Long 1983, 1991; Kluge et al. 2017; Pandit 2017; Nowak et al. 2020). A total of 10,000 plant species are found in this mountain system, of which nearly 4000 are endemics (Manish and Pandit 2018). Despite this high plant diversity and endemism, it needs to be studied more about the causal factors behind the development of such high biodiversity and endemism (Manish et al. 2021). Given the fact that the development of the Himalaya started ~55 ± 10 million years ago (Mya), the high biodiversity and endemism in the region become more intriguing (Royden et al. 2008). Many authors have attributed the development of high biodiversity and endemism in the Himalaya to morpho-tectonic events (Pandit 2017; Ding et al. 2020), while others have argued for the changes in climate and other abiotic factors such as soil, landforms, etc. as the major drivers for species diversification and radiations (Hoorn et al. 2013; Wen et al. 2014; Favre et al. 2015). Still, others argue for biotic mechanisms, such as changes in morphological and physiological traits, evolution of niches, biotic adaptations, etc. as greater contributors to species diversification and radiations (Wen et al. 2014; Ebersbach et al. 2018). Studies that attempt to link all of these factors together are therefore needed to explore the interconnectedness of the buildup of mountain systems and the development of biodiversity in the Himalaya.

There have been many reports that have attributed high plant endemism in both Nepal and Bhutan to a multitude of factors, including high habitat heterogeneity, isolated habitats, steep productivity, and environmental gradients, high precipitation, etc. (Vetaas and Grytnes, 2002; Kluge et al. 2017; Tiwari et al. 2019). Very few studies have attempted to look for evolutionary clues to explain high endemism in the region (Khan et al. 2019; Rana et al. 2021). However, most such studies have been limited to focusing on just a single taxon or being localized to a geographical extent. In this study, we have attempted to overcome these limitations by analyzing the evolutionary history of 312 endemic plant species of Nepal and Bhutan using the family-level phylogenetic supertrees

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and ancestral area reconstruction trees as per the broad protocols outlined in Manish et al. (2021). We have attempted to analyze the diversification patterns and diversification rates and reconstruct ancestral distribution areas of endemic plant species in the Nepal and Bhutan Himalaya in different geological time periods. Particularly, we sought answers to the following specific questions in this study: (i) What were the major time periods and patterns of endemic species diversifications in Nepal and Bhutan Himalaya? (ii) What were the ancestral source areas from where the initial colonizing plant species migrated to Nepal and Bhutan Himalaya?

Material and methods

Study area

This study included Eastern Himalaya (Bhutan) and Central Himalaya (Nepal). Bhutan is situated in the Eastern Himalaya, spanning from latitudes 26° 45' N to 28° 10' N and longitudes 88°45' E to 92°10' E (Figure 1). Its length is approximately 340 km, covering an area of around 40,077 square kilometers (sq. km). The country shares borders with the Tibetan plateau of China in the north, the Indian States of Sikkim in the west, West Bengal and Assam in the south, and Arunachal Pradesh in the east. The topography is predominantly rugged and mountainous (Figure 1). The regions above 4200 m constitute 20.5% of the total land (MoA 1997) and are characterized by perpetual snow and ice, forming glaciers and glacial lakes. The climate exhibits significant variation based on altitude. Bhutan lies on the southern face of the eastern part of the Great Himalayan range. It is divided broadly into three physiographic zones, viz., Southern Foothills, Lesser Himalaya, and Higher Himalaya. One conspicuous feature of the Bhutan Himalayas is their abrupt rise in altitude from south to north in comparison to the other parts of the Himalayas.

Nepal, a landlocked country nestled in the Himalayan foothills, spans from 26°20' to 30°10' north latitude and 80°15' to 88°19' east longitude (Figure 1). It shares borders with the Tibetan region of China in the north and India in the east, south, and west. Nepal is approximately 128 kilometers wide, 880 kilometers long, and covers a total land area of 1,47,516 sq. km. Positioned uniquely in the central Himalayas, Nepal features diverse phytogeographical provinces with a range of vegetation types, from tropical lowland rainforests characterized by *Shorea robusta*, to temperate oak and conifer forests in the mid-hills and dwarf scrubs of rhododendron and alpine meadows in higher elevations. The country's flora integrates various elements, including Western and Central Asiatic, Sino-Japanese, Southeast Asiatic, African-Indian desert, and typical Indian floristic elements (Welk 2016), reflecting a rich biodiversity. Additionally, Nepal occupies a transitional zone in the central Himalayas, serving as a botanical bridge between the eastern and western Himalayan floras (Shrestha and Joshi 1996).

Species records

We used published records, including national, local, and regional floras, checklists, and national and international databases to collate species-presence records of endemic plant species in the Nepal and Bhutan Himalaya. For this study, we defined "endemic species" as one that had its geographical distribution limited to the international political boundaries of the two nations (Nepal and Bhutan). All the published records were searched for two major attributes with respect to the species information: (i) Extent of geographical distribution of the species, (ii) Family to which the species belonged. The synonyms of species were checked using the WFO Plant List database (https://wfoplantlist.org/plant-list) and such species (synonyms) were excluded from further analysis.

Analysis of diversification time and diversification rates and ancestral area reconstructions (AAR)

For analyzing the patterns of diversification times and diversification rates across different geological time periods and the ancestral area reconstructions of the plant endemic plant species of

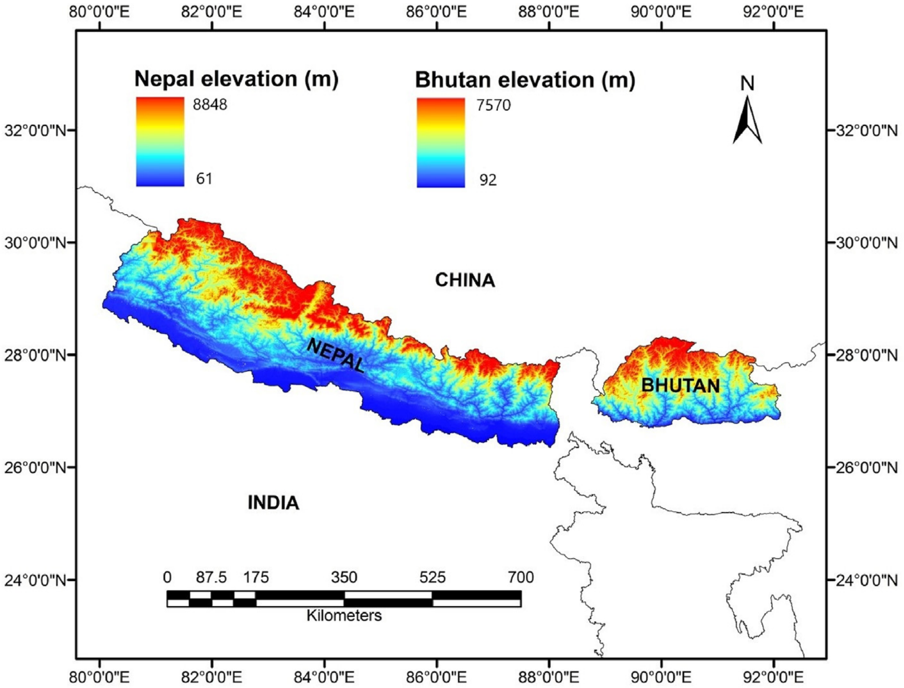

Figure 1. Origin and diversification of endemic seed plants in Central Himalaya, Nepal, and Eastern Bhutan. The map represents the elevational profile and geographical extent of both the study areas.

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Nepal and Bhutan, we used the broad protocols of Manish et al. (2021) with some modifications. Basically, we used the protocol of Manish et al. (2021) for the following: (i) Preparation of family-level phylogenetic supertrees for endemic plant species of Nepal and Bhutan, (ii) classification of diversification times and diversification rates in discrete geological time period bands, (iii) formula for calculating the percentage family diversification (PFD), diversification rates (DR), and percentage node instance (PNI) values, (iv) determining ancestral distribution areas of the congeneric species for the endemic plant species of Nepal and Bhutan to be used as an input in ancestral area reconstructions (AAR) analyses.

To determine the patterns of diversification times and diversification rates, we prepared family-level phylogenetic supertrees for endemic plant species of Nepal and Bhutan using the Phylomatic tool in Phylocom 4.2 software (Webb et al. 2008) with the Angiosperm Phylogeny Group IV seed plant tree (R20160415.new) of Gastauer et al. (2017) as a base. The resulting family-level phylogenetic supertrees were then calibrated using the branch length adjustment algorithm (BLADJ) utilizing the angiosperm-dated tree of Bell et al. (2010) in Phylocom to produce a pseudo-chronogram that gave diversification times of families in Mya. The diversification time of families thus obtained were grouped and classified into 4 discrete geological time period bands pertaining to different stages of the formation of the Himalaya according to Favre et al. (2015): (i) 55-45 Mya (period of India-Eurasia collision and start of the formation of the Himalaya); (ii) 45-35 Mya (period of early uplift of the Himalaya); (iii) 35-20 Mya (period of the onset of the modern-day South West Indian monsoon system); (iv) 20-10 Mya (period of aridification of Central Asia and further uplift of the Himalaya). In the next step, percentage family diversification (PFD) and diversification rates (DR) for each of the 4 geological time period bands using the formula proposed by Manish et al. (2021).

$$PFD = \left(\frac{At}{A_T}\right) \times 100$$

where PFD stands for percentage family diversification; at represents the number of plant families that diversify over a given period of time; and A_T stands for the total number of plant families found in Nepal and Bhutan.

$$DR = \left(\frac{PFD}{T}\right)$$

where T is the duration in millions of years, DR is the diversification rate, and PFD is the percentage family diversification.

AAR analyses for endemic plant species of Nepal and Bhutan were performed using the Bayesian Binary Markov Chain Monte Carlo (BBM) method with default settings in RASP 3.2 software (Yu et al. 2015). For this purpose, genera level phylogenetic supertrees and ancestral distribution areas for different taxa were used as inputs in AAR analyses in RASP software. Genera level phylogenetic supertrees were prepared for Nepal and Bhutan plant endemics using the same Phylomatic tool and BLADJ algorithm in Phylocom software (as described in the previous paragraph). As ancestral distribution areas cannot be obtained for endemic species (since they have originated and evolved within the region only), we sourced the ancestral distribution areas of the congeneric species from Manish et al. (2021) and used it as an input in AAR analyses. The BBM analyses returned the most likely ancestral states (MLS) for every genus of Bhutan and Nepal plant endemics. These MLS occurrences were further used for calculating percentage node instance (PNI) values using the formula proposed by Manish et al. (2021). The PNI values were used for interpreting the most likely biogeographic source areas for both Bhutan and Nepal plant endemics in the study area.

These MLS occurrences were further used for calculating percentage node instance (PNI) values as follows:

$$PNI = \left(\frac{Na}{Nb}\right) \times 100$$

where PNI is the node instance percentage; Na is the number of times a distribution area becomes an MLS, and Nb is the total number of times all distribution areas become MLS.

The PNI values were used for deducing the most likely biogeographic source areas for both Bhutan and Nepal plant endemics in the study area.

Results

Species richness and diversification

The floristic database we compiled revealed that the endemic plant species in Nepal and Bhutan belonged to 46 and 37 families, respectively. The most speciose families (families with the largest number of species) in Nepal were Apiaceae (28), Asteraceae (22), Fabaceae (21), Saxifragaceae (21) and Papaveraceae (20). In Bhutan, Orobanchaceae (25), Orchidaceae (17), Rosaceae (12), Poaceae (7), Primulaceae (7), and Saxifragaceae (7) were the most speciose families.

Our analyses of diversification times and diversification rates of plant endemics revealed that the maximum percentage of family diversifications in Nepal (PFD = 33%) occurred during 35-20 Mya, i.e. geological time corresponding to the onset of the monsoon system (Figure 2a; Figure S1). The family diversification rates were also the highest (DR = 2.20) during this 35-20 Mya (Figure 2b; Figure S1). There was a 65% increase in percentage family diversifications and a 10% increase in diversification rates in Nepal endemics during the 35-20 Mya time period (Figure 2a, b). Interestingly, during 20-10 Mya (period of further uplift of the Himalaya and Central Asia aridification), no family diversifications and diversification rates were observed in Nepal (Figure 2a, b). In Bhutan, the maximum percentage of family diversifications and diversification rates were observed during 55-45 Mya, i.e. the time of collision and start of the formation of the Himalaya (Figure 2a, b; Figure S2). The number of family diversifications decreased with time in Bhutan, with the least number of family diversifications observed during 20-10 Mya (Figure 2a; Figure S2).

Ancestral area reconstructions

Our AAR analyses revealed that both in Nepal and Bhutan, the majority of the endemics owe their origin to taxa that migrated from SE Asiatic Malaysian and SE Chinese regions (Figure 3a, b; Figures S3, S4). In Nepal and Bhutan, SE Asiatic Malaysian and SE Chinese regions together emerged as ancestral biogeographic states in 63% and 74% of ancestral state distributions, respectively (Figure 3a, b; Figures S3, S4). After SE Asiatic Malaysian and SE Chinese regions, Sino-Japanese region emerged as the most likely ancestral biogeographic source region of plant endemics in Nepal and Bhutan, by occurring in 53% and 70% of ancestral state distributions, respectively (Figure 3a, b; Figures S3, S4).

Discussion

The Himalayan region represents a substantial portion of global climate diversity, offering a unique opportunity to compare the history of species accumulation across various climates within a

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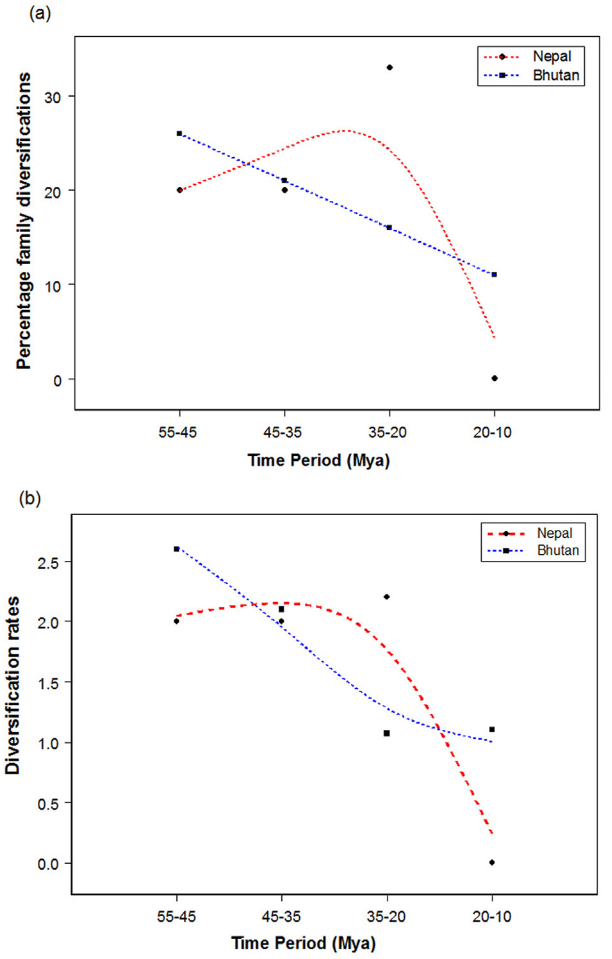

Figure 2. Diversification patterns of endemic plants in Nepal and Bhutan during the major geological time periods corresponding to the different stages of the formation of the Himalaya. Diversification patterns were analyzed for different time periods in terms of: (a) percentage family diversifications, and (b) diversification rates (the lines in the plots are fitted using the spline smoothing function).

geographically cohesive area. Higher elevations in this region, which straddles the freezing barrier, are snowbound, whereas the lowlands in the subtropical east receive around three times as much precipitation as those in the northwest (Bookhagen and Burbank 2010; Rana et al. 2019). There is a noticeable zonation in plant richness even though plants from warm, wet areas in the eastern low elevations may travel rather easily to both the low elevations in the northwest and the high elevations in the east. This suggests that climatic controls, rather than geographical barriers, play a crucial role in the establishment of plants.

The results of the present study suggest that maximum diversifications and diversification rates of endemic plants occurred during 35-20 Mya in the Nepal Himalaya. Literature suggests that 35-30 Mya was the time period when the Southwest monsoon system, similar to that of the present-day monsoon system in the Indian subcontinent in terms of seasonality and intensity, originated in the Himalaya (Clift and Webb 2019). Nepal Himalaya being a part of Central Himalaya is much drier and possesses more seasonal variation than the Eastern Himalaya (Singh and Singh 1987). Thus, it can be assumed that the maximum endemic species started diversifying in the Nepal Himalaya when the monsoon system intensified. Monsoons have been reported to govern the processes of landform diversification and the formation of deep ridges and valleys in the Himalayan region, and the deep ridges and valleys could have easily formed pockets of isolated habitats and thereby served as regions of species diversification in the Himalaya (Bookhagen and Burbank 2010). The greater diversity of flora in the central Himalaya (Nepal) is also attributed to the mixing of drier Western and Central Asiatic floral provinces and African Indian desert elements toward the western part of Nepal (Welk 2016). It has been reported that the Himalaya achieved the main period of uplift (5.5 km) during the early and middle Miocene by 15 Mya (Ding et al. 2017), which resulted in intensified monsoon and warming temperatures in northern India. It is further highlighted that warming temperatures at the thermal maximum facilitated the dispersal of evergreen to semi-evergreen mega-thermal and lower montane rainforest elements from Myanmar westward along the Himalayan foothills. This is supported by the abundant leaf and wood fossils and palynomorphs in the Siwalik sediments of northern India (Khan et al. 2016; More et al. 2016; Ding et al. 2017).

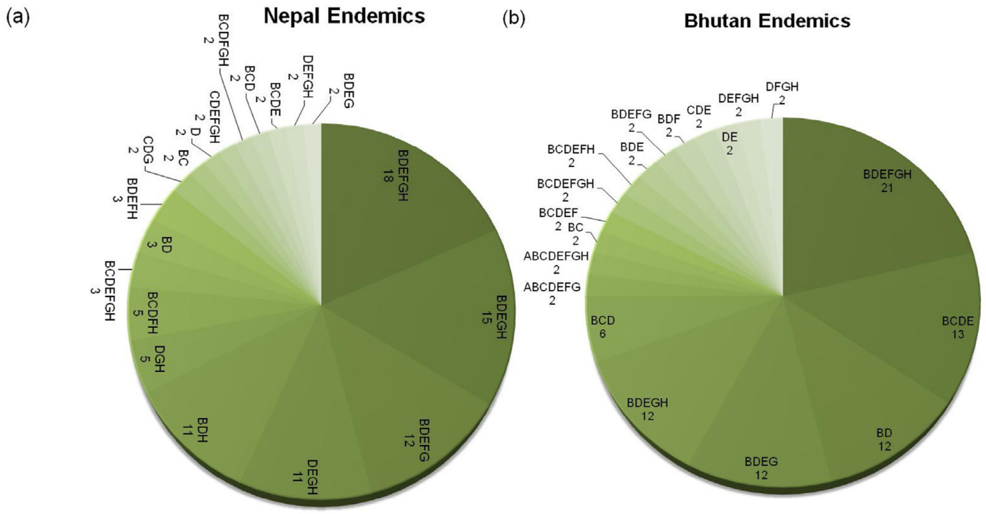

Figure 3. Ancestral area reconstruction analyses (AAR) for: (a) Nepal plant endemics, and (b) Bhutan plant endemics. Ancestral biogeographic source areas are coded as follows in both the subfigures: A-Tropical; B-Southeast Asiatic Malaysian; C-Indian; D-SE Chinese; E-Sino-Japanese; F-Irano-Turanian; G-Centrasiatic; H-Holarctic. The numbers below the alphabetical notations (ancestral biogeographic source areas) in both the subfigures represent the percentage node instances (PNI) values.

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For Bhutan Himalaya, our results indicated that the maximum diversifications and diversification rates were during 55-45 Mya (the period of the India-Eurasia collision and the start of the formation of the Himalayan mountains). However, it must be noted that the timing of India's collision with Eurasia and the variations in this process along the Indian front have been debated for decades (Patriat and Achache 1984; Hu et al. 2016). Various models of India-Eurasia collision and the simultaneous evolution of the Himalayan Mountain system have been proposed (reviewed in Suo et al. 2022). According to the first model, the India-Eurasia collision first happened along the western Himalayan syntaxis, and then the suturing processes moved eastwards (Tapponnier et al. 1981; Rowley 1996). The second model suggests collision along the eastern Himalayan syntaxis and the evolution of the Himalayan mountain ranges from the east-west direction (Liang et al. 2013). The third model suggests that the collision occurred close to the Lhasa Terrane (Tong et al. 2019). The fourth model postulates that India collided with Eurasia in the Yarlung-Tsangpo Suture Zone, and then the evolution of the Himalaya progressed in both the eastward and westward directions (Ding et al. 2001, 2016). The fifth model suggests the simultaneous onset and evolution of the Himalaya along the entire Himalayan orogenic belt (Zhu et al. 2005). Therefore, it is difficult to pinpoint the exact direction of the evolution of the Himalayan mountain systems. While the slowdown in the Indian plate's drift around 50 million years ago is often viewed as a direct response to the initial collision (Copley et al. 2010), geological indicators such as stratigraphy, sedimentology, metamorphism, and paleomagnetism along the suture frequently yield inconsistent ages for this event (Hu et al. 2016). Literature indicates that when the landscapes in Bhutan were evolving in the Miocene, it possessed a tropical environment similar to the Southeast Malaysian region (Khan et al. 2019). This would have offered ample opportunities for the taxa to migrate from the Southeast Malaysian region into Bhutan. The India-Eurasia collision also drained out the erstwhile Tethys Sea and resulted in the formation of new landforms with many interconnected land bridges between India and Southeast Asian regions (Manish and Pandit 2018). The migrating taxa as a result of these events would have started to colonize the newly formed habitats rapidly due to very little competition and abundant food availability. This could have led to high niche differentiation and the formation of new species complexes in the region (Bhutan Himalaya).

Historical records demonstrate the critical impact that climate variations have played in plant evolution, extinction, migration, and distribution in the Himalaya (Rana et al. 2019). Significant floral and faunal turnover was notably caused by the increased cooling at the Eocene-Oligocene boundary, approximately 34 Mya, which occurred globally, including in Asia (Buerki et al. 2013; Sun et al. 2014; Pound and Salzmann 2017). Subsequently, between 8.5 and 6 Mya, a period of drying and global cooling impacted temperate regions, leading to a transition from forest to grassland in the Western Himalaya (Badgley et al. 2008). This shift notably influenced plant dispersal and speciation at higher elevations in the Himalaya and southern China (Zhao et al. 2016; Xing and Ree 2017; Deng et al. 2018).

Conversely, pollen data point to a rather stable climate, marked by year-round warmth and steady precipitation in the eastern Himalayan lowlands for the previous 15 million years (Khan et al. 2019; Rana et al. 2019). The northwest Himalaya has seen a major decline in forests during the past two million years, especially during glacial maxima. Numerous Himalayan species were compelled by this restriction to migrate eastward into more tropical and stable climate zones (Owen et al. 2002; Mehrotra et al. 2005; Vögeli et al. 2017; Srivastava et al. 2018). However, the Paleocene records of legumes suggested that these plants may have migrated to India from Africa via the Ladakh-Kohistan Arc during the latest Cretaceous to Paleocene (Bhatia et al. 2022).

Conclusion

The Central and Eastern Himalaya both exhibited a higher number of endemic flowering plants, although Central Himalaya showed a greater richness of endemic species of flowering plants than Eastern Himalaya. Our results showed that the maximum diversification of endemic flowering plants occurred earlier in the Eastern Himalaya (Bhutan: 55-45 Mya) than in the Central Himalaya (Nepal: 32-20 Mya). Also, the diversification was associated with the formation of the Himalayan mountains (India-Eurasia collision) and the origin of the monsoon system. Ancestral area reconstruction indicated that the majority of the plant species in the Central and Eastern Himalaya have diversified from taxa that migrated from the Southeast Asiatic Malaysian and Southeast Chinese regions. However, more in-depth studies focused on the impact of phase-wise gradual uplift of Himalayan mountains, long-term climate variation, migration history, and floristic composition of the adjoining landscape on plant community assemblies are required to make such a generalization.

CRediT authorship contribution statement

Achyut Tiwari: Writing – review & editing, Writing – original draft, Supervision, Resources, Investigation, Conceptualization. **Basu Dev Paudel:** Writing – review & editing, Methodology, Data curation. **Kumar Manish:** Writing – review & editing, Visualization, Supervision, Software, Resources, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that there is not any conflict of interest with this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.japb.2024.11.010.

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