PLANT DIVERSITY GRADIENTS ALONG THE HIMALAYA: A COMPARISON BETWEEN THE EAST AND THE WEST

Thesis submitted to the

Saurashtra University, Rajkot (Gujarat)

for the award of the Degree of

DOCTOR OF PHILOSOPHY
IN
WILDLIFE SCIENCE

By

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January 2018

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CERTIFICATE

This is to certify that the thesis by Mr. Suresh Kumar entitled "Plant diversity gradients along the Himalaya: A comparison between the east and the west" is an original and independent research work submitted to the Saurashtra University, Rajkot (Gujarat), for the award of the degree of Doctor of Philosophy in Wildlife Science.

Mr. Suresh Kumar has put in more than six terms of research work embodied in this thesis under our guidance and supervision. The work presented in this thesis has not been submitted for any degree of any other University or Institution.

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The research work was appreciated by all who were present and the comments made by the faculty and researchers are included in the thesis.

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Executive summary

Patterns and causes of latitudinal and elevational diversity gradients have gained increasing attention in the field of macroecology. A monotonic decline in species richness from low to high latitudes and elevations was widely accepted as the common pattern for a long time. However, reviews of the available literature on patterns of species diversity along elevational gradients show that species richness often does not monotonically decline with elevation. Global reviews of species richness along elevational gradients in many taxa report three generally dominant patterns, i.e. decreasing richness with increasing elevation, a plateau in richness across low elevations, and a unimodal pattern with a mid-elevation peak. Like many other taxa plants also show highest species richness in the tropics and the richness decreases with increasing latitude. Along elevational gradients mid-elevational peaks are regularly described, and richness peaks of herbs are at higher elevations than those for woody plants. In this thesis, I analyse the elevational and latitudinal patterns of plant species richness across the Himalaya.

Two methods, i.e. "*range interpolation*", and "*field sampling*" have been used for studying the plant diversity gradients. Both methods are prone to the risk of deviation from actual patterns of diversity. Interpolation of species ranges is associated with under-sampling at the edges which results in an accumulation of species towards the centre. On the other hand, field sampling results in the estimation of only a small fraction of the total richness and raises the question of how to ascertain true richness at a location. Therefore, while studying elevational diversity gradients, a robust approach based on a combination of methods need to be applied to overcome potential sampling biases. Given the different issues associated with each method, concordant results would provide supporting evidence that the patterns are real.

Possible causes of the latitudinal and elevational diversity gradients suggested in literature, can be grouped into four categories, i.e. (i) *Climatic Hypothesis*; based on the impact of current abiotic conditions on species richness, (ii) *Spatial Hypothesis*; based on impact of spatial extent and spatial constraints on the species richness, (iii) *Historical Hypothesis*; based on processes occurring across evolutionary time scales and their impact on species richness, and (iv) *Biotic Hypothesis*; involving ecological interactions among species e.g. ecotone effects, source-sink dynamics and habitat heterogeneity. Given the

difficulties associated with testing these multiple hypotheses, the debate on the causes of diversity gradients remains an outstanding question.

The Himalaya is the highest and largest mountain system on earth. The unique biogeographic location of Himalaya at the confluence of four biogeographic regions, *viz.* the Palearctic, Saharo-Arabian, Sino-Japanese and Oriental, provides a wide range of ecosystems, habitats and dispersal corridors for the colonisation of a multitude of floral assemblages. A pattern of mid-elevational peaks in plant species diversity along the elevational gradient has been reported based on limited sampling in various parts of this mountain range. However, a comprehensive account of the Himalayan flora covering patterns of plant species richness and factors influencing these patterns has not been presented so far. I carried out this study with the goal of understanding the biogeographic, phylogenetic and climatic determinants of latitudinal and elevational diversity gradients of Himalayan plants. The broad research objectives were as follows:

1. To evaluate phytogeographic and phylogenetic affinities of the Himalayan flora.
2. To assess the patterns of plant species richness along elevational and latitudinal gradients of the Himalaya, based on an exhaustive literature survey.
3. To determine tree richness patterns in the Himalaya based on field research as well as the literature survey, and examine reasons for the pattern.

I examined the available 31 published floras across different regions of the Himalaya, including Nepal, Bhutan and Indian Himalayan states to evaluate all reported seed plant species. After updating the taxonomic inconsistencies, I found a total of 10,503 species of seed plants recorded in Himalayan floras, including 7,149 native non-endemic species, 2,148 endemic species and 1,206 alien species. The seed plants of Himalaya include; 1,382 trees, 1,542 shrubs, 6,350 herbs, 573 woody climbers, 285 herbaceous climbers and 371 epiphytes. For the present analysis I excluded trans-Himalayan region since it covers the areas beyond the elevational gradients and also small parts of Himalaya in Pakistan and China for which floras were unavailable. More discoveries of plant species remain to be made from Himalaya. For example, from Arunachal Pradesh in the easternmost region of Himalaya, comparatively fewer species are reported than adjacent Bhutan & Sikkim (Arunachal Pradesh: 4503 sps. *vs* Bhutan & Sikkim: 6284 sps.). Given that geographical area of

Arunachal Pradesh is two times larger than Bhutan region this discrepancy in species richness may be a result under-exploration in Arunachal Pradesh.

Along the latitudinal gradient from east to northwest Himalaya, seed plants together show a threefold decline in species whereas trees show a fivefold decline in species. Along the elevational gradient, the eastern Himalayan regions show a mid-elevation peak both in all seed plants as well as trees, whereas the northwest Himalaya shows a low-elevation plateau. Species richness across Himalaya shows a highly positive correlation with annual precipitation and negative correlation with the annual temperature range. CCA shows that different life forms are influenced differently by climatic variable, e.g. epiphytes are highly influenced by precipitation and isothermality whereas trees are affected by temperature and shrubs by seasonality.

I compared elevational ranges of all species recorded in the Himalayan floras. Species richness peak at approximately 1000m asl across the whole Himalaya. However, 1,461 species are not recorded at the lowest elevations in these floras but are known to be present in the north Indian plains. On extending the ranges of these species, the 1000m peak remains but is much less pronounced. Native species account for the 1000m peak, and the aliens (both cultivated and naturalised) show a monotonic decline with elevation. The elevational richness of native species shared with surrounding regions of Himalaya shows a monotonic decline for species ascending from the plains of north India (as it must), similar peak at 1000m for species shared with Yunnan and Myanmar, and a peak at 3000m for species shared with Tibetan plateau.

Native species of Himalaya have either colonised or evolved during a long geological period whereas alien species have colonised recently. Concordance of biogeographic and climatic affinities of natives and aliens for elevational and latitudinal distribution will implicate the importance of climatic controls in establishment. Thus, I compared the richness patterns of aliens and natives in the east and northwest Himalaya. Species with different climatic affinities, i.e. tropical and temperate, show similar elevational patterns in both the groups. Highest number of natives are shared with Africa and Australia whereas highest number of aliens are from north and south America. In spite of their different sources of origin, both natives and aliens show consistent patterns, i.e. species shared with tropical continents show a monotonic decline of species with elevation, whereas those shared with

Europe show peak at 2,000-3,000m. Nestedness values are much higher in aliens as compared to natives along the elevational gradients. This implies that alien species present at high elevations tend to be a subset of those found at low elevations indicating a strong role of directional ecological filtering in alien species establishment across Himalaya.

Phylogenetic beta diversity turnover between plant assemblages across Himalaya yielded six distinct floristic regions showing both latitudinal and elevational transitions in plant communities. Species with tropical affinities dominate in the eastern Himalaya whereas cosmopolitan species dominate in the northwest. Temperate species are distributed equally across the whole Himalayan range, pointing out the similarity in the climatic conditions of high elevations across Himalaya. Phylogenetic evaluation of Himalayan flora based on the family and species level phylogenies shows that filtering of clades has played a strong role in shaping the latitudinal diversity gradient from east to northwest Himalaya. In comparison to the null models of the whole Himalayan species pool plant communities of eastern Himalaya are phylogenetically ~~clustered~~ overdispersed possibly due to a ~~few~~ dominant tropical clades, and ~~over-dispersed~~ clustered in the northwest. However, along the elevational gradient, phylogenetic clustering in plant communities is very weak.

Detailed analysis of the distribution of tree species across the Himalaya shows that eastern Himalaya harbours five times higher species than northwest. Beta diversity of tree species shows two turnover zones along the latitudinal gradient from east to northwest Himalaya. Highest beta diversity is seen between Eastern Nepal and Central Nepal followed by Uttarakhand and Himachal Pradesh. Thus the beta diversity measures divide the Himalayan region into three distinct floristic regions, i.e. eastern, central and western Himalaya. Latitudinal distribution of trees shows that most of the species in the northwest Himalaya are also present in the eastern Himalaya. A total of 90 species are distributed across all eight sub-regions which constitute ~57% of species in Jammu & Kashmir in the northwest but only ~12% species of Arunachal Pradesh in the easternmost region of the Himalaya. However, considering Arunachal Pradesh as data deficient, 117 species are distributed from Bhutan & Sikkim to Jammu & Kashmir which shows even higher sharing of species between east and northwest Himalaya. Elevational range sizes show an increasing trend from the tropical regions of east to temperate regions of northwest Himalaya. In particular, in Jammu & Kashmir range size is much larger in low-elevations than the range size of species in Arunachal Pradesh at the same elevations. Along elevational gradients, the range size increases with elevation.

Comparison of elevational richness patterns of trees obtained by two sampling methods, i.e. "*range interpolation*" and "*field sampling*" along two elevational gradients one each in the east and northwest Himalaya shows consistent patterns suggesting least influence of biases associated with the different methods. North Bengal and Sikkim in the eastern Himalaya show a peak in tree species richness at 500-1000m whereas Jammu & Kashmir in northwest Himalaya shows a low-elevation plateau in richness with increasing elevation. Both tree density and girth size are not consistently associated with species richness along the elevational gradient in the east or northwest Himalaya. However, girth sizes tend to be larger at the mid-elevations both in the east and northwest Himalaya. These results support a general body of research that relatively cold temperature and moderately high precipitation at mid-elevations may lead to fast growth and slow decomposition, thus larger girth sizes.

More detailed analysis of richness pattern along the elevational gradient of North Bengal and Sikkim in eastern Himalaya revealed that tree species richness peaks at 500-1000m is not consistent with other metrics like diversity, abundance, density etc. During field sampling, I encountered a total of 269 tree species (34% of those in the local floras) with the highest number of species at 500m (106 species). Further, species rarefaction curves imply that the 500m elevation is the least well sampled as compared to other elevation zones. I compared the species richness pattern with diversity indices along the elevational gradient confirming that this is the position of highest richness. Fisher's alpha index which is least influenced by evenness shows a consistent pattern with species richness whereas the Shannon and inverse Simpson indices which are influenced by species evenness shows the highest diversity is at foothills which is reduced highly at 1000-1500m, even as richness is high at this elevation. This is because at 1000m three tree species comprise >40% of all individuals and at 1500m three tree species comprise >50% of all individuals. In contrast at 200m and 500m, the highest abundance of top five species ranges only between 5-9%.

Species turnover, as measured by beta diversity, was highest between 1500m and 2000m along the elevational gradient. The number of species encountered is very similar at these two elevations in the field data (54 and 49 respectively), implying a significant turnover in composition. These results suggest the 1500-2000m belt is a critical transition zone between sub-tropical and Himalayan temperate vegetation in the east, which marks the elevation at which freezing regularly occurs. Annual mean temperature and annual precipitation values extracted from worlclim data at 1000 random points along the elevational gradient for this region shows a linear decline in both variables. Similarly, actual evapotranspiration also shows a linear decline along the elevational gradient. Given the fact that the tropical-temperate transition zone is higher than the species richness peak itself and values for climatic variables decline linearly with elevation, neither mixing of floras nor climate alone seem able to account for the peak.

In order to explain the peaks in species diversity, I propose a simplistic model based on dispersal coupled with climate. Climatic conditions along foothills and adjacent plains are assumed similar and become monotonically harsher with increasing elevation. I assume climate sets both the number and identity of species. At the foothills therefore, dispersal of species from plains will not introduce new forms but at the elevations adjacent to foothills, species can receive new forms from both below as well as higher up. Thus, a two-way dispersal at the elevations adjacent to foothills maintains higher species richness as compared to foothills. However, beyond these elevations tree species richness is dominated by the linear decrease set by climate.

The thesis is organized into five chapters.

Chapter 1. This chapter is an introduction to the study. I present a broad review of the literature, rationale behind this study, study system and general methods. The first part of this Chapter focus on a review of species richness pattern across gradients at the global level and I then summarise all studies describing elevational richness patterns of plants in Himalaya. In the second part, I highlight the rationale behind this study and then briefly describe the study system and general methods employed for the thesis. The remaining four chapters address an independent research question and follow a general structure including an introduction to the research question, detailed analytical methods, results and discussion on the results.

Chapter 2. This chapter addresses species richness patterns, biogeographic affinities and climatic control on the assembly of native and alien floras of Himalaya based on a thorough literature survey. I compare latitudinal and elevational richness patterns of the native plants of Himalaya who have been assembled during the long geological history of Himalaya with the more recently introduced alien species. I evaluate the relation of major climatic variables with species richness and elevational nestedness to test the role of local climate and biotic interaction in the process of plant community assembly across Himalaya.

Chapter 3. In this chapter, I test the role of tropical niche conservatism theory in shaping the latitudinal and elevational diversity gradients of seed plants across Himalaya. I used a family level and a species level phylogeny to test for various phylogenetic affinities of Himalayan flora. I evaluated phylogenetic clustering of plant communities within different regions of Himalaya. Phylogenetic beta diversity was calculated among the plant assemblages to identify phylogenetically distinct floristic regions across the Himalayan latitudinal and elevational gradient.

Chapter 4. Trees are the most studied group and have better information in the secondary literature. Therefore, in this chapter, I scaled down my analysis to the distribution patterns of only tree species across the Himalaya. I describe the latitudinal and elevational richness patterns and test various ecological metrics like beta diversity, nestedness, distribution ranges etc. to evaluate the historical process of species dispersal from east to northwest Himalaya. I further compare the results obtained from two methods, i.e. "*range interpolation*" and "*field sampling*" along two elevational gradients to understand the richness pattern of trees in the east and northwest Himalaya.

Chapter 5. In this chapter, I conducted a detailed analysis to understand the position and causes of the mid-elevation peak in tree species richness along a single elevational gradient in North Bengal & Sikkim in eastern Himalaya. I compare species richness with various other ecological metrics like diversity indices, beta diversity, species abundance distributions to understand the intricacies of community assembly along the elevational gradient. I further evaluate the patterns of climatic variables along the same elevational gradient. Finally, I propose a dispersal model based on the source-sink dynamics coupled with climate which predicts a similar low-elevation peak in trees as has been recorded in this study.

CHAPTER 1

Introduction

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Introduction

1.1 Background

Species richness patterns along latitudinal and elevational gradients is one of the popular fields of research in macroecology. A monotonic decline in species richness from low to high latitudes and elevations was widely accepted as the prevalent pattern for a long time (Stevens, 1989, 1992). However, reviews of available literature on the patterns of species diversity along the elevational gradients show that species richness may not be necessarily monotonic (Rahbek, 1995, 2005; Grytnes & McCain, 2013). A recent global review on elevational biodiversity gradients shows a unimodal pattern with mid-elevation peaks in 63% of studies (Guo *et al.,* 2013). Early evidence of mid-elevational peaks in species richness is present in the vegetation community assemblage studies of Santa Catalina and Siskiyou Mountains in the US, which showed both monotonically decreasing species richness with increasing elevation and a humped pattern with maximum species richness at intermediate elevations (Whittaker, 1960; Whittaker & Niering, 1965). However, for a long time, most studies on broad-scale species diversity patterns focused on latitudinal gradients, and elevational gradients were considered to mirror latitudinal patterns (Stevens, 1989, 1992). Mid-elevational peaks were first brought into focus in a global review on elevational biodiversity patterns by Rahbek (1995).

McCain (2005, 2007a, 2009, 2010) performed a series of global meta-analyses of elevational species richness patterns among taxonomic groups. A unimodal richness pattern with the highest richness at intermediate elevations was evident for non-flying small mammals, i.e. rodents, shrews and marsupials (McCain, 2005) whereas two global patterns were equally common in bats, decreasing species richness with increasing elevation and unimodal richness peak (McCain, 2007a). Birds show more variation in their elevational richness patterns: 30% gradients consist of monotonic declines, 43% have high diversity across most of the lower part of the gradient and then decrease, and 27% have unimodal richness (McCain, 2009). More than half of the elevational gradients for reptiles show a decline in species richness with increasing elevation, 25% have a low plateau, and 21% have a unimodal richness pattern (McCain, 2010).

A global analysis of elevational species richness patterns on ferns by Kessler *et al.* (2011) shows that 35% studies found hump-shaped curves with maximum richness somewhere between the gradient extremes, 20% found monotonic decline, 25% monotonic increases and 20% showed no change in species richness with elevation. Although global analyses of angiosperm species richness along elevational gradients are not available, mid-elevational peaks are regularly described, and diversity peaks of herbs are at higher elevations than those for woody plants (Guo *et al.*, 2013). Thus, the evident global trend of species richness along elevational gradients follows four main patterns, i.e. decreasing richness with increasing elevation, plateaus in richness across low elevations, a low-elevation plateau with a mid-peak and a unimodal pattern with a mid-elevation peak (McCain & Grytnes, 2010). However, sampling procedures are often unclear since most of the analyses are based on interpolating ranges from secondary sources, and various artefacts have not been properly controlled for many of these studies.

Two methods have been used for studying the elevational diversity gradients. First, ranges are interpolated between highest and lowest records for a species from secondary literature sources "*range interpolation*", and a species is assumed present everywhere between its highest and lowest record (Grytnes & Vetaas, 2002; Bhattarai *et al.,* 2004; Bhattarai & Vetaas, 2006; Grau *et al.,* 2007). Second, selected quadrats or transacts are used to collect field samples along the elevational gradient "*field sampling*" (Carpenter, 2005; Acharya *et al.*, 2011). Both methods are prone to the risk of deviation from actual patterns of diversity. Interpolation of elevational ranges has the major problem that under-sampling results in an underestimation of the species range, with a consequent accumulation of species at mid-elevations (Grytnes & Vetaas, 2002). Interpolation also creates the possibility that ranges are overestimated, particularly for charismatic species where a single individual beyond the normal range limit is noted (Price *et al.*, 2014). The alternative approach that of field samples circumvents these problems, but results in only a small fraction of the total richness being recorded, and raises the question of how to ascertain true richness at a location (Gotelli & Colwell, 2001; Slik *et al.*, 2015). Limited comprehensive field-based studies are available because of the difficulty of gathering such data for numerous species along geographical or ecological gradients. Therefore, while studying elevational diversity gradients, a robust approach based on a combination of methods need to be applied to overcome potential sampling biases. Given the different issues associated with each method, concordant results would provide supporting evidence that the patterns are real.

Assuming mid-elevation peaks are real, Grtynes & McCain (2013) summarised their possible causes into four categories: climatic hypotheses based on current conditions, hypotheses of the area and spatial constraint, historical hypotheses invoking processes occurring across evolutionary time scales, and biotic hypotheses involving ecotone effects, source-sink dynamics and habitat heterogeneity. The climatic hypothesis suggests that tolerance of climatic factors such as temperature, precipitation and primary productivity may put restrictions on species occurring at different elevations. Grytnes & McCain (2013) proposed that rainfall often follows a more complex relationship with altitude and maximum rainfall is often found at an intermediate elevation which in turn increases the productivity, resulting in more species diversity. Many studies have shown a positive relationship of species richness with precipitation, temperature and productivity, at least across biogeographical regions (Pianka, 1966; Heaney, 2001; Evans *et al.,* 2005; McCain, 2007b; Kreft & Jetz, 2007).

Species-area relationship is often suggested explaining elevational species richness patterns, predicting more species in elevational bands that cover more area (McCain, 2007b) but this has been difficult to invoke as an explanation of mid-elevation peaks. A null model, the mid-domain effect (Colwell & Hurtt, 1994; Colwell & Lee, 2000) has also been proposed to explain hump-shaped richness patterns along elevational gradients. However, in most of the studies the fits to the model are low (Dunn *et al*., 2007; Price *et al*., 2014). Many evolutionary explanations have also been offered to explain mid-elevational peaks, the most prominent among them is based on climatic niche conservatism (i.e. many species are restricted to the climate of the ancestor) and is referred to as the montane-museum hypothesis (Kozak & Wiens, 2010). Another hypothesis termed as the mass effect, suggests an accumulation of dispersing species from lower and higher elevations into mid-elevations. Since migrants can be received from two sides in the middle whereas only from one side at top and bottom, thus highest overlap of the sink populations occurs at mid-elevations (Lomolino, 2001; Grytnes & Vetaas, 2002; Grytnes, 2003; Grytnes *et al.,* 2008). Relationships between diversity pattern and underlying phylogenetic history of species have been assessed for understanding elevational diversity gradients (Wiens *et al.,* 2007).

The Himalayan region exhibits one of the steepest bioclimatic gradients in the world ranging from tropical to high alpine and nival zones. Such a sharp gradient within a short distance, coupled with unique biogeographic location, geo-diversity and topographic variation is associated with an exceptionally rich biodiversity. Hence, this region has been identified as a global biodiversity hotspot (Myers *et al.*, 2000). Located at the confluence of four zoogeographic regions, *viz.* the Palearctic, Saharo-Arabian, Sino-Japanese and Oriental (Holt *et al.*, 2012), Himalaya provides a wide range of ecosystems, habitats and dispersal corridors for the colonisation of a multitude of floral assemblages. Vascular plants in the Himalaya are distributed along an elevational gradient of *ca* 60m to 6400m above sea level (Molnar, 1986; Grytnes & Veetas, 2002). A prominent pattern of mid-elevational peaks in plant species diversity along the elevational gradient has been reported in various parts of the mountain range (Vetaas & Grytnes, 2002; Oommen & Shanker, 2005; Khuroo *et al.*, 2011). Published estimates of taxonomic diversity in the Indian Himalayan region include about 8000 species of angiosperms, 44 species of gymnosperms, 600 species of pteridophytes, 1,737 species of bryophytes, 1,159 species of lichens and 6,900 species of fungi (Singh & Hajra, 1997).

Many local and regional studies have assessed the patterns of species richness along elevational gradients in different mountain systems of the world including Himalaya. Various studies conducted in Himalaya on the elevational diversity patterns of plants is presented in the table (Table 1.1). Summary of these studies shows that in the case of the Himalaya, unimodal diversity peaks are prevalent, contrary to the global scenario of different kinds of diversity gradients being common. Guo *et al.* (2013) observed that mountains presenting greater elevational extent were more likely to display unimodal patterns. Except a few studies based on field sampling, most of the studies in Himalaya have interpolated the species ranges from secondary sources for reporting the elevational diversity patterns thus are subjected to range interpolation bias (Grytnes & Vetaas, 2002). Thus a careful review of the methods employed in these studies and the reported patterns across Himalaya is crucial to understand the plant diversity patterns of the Himalaya.

Table 1.1 Studies on species richness along elevational gradients in Himalaya.

Life forms and gradient	**Method**	**Location**	**Richness pattern**	**Authors**
Plants (100-6000m)	Range interpolation	Nepal	Unimodal peak at 1500-2500m	Grytnes & Vetaas, 2002
Plants (250-4250m)	Range interpolation	Nepal	Unimodal peak at 1000m	Carpenter, 2005
Plants (100-5000m)	Range interpolation	Nepal	Unimodal peak at 1500-2500m	Veetas & Grytnes, 2002
Plants 100-5000m	Range interpolation	Bhutan	Unimodal peak at 2000m	Kluge *et al.*, 2017
Plants 300-5300m	Range interpolation	Sikkim	Unimodal peak at 1800m	Manish *et al.*, 2017
Plants (100-1500m)	Field sampling	Nepal	Unimodal peak at 700m	Bhattarai & Vetaas, 2003
Trees (200-2200m)	Field sampling	Arunachal Pradesh	Unimodal peak at 600-1000m	Behera & Kushwaha 2007
Trees (300-4700m)	Field sampling	Sikkim	Unimodal peak at 1500m	Acharya *et al.*, 2011
Trees (100-4300m)	Range interpolation	Nepal	Unimodal peak at 1000m	Bhattarai & Vetaas, 2006
Woody flora (100-5000)	Range interpolation Field sampling (interpolated)	West Himalaya Uttarakhand	Unimodal peak at 1500-2000m Unimodal peak at 2000m	Oommen & Shanker, 2005
Woody flora (500-4800m)	Range interpolation	Kashmir	Unimodal peak at 2000m	Khuroo *et al.*, 2011
Orchids (100-5200m)	Range interpolation	Sikkim	Unimodal peak at 1500m	Acharya *et al.*, 2011
Ferns (100-4800m)	Range interpolation	Nepal	Unimodal peak at 2000m	Bhattarai *et al.*, 2004
Bryophytes Ferns (100-5500m)	Range interpolation	Nepal	Unimodal peak at 2700m Unimodal peak at 2000m	Grau *et al.*, 2007

In addition to the altitudinal gradient, Himalaya also provides a sharp gradient of moisture with decreasing precipitation from southeast to northwest. This gradient has been interpreted as a primary driving factor for the decrease in avian diversity from southeast to northwest Himalaya (Price *et al.,* 2011; Ghosh-Harihar & Price, 2014; White, 2016). However, studies on understanding similar gradients of plants along Himalaya have not been conducted so far. One reason to study plants is that it is possible that birds are responding to their underlying resource base provided by plants. In this way, floral species diversity may drive faunal diversity in general. Himalaya thus provides an excellent natural setting for testing models on the mid-elevation peaks by comparing the patterns obtained from interpolated ranges with the actual systematic sampling along the complete elevational gradient, and by asking how patterns change from southeast to northwest (Ghosh-Harihar & Price, 2014). In this study, I employed range interpolation method, and combined this with a detailed sampling along the elevational gradients in Himalaya.

1.2 Study rationale

My review of the literature found two primary methods for understanding the diversity gradients, i.e. *range interpolation* and *field sampling* (Table 1.1). Both methods have associated biases which may result in spurious patterns in diversity gradients. Geographical scales of studies also varies ranging from a part to complete gradient or even global reviews based on literature . In this study, I compiled a complete flora of Himalayan mountain range from the available published floras for the region to understand the patterns of plants diversity, ranging from the local scale to complete Himalayan scale. To ask how the flora has been assembled, I evaluated the biogeographic affinities of each plant species. Taking into consideration the biases in diversity gradient studies, I employed both methods, i.e. range interpolation from published literature and sampling of trees along the elevational gradient to compare the patterns. Two climatically contrasting elevational gradients, i.e. wetter and more tropical in the southeast Himalaya and drier and more temperate in the northwest Himalaya were focused for comparison of the methods of studying diversity gradients. The broad research objectives for the study were as under:

a) To evaluate biogeographic and phylogenetic affinities of the Himalayan flora.
b) To assess the patterns of plant species richness along elevational and latitudinal gradients of the Himalaya, based on an exhaustive literature survey.
c) To determine tree richness patterns in the Himalaya based on field research as well as the literature survey, and examine reasons for the pattern.

1.3 Study system

I divided the Himalayan mountain range into six administrative units to compile all seed plants (Gymnosperms and Angiosperms) within these sub-regions, because published floras often spanned one of these regions. These sub-regions (from southeast to northwest) are Arunachal Pradesh, Bhutan & Sikkim, Nepal, Uttarakhand, Himachal Pradesh and Jammu & Kashmir excluding trans-Himalaya (Fig. 1.1). All the published floras within these sub-regions were consulted to enlist a complete checklist of plants, with their lowest and highest elevational ranges. I conducted field surveys of trees along two elevational gradients (~100-4000m in east and ~300-3500m in west) in eastern and western Himalaya. Eastern Himalaya includes study sites in Chapramari Wildlife Sanctuary and Neora Valley National Park in Northern West Bengal, and Khangchendzonga National Park in Sikkim, whereas western Himalayan sites include Ramnagar Wildlife Sanctuary, Udhampur, Batote and Kishtwar Forest Divisions in Jammu & Kashmir.

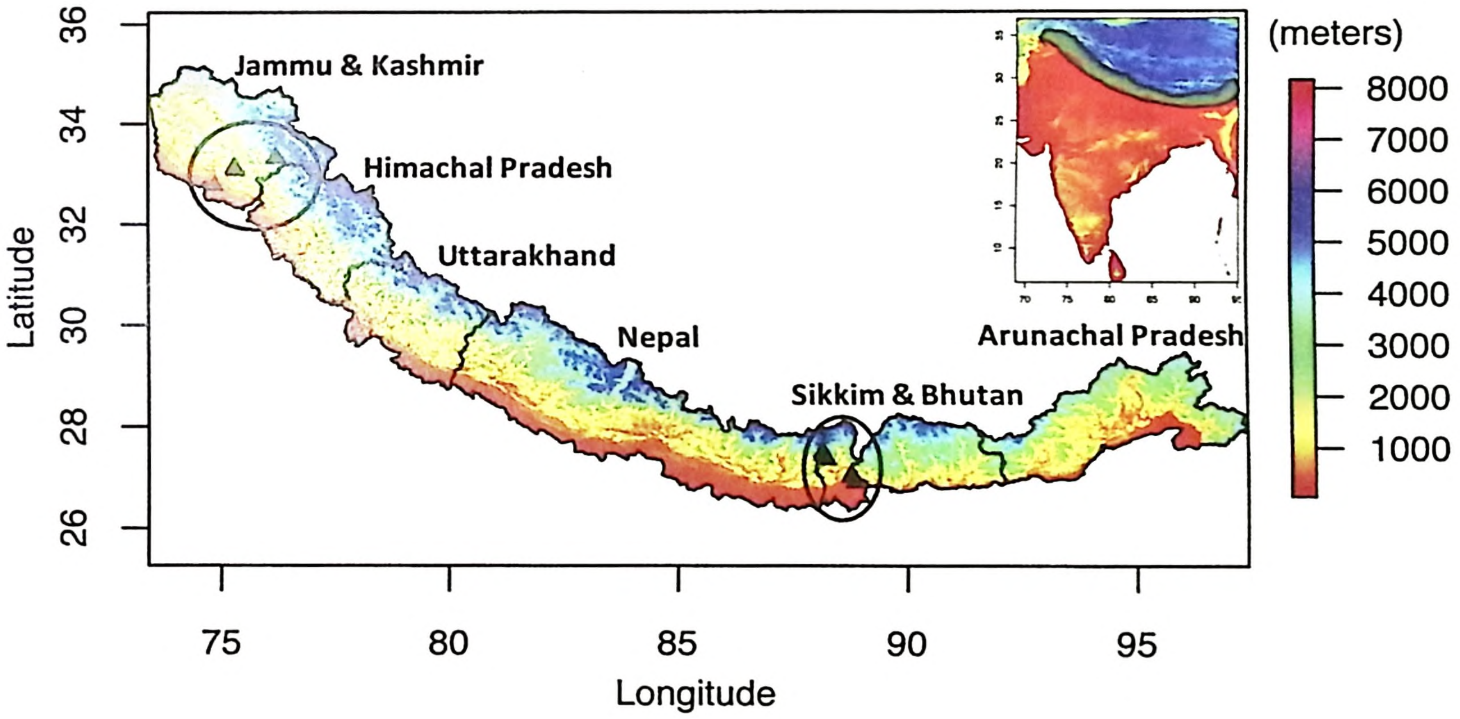

Figure 1.1 Digital elevation model of Himalayan range divided into six sub-regions (excluding trans-Himalaya and small regions in Pakistan and China). The triangles denote sites for field sampling of trees located in east and northwest Himalaya.

1.4 General methods

1.4.1 Data source

A total of 31 floras published in 42 volumes and nine parts available for six sub-regions within Himalaya (Fig. 1.1) were examined to enlist all reported seed plant species

(Rana & Rawat, 2017). All botanical names reported in floras were updated for taxonomic uniformity with currently accepted names as available in the global working list of plants species at www.theplantlist.com and names considered as synonyms were catalogued in a separate column as synonyms of the accepted species (>3000 synonyms). Information on life forms, distribution range and elevational range of plant species was also compiled for each of the six geographical regions. Biogeographic affinities and global distributional ranges of all species were catalogued from published literature and available global online plant databases. Based on their distributions all species were classified into three distribution categories, i.e. endemic, native and non-native.

Trees were sampled during a period of 18 months between April 2014 to December 2016 along two elevational gradients at same elevations at every 500m in eastern and northwestern Himalaya. Locations of field sampling are given in study area (Fig. 1.1). Sampling was conducted based on species accumulation curves in multiple quadrats of size 0.1ha at every elevation zone. Additional sampling of four big grids of size 5ha each was conducted at foothills and 2000m both in eastern and northwestern Himalaya.

1.4.2 Data Analysis

I calculated the number of plant species in every 100m band along the elevation gradients in six geographic sub-regions using R (R Core team, 2016). I used subsets of species with different biogeographic affinities, life forms and distribution ranges to understand their distribution patterns within the Himalaya. For analysis of field sampling data, "vegan" (Oksanen *et al.*, 2016) and "sads" (Prado *et al.*, 2015) packages in R were used to calculate diversity indices, beta diversity, species rarefaction curves, species nestedness and species abundance distributions along the elevational gradients. Bioclimatic variables from worldclim data (Hijmans *et al.*, 2005) were interpolated for the Himalayan region using the "raster" (Hijmans, 2016) and "sp" (Pebesma & Bivand, 2005; Bivand *et al.*, 2013) packages in R for evaluating the relationship of plants with climate. For phylogenetic analysis of Himalayan plants, I used R packages "ape" (Paradis *et al.*, 2004), and "picante" (Kembel *et* al., 2010). Detailed data analysis methods for different chapters are written in the methods part of respective chapter.

CHAPTER 2

Biogeographic affinities and diversity patterns of the Himalayan flora

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2.1 Introduction

The mountainous regions in the tropical and sub-tropical latitudes contain higher species diversity when compared to the tropical lowlands (Orme *et al.*, 2005; Jenkins *et al.*, 2013). This may be attributed to ease of access from a large tropical species pool, the creation of species as a result of many barriers within a mountain chain, and a great diversity of climatic conditions that allow species accumulation at different positions along the elevational gradient (Graham *et al.*, 2014). Mountain chains are also barriers that separate geographical regions, resulting in the development of distinctive biotas more or less in isolation (Holt *et al.*, 2013) and colonisation from these regions can also augment local species richness. Whether or not species have formed as result of barriers within the mountain chain or immigrated from elsewhere, the build-up of local species richness depends both on access to the locality and persistence there.

Holt *et al.* (2013) identified 11 zoogeographic realms across the world based on the distinctiveness of the fauna each realm contains. Four of these meet in the Himalayan region, and potentially species from each, as well as other more distant regions, contribute to assembly of the native Himalayan flora. This process has taken millions of years (e.g., Xing & Ree, 2017). This historical assembly of native species has been augmented by recently introduced species in Himalaya as a result of human-mediated exchange (Khuroo *et al.*, 2012). These introductions of alien species have mainly occurred over the last few centuries (Sax *et al.*, 2007; Hulme *et al.*, 2009; van Kleunen *et al.*, 2015; Seebens *et al.*, 2017). Not only have dispersal barriers been broken, but disturbance of local communities facilitates establishment and persistence of introduced species. Globally about two-thirds of 880 invasive plants (alien species causing economic or environmental harm) reviewed by Turbelin *et al.* (2017) have been deliberately introduced for agriculture or horticulture, implying initial conditions for establishment often involved removal of biotic enemies (competitors, pests, etc.). Introduced species often augment local species richness (Sax, 2001; Pyšek & Richardson, 2006), but still alien species are restricted to selected locations. Aliens with broad climatic tolerances have been reported to be more successful than those with narrower tolerances (Sax, 2001; Pyšek & Richardson, 2006; Alexander *et al.*, 2016). Establishment and persistence of the introduced species is more likely in localities that match climate in their native range (Sax, 2001; Feng *et al.*, 2011). While many plant introductions are accidental, I expect them to occur most often in places where many people are engaged in agriculture or horticulture, which is generally at the base of the mountains. Several studies generate support for so-called directional ecological filtering, whereby introductions are predominantly at the base, and only species with broad climatic tolerances establish at high elevations (Haider *et al.*, 2010; Alexander *et al.*, 2011; Marini *et al.*, 2013; Steyn *et al.*, 2017). This filtering process implicates that both access and local conditions are a cause of linear declines in aliens from the lowest to highest elevations.

In this Chapter, I ask how access and local conditions have contributed to the assembly of the Himalayan flora by quantifying the relationship of plant richness with climate, affinities of the flora to other regions of the world, and comparing native species to alien naturalised species, which have a colonisation history quite different from natives. Across the entire Himalaya, I compare patterns in the distribution of native species to those that have been introduced. I evaluate patterns of both natives and aliens in the context of the directional ecological filtering hypothesis, which plays a vital role for the location of introduction in driving richness patterns, and use similarities and differences between native and alien richness patterns to evaluate underlying causes of native richness distributions. If local climatic controls are important in affecting the establishment of both natives and aliens, I generate two predictions that can be used to ask how much local factors determine species richness patterns in the natives. First, natives and aliens should both occupy localities that roughly correspond to the climate of origin. Second, concordant patterns of richness in natives and aliens across the Himalaya, both geographically and across elevations, imply a direct influence of climate on species richness, given the different modes of dispersal, locations of origin, and differences in time since establishment.

2.2 Methods

2.2.1 Data source

While the Himalaya is thought to be one of the world's biodiversity hotspots (Myers *et al.*, 2000), including for plants (Kier *et al.*, 2005; Kreft & Jetz, 2007), plant richness patterns across the Himalaya remain poorly known (Kier *et al.*, 2005). Nevertheless, previous assessments of plant distributions from the literature have not made use of all available knowledge and instead relied on one or a few compilations that evaluate specific Himalayan regions, such as Nepal (e.g., Grytnes & Vetaas, 2002; Feng *et al.*, 2016), Bhutan (e.g., Kluge *et al.*, 2017) or the west Himalayan states of India (Oommen & Shanker, 2005). One known problem is that compilations based on Himalayan floras span only a small area at low elevations so that the number of species at these elevations is known to be under-reported (Grytnes & Vetaas, 2002; Feng *et al.*, 2016). This can be corrected by using floras from the plains of India. Here, I evaluate all 31 Himalayan floras available (which come in 43 volumes and nine parts in total; Appendix-1), as well as additional floras from the plains of India (Appendix-1; websites). From these, I describe both elevational and geographical richness patterns. A comparison of richness patterns across the entire Himalaya has not been previously reported, apart from those derived from a crude worldwide assessment, based on interpolation from a few census points (Kreft & Jetz, 2007).

The floras cover either individual Indian Himalayan states, Bhutan, Nepal or more local areas within these larger sub-regions. I assessed all species listed in these floras against the updated list of botanical names available from www.theplantlist.com (The Plant List, 2013). The assessment resulted in the elimination of >3,000 synonyms leaving a total of 10,503 species reported from the Himalaya (Table 2.1). According to the Plant List, of the 10,503 species, 1,134 have been insufficiently studied to resolve taxonomic conflicts and may still contain some synonyms, whereas the other 9,369 species have been evaluated. Nevertheless, I consider all 10,503 species here. Species were classified as native or alien based on the distribution records in the United States Department of Agriculture, Germplasm Resources Information Network (GRIN) (www.ars-grin.gov/npgs). Khuroo *et al.* (2007), and Bhattarai *et al.* (2014) have previously compiled data on some aliens from the Himalaya, but the USDA website gives extensive updates and modifications to these records. A subset of aliens is so-called invasive species, defined as those causing economic or environmental harm. These were identified from the Global Invasive Species database (www.iucngisd.org/gisd) and Invasive Species Compendium (www.cabi.org/isc).

Every flora was confined to one of six distinct sub-regions, i.e. Arunachal Pradesh, Bhutan, Sikkim and adjoining hill districts of West Bengal (henceforth the Bhutan region), Nepal, Uttarakhand, Himachal Pradesh, and Jammu & Kashmir (Fig. 1.1). I compiled reported elevational ranges for each region separately based on the minimum and maximum elevation reported in all floras for that specific region. In some cases, a species elevational range was not reported in one region, and then I substituted the elevational range in the adjacent region. For each species, I also recorded its minimum and maximum elevation from anywhere across the Himalaya. I cross checked all species for their presence in the Indian plains using seven online plant distribution databases (www.efloras.org, www.catalogueoflife.org, www.ars-grin.gov/npgs, www.gbif.org, www.efloraindia.nic.in, www.flora.indianbiodiversity.org, www.sites.google.com/site/efloraofindia) and modified the lowest ranges of the species from the floras accordingly. In fact, a large number (1,461) of species present in the plains of India have elevational ranges recorded in the Himalayan floras as not extending to the lowest elevation in the region (about 150m in the east and 300m in the west). I modified the lower elevational ranges of these species to match the lowest elevation in the region. An additional 1,233 species do not have either upper or lower elevational ranges recorded in the floras (1,047 natives, 186 aliens). Of these, 266 species are known to be present in the plains. For illustrative purposes, I added these to the richness values between 100m and 300m. The majority of the remaining 967 species are rare and poorly studied. I do not consider them in analyses of elevational range.

To help interpret elevational patterns I also assessed the distribution of different life forms as indicated in the Himalayan floras (i.e. trees, shrubs, herbs, woody climbers, herbaceous climbers and epiphytes).

2.2.2 Distributions and affinities

The distribution of a species across the Himalaya was based on its presence/absence within one of the six sub-regions because fine-scale distribution maps are not available. For each of the sub-region, the number of species in each 100m elevational band between 100m and 5,000m elevation was calculated as all species whose elevational range at least partly overlapped that band (I also considered 50m and 200m elevational bands, found similar results, and do not report them here). Hence, of necessity, I ignored fine scale geographical distribution: I do not present measures of local richness but rather integrated richness for each region within an elevation. Species richness across the Himalaya was smoothed from these data by using the inverse distance weight interpolation method in the R package "gstat" (Gräler *et al.*, 2016).

Each species was catalogued as present in four areas surrounding the Himalaya, i.e. Indian Plains, Myanmar, Yunnan and Tibet using the online plant distribution databases listed above. Species were classified into three biogeographic categories, i.e. tropical, temperate and cosmopolitan based on the affinities of their plant genera as categorised by Wu (1991). Accordingly, every species in a genus is assigned the same category. These data are unavailable for 525 species (<5%) which I excluded from these analyses. I also recorded the occurrences of each species on other continents (Africa, Australia, Europe, North America and South America, Hollis & Brummitt, 1992; www.ars-grin.gov/npgs).

2.2.3 Nestedness analysis

A critical test of the directional ecological filtering hypothesis is that species far from the point of introduction should be a subset of those at the point of introduction (Alexander *et al.*, 2011; Steyn *et al.*, 2017). I evaluated nestedness for natives and aliens along the elevational gradients in the Bhutan region in the east and Jammu & Kashmir in the northwest. Following Alexander *et al.* (2011) I used the nestedness metric based on overlap and decreasing fill (NODF) developed by Almeida-Neto *et al.* (2008), in the R package "vegan" (Oksanen *et al.*, 2016).

2.2.4 Climate data

Climate, notably actual evapotranspiration, strongly correlates with plant richness across the world (Kreft & Jetz, 2007). Therefore, I asked how well distributions of natives and aliens match various climate parameters. I obtained a digital elevation model of the Himalayan region (Fig. 1.1) from the global Shuttle Radar Topography Mission (SRTM) 90m resolution layer (http://srtm.csi.cgiar.org/, Jarvis *et al.*, 2008). I resampled the DEM of Himalayan region into 1,145 grids of size 0.2×0.2 degrees each and using the elevational information of each grid, I assigned the species richness in every grid within the six sub-regions based on species ranges overlapping in the respective grid. I extracted bioclimatic variables for each of these grids from the worldclim database (www.worldclim.org/, Hijmans *et al.*, 2005), using R packages "raster" (Hijmans, 2016) and "sp" (Pebesma & Bivand, 2005; Bivand *et al.*, 2013). I confined the analysis to six most important bioclimatic variables which are least correlated. Since all other variables are correlated with these six variables thus have less explanatory power. A correlation test was conducted, and two most important bioclimatic variables were shown as maps to compare the patterns of species richness with climate. Canonical correspondence analysis (CCA) was conducted between these six bioclimatic variables and different life forms of native plants distributed across six sub-regions in Himalaya using R package "vegan" (Oksanen *et al.*, 2016). The bioclimatic variables included in the analyses are; BIO1 (Annual Mean Temperature), BIO2 (Mean Diurnal Range), BIO3 (Isothermality), BIO4 (Temperature Seasonality), BIO7 (Temperature Annual Range) and BIO12 (Annual Precipitation).

2.3 Results

2.3.1 Plant species richness in the Himalaya

A breakdown of the 10,503-recorded species into various categories is given in Table 2.1. In total, the list includes 9,297 native species and 1,206 alien species. Of these 657 species are cultivated (e.g. the cabbage and the pea; 149 natives and 508 aliens) which I excluded from most analyses. The remaining aliens I consider to be naturalised, although 323 of these are less certain than the others. Finally, 160 species names in the floras were not present in the global working list of plants, and I ignored them from analyses due to limited information on these species. Among the 9,148 native species, 2,148 (~24%) are endemic to the region under study. However, 506 of the endemic species are still taxonomically unresolved in The Plant List (2013). This is 45% of all Himalayan unresolved species and suggests the percentage of endemics may decrease after further research since many of these species could be synonyms of other native species.

Table 2.1 Distribution of Himalayan plant species classified in different categories.

Nativity	**Species**	**Life forms**	**Species**	**Habit**	**Species**
Native non-endemics	7149	Trees	1382	Native wild	9148
Native endemics	2148	Shrubs	1542	Native cultivated	149
Aliens	1206	Herbs	6350	Alien naturalised	144
		Woody Climbers	573	Invasive	231
		Herbaceous climbers	285	Alien uncertain	323
		Epiphytes	371	Alien cultivated	508
Total	**10503**		**10503**		**10503**

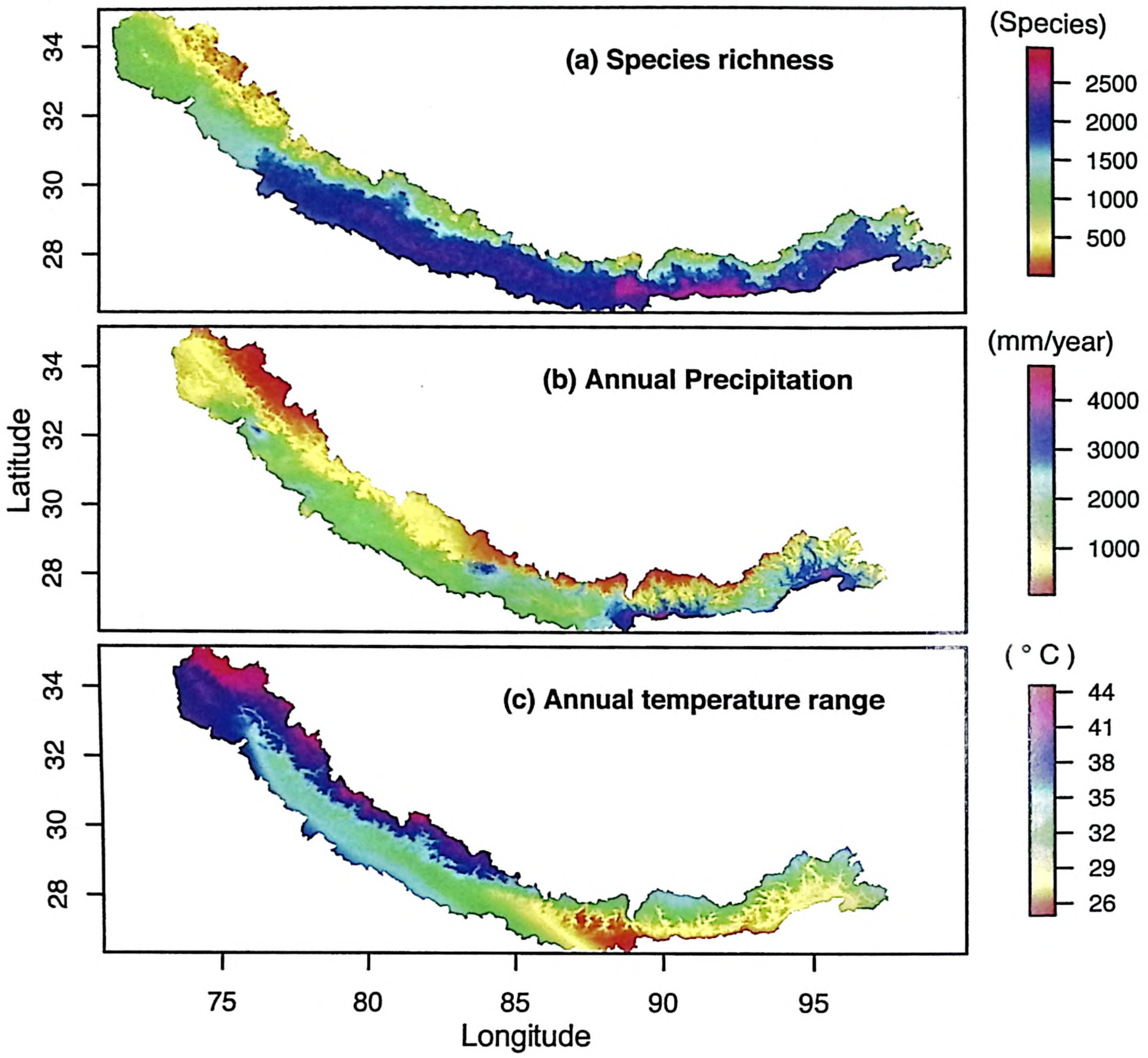

Figure 2.1 Maps of Himalayan region as studied. **(a)** Plant species richness. **(b)** Annual precipitation. **(c)** Annual temperature range. The eastern Himalaya has higher precipitation than the northwest and is less seasonal.

Plant species richness shows a threefold decline from east to northwest Himalaya (Fig. 2.1). The only exception is Arunachal Pradesh in eastern-most region of Himalaya, where comparatively fewer species are reported than adjacent and western Bhutan region (Arunachal Pradesh: 4503 sps. *vs* Bhutan region: 6284 sps.). Considering the facts that geographical area of Arunachal Pradesh is two times larger than Bhutan region and since the region is also comparatively more tropical in climate, this discrepancy in species richness may be a result of fewer species reported from the region due to under-exploration. Given the remoteness and past political disturbances in Arunachal Pradesh, comparatively fewer efforts have been made for research and exploration of the plant diversity in the region. However, another possibility for this discrepancy could be position of Arunachal Pradesh at comparatively higher latitude, but this is very unlikely since sufficient geographical area adjacent to Bhutan is available at the same latitude. Thus species richness should match in the two adjacent sub-regions.

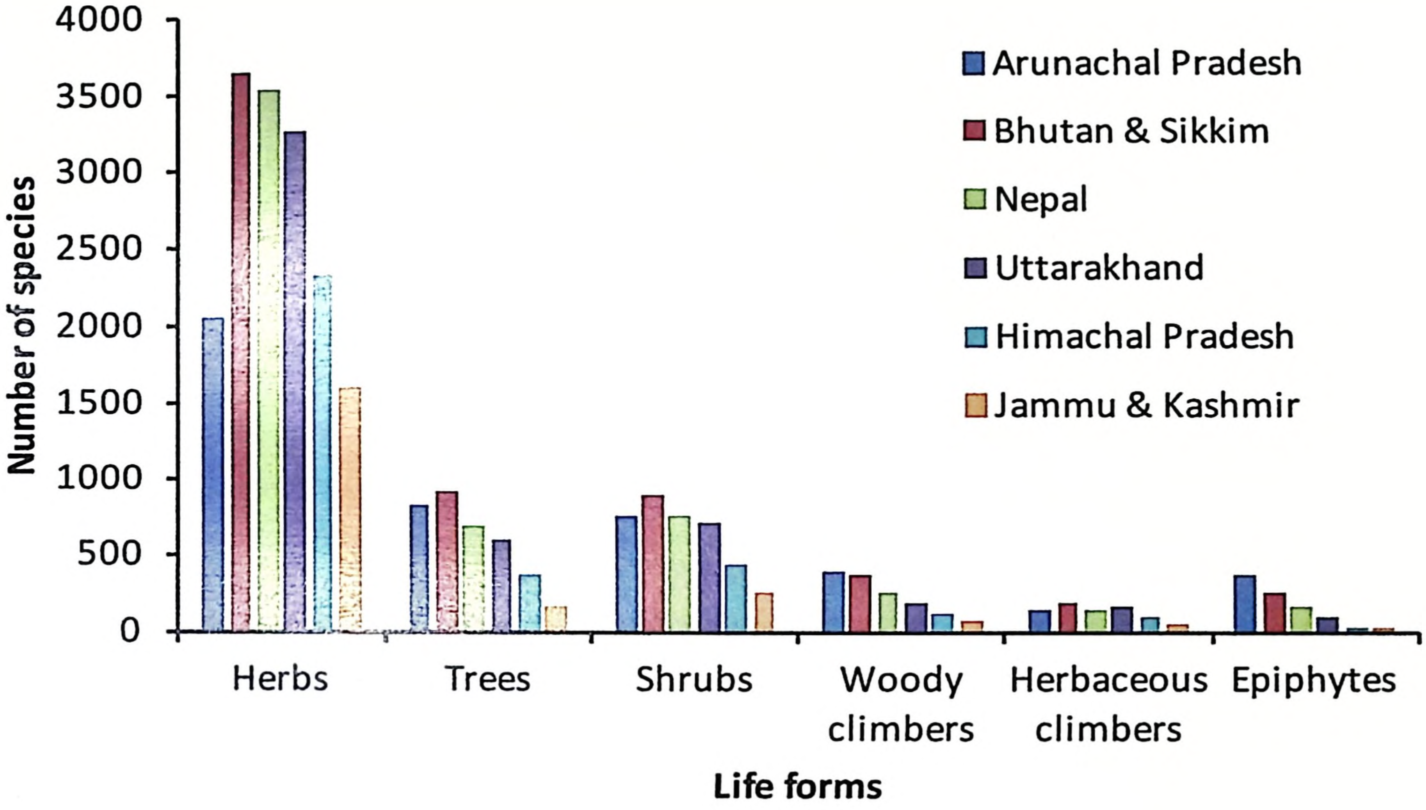

Figure 2.2 Distribution of different life forms of plants in six sub-regions of Himalaya. All life forms show a decline in species richness from east to northwest, except for Arunachal Pradesh.

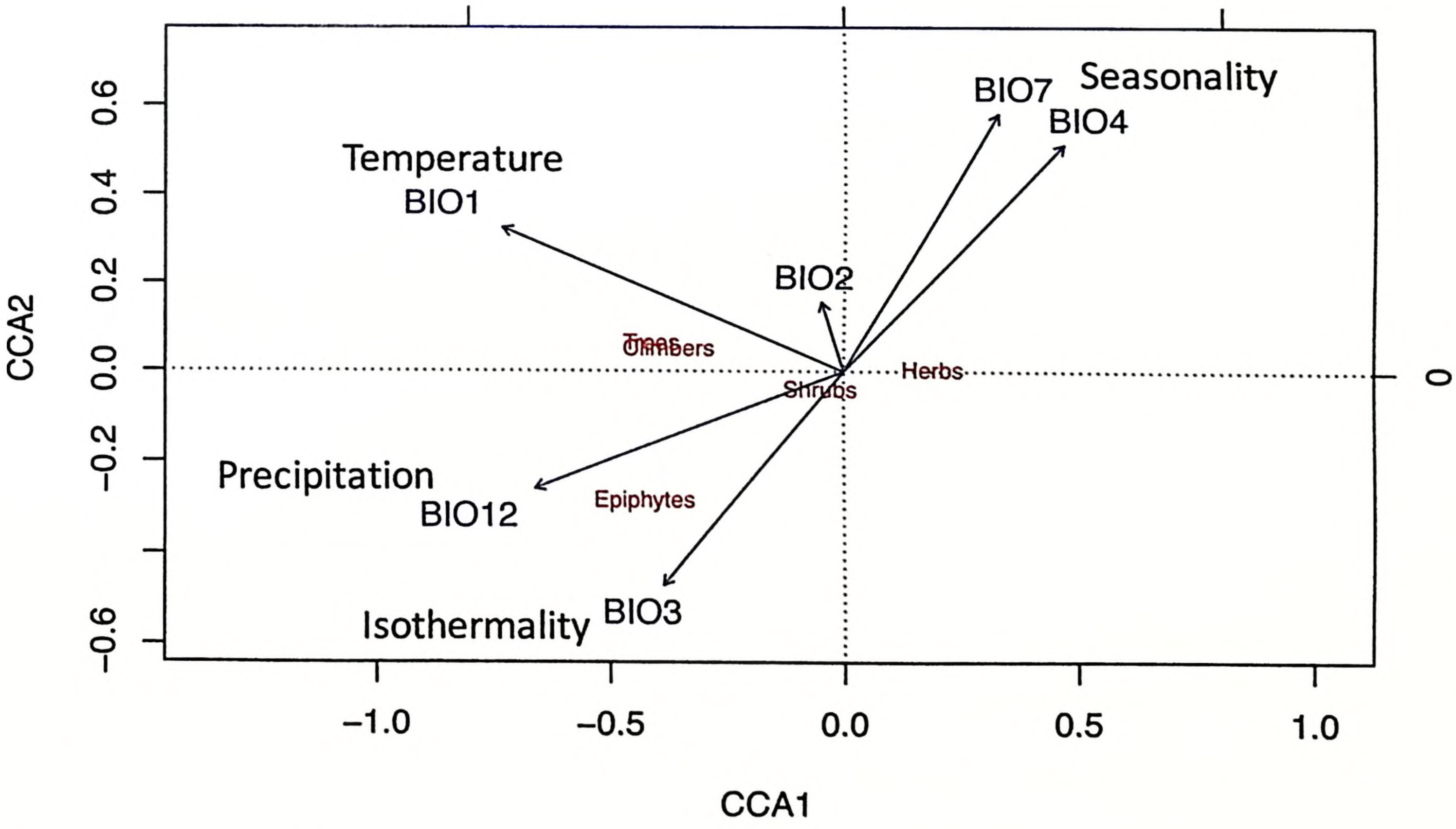

Figure 2.3 Biplot from canonical correspondence analysis (CCA) showing the relationship between life forms of plants and six crucial bioclimatic variables across Himalaya.

All life forms of seed plants in Himalaya also show a sharp decline in species number from east to northwest Himalaya (Fig. 2.2). However, the discrepancy in species richness is again present in Arunachal Pradesh. Specifically, number of herb species is very less in Arunachal Pradesh (2046 sps.) than Bhutan region (3649 sps.). In contrast, number of species reported in few well-studied life forms like epiphytes (mostly Orchids) and woody climbers is higher in Arunachal Pradesh than Bhutan. The CCA indicated a clear relationship between plant life form richness and climatic variables (Fig. 2.3). In CCA, 75% of the variation is explained by the constrained model. The first two constrained axes accounted for a variation of 6.3% and 1.4% of the fitted variation. The permutation test for CCA under reduced model with 999 permutations shows a highly significant correlation ($p < 0.001$). Epiphytes are highly influenced by precipitation and isothermality, whereas trees are influenced by temperature and shrubs are influenced by seasonality (Fig. 2.3).

2.3.2 Elevational richness patterns of aliens and natives

Considering documented elevational ranges of all seed plants in the Himalayan floras, interpolated species richness peaks at approximately 1,000m (Fig. 2.4a). When I extended lower ranges by adding the 1,461 species not recorded at the lowest elevations in the Himalayan floras but known to be present in the Indian plains the peak remains but is much less pronounced (Fig. 2.4a). All future plots in the thesis include this modification. An additional 266 species have no recorded upper elevational limit but are known to be present in the plains. I considered these to have an upper limit of 300m and this addition is shown by the filled circles in Fig. 2.4a. For aliens, the addition of these species makes a significant difference to the patterns, and I show them in other plots as well, but for natives, they form only a small fraction of the total so are not included.

In Fig. 2.4b I partition the solid line of Fig. 2.4a into endemic natives, non-endemic natives and aliens. The largest class, natives, follow the 1,000m peak, whereas aliens show a monotonic decline with elevation. Native non-endemics and most aliens extend out to one of four regions, the Indian plains, China, Myanmar, and Tibet. The richness peak at 1,000m is attributable to native endemics (Fig. 2.4b) as well as species shared with the southeast mountains of Yunnan and Myanmar (Fig. 2.4c). Note that native species present in the Indian plains must show a monotonic decline in number with increasing elevation, but that is not true for the high elevation Tibetan species. Both cultivated and naturalised alien species show a monotonic decline in richness with elevation (Fig. 2.4d).

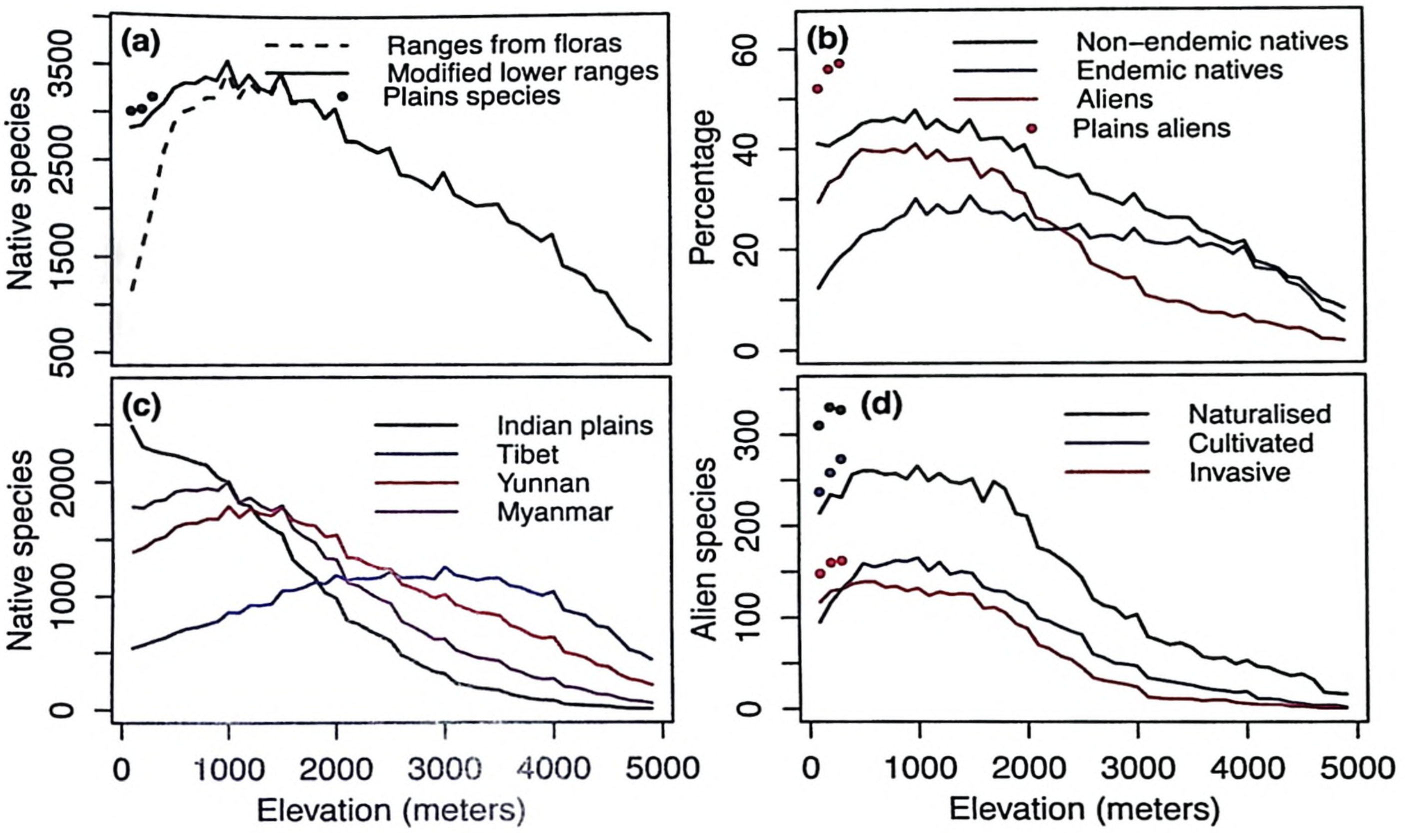

Figure 2.4 Elevational richness patterns of seed plants in the Himalaya **(a)** Total species richness **(b)** Patterns of native, endemic and naturalised aliens, expressed as a fraction of the total in each class. **(c)** Patterns of native species shared with the surrounding regions **(d)** Patterns of cultivated, naturalised and invasive alien species.

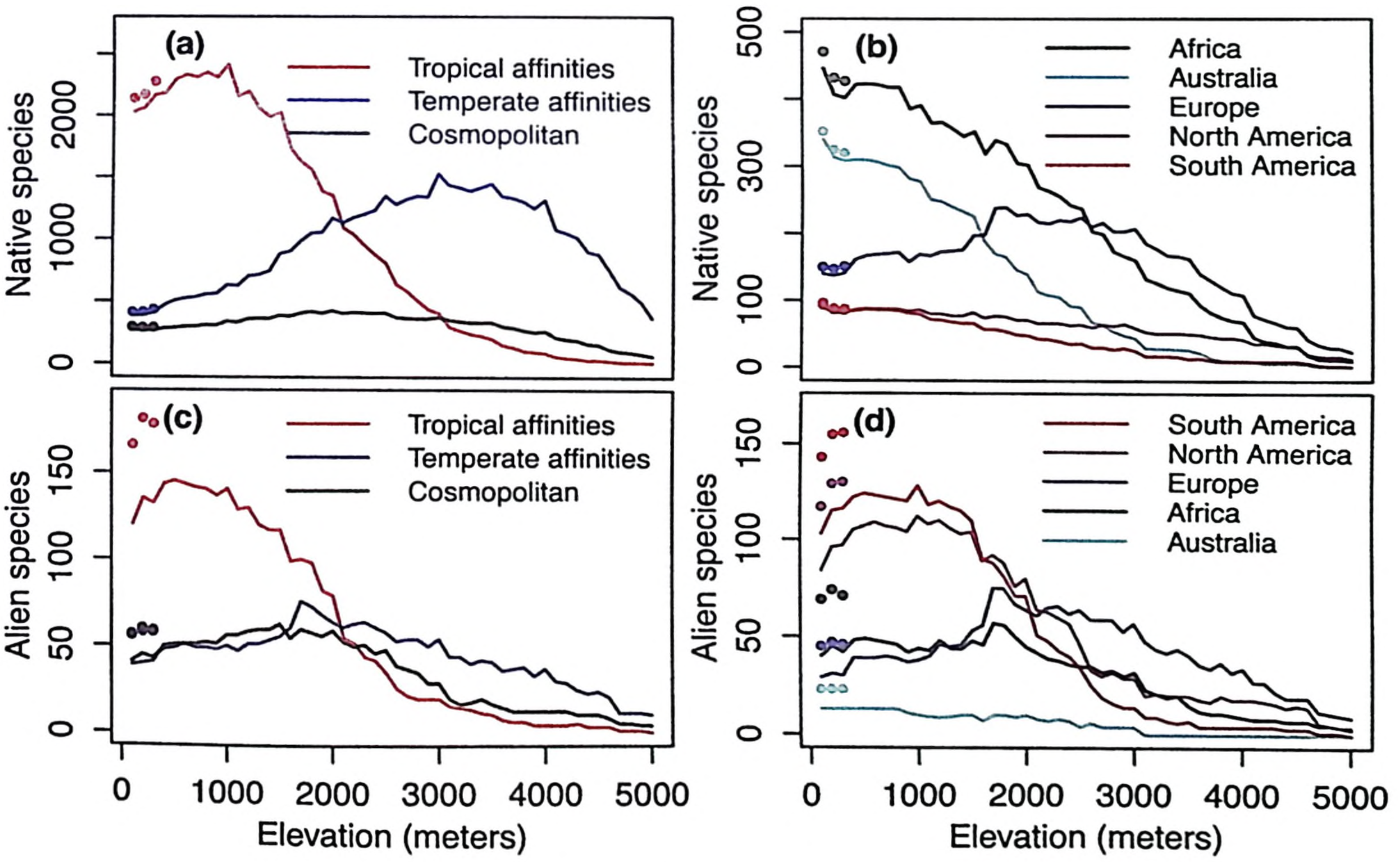

Figure 2.5 Elevational richness patterns of native and aliens plant species in Himalaya **(a)** Patterns of native species shared with other continents. **(b)** Patterns of native species with different biogeographic affinities. **(c)** Patterns of alien species shared with other continents. **(d)** Pattern of alien species with different biogeographic affinities.

In figures 2.5 and Fig 2.6, the upper row illustrates native patterns and the lower row alien patterns. The peak at 1,000m is attributable entirely to those species with tropical affinities (Fig. 2.5a), which form the majority. In contrast, the richness of naturalised aliens with tropical affinities monotonically declines with elevation (Fig. 2.5c). Native species with temperate affinities have a richness peak at 3,000m, whereas aliens with temperate affinities have their highest richness at the base, and show a decline above 2000m. The alien patterns are again consistent with introductions predominantly coming in through the lower elevations, with relatively few species extending to high elevations.

The data shows two remarkable features. First, many native species are shared with other continents (Africa, 701 species; Europe, 465; Australia, 409; North America, 167; South America, 122). Second, aliens show very different affinities from natives with contrasting patterns in number of shared species (North America, 366 species; South America, 364; Europe, 305; Africa, 252; Australia 88). The elevational richness of these groups is as expected for the climatic affinities of the continent they are shared with (Fig. 2.5b, 2.5d, compare with Fig. 2.5a, 2.5c). Both natives and aliens shared with tropical continents show a monotonic decline of richness with elevation. On the other hand species shared with Europe shows a peak in richness at 2,000-3,000m.

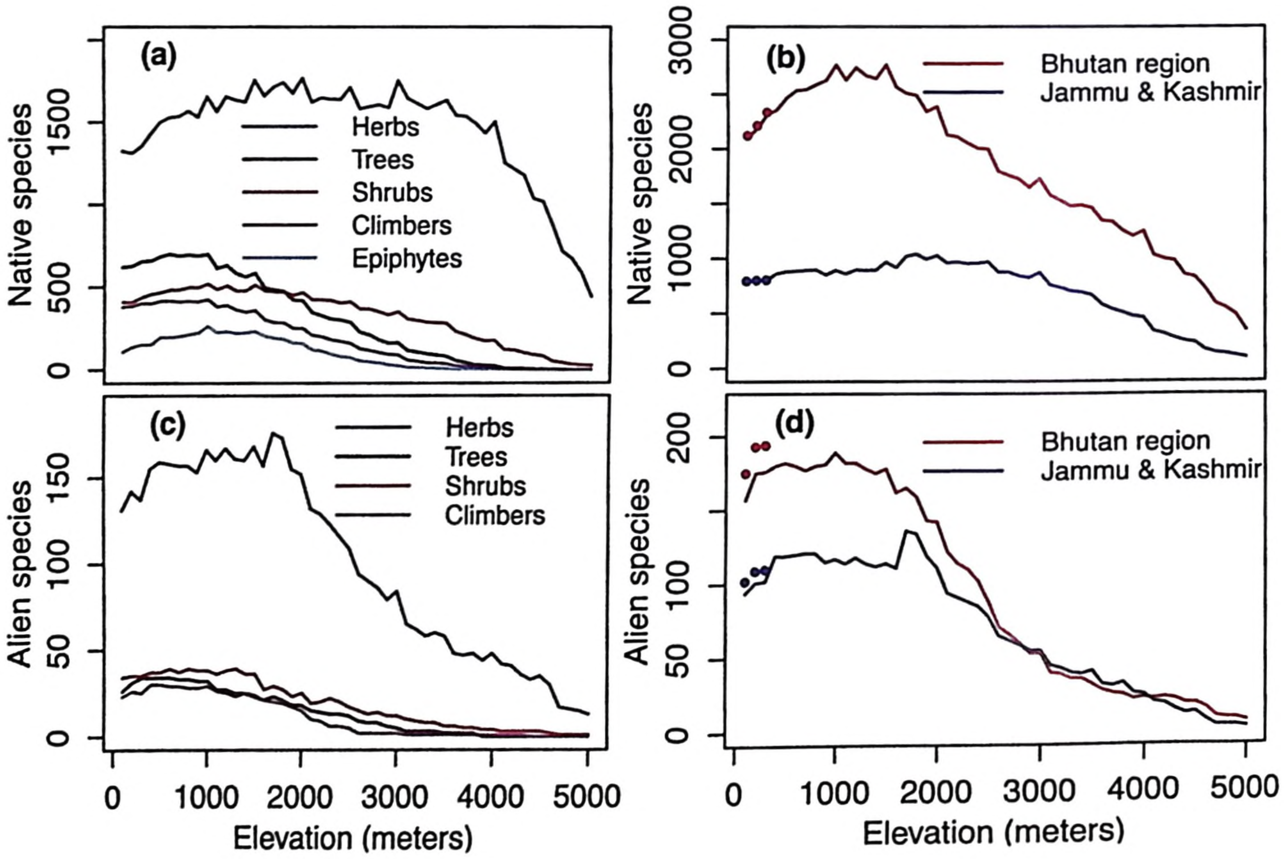

Figure 2.6 Elevational distribution patterns of native and alien species in the Himalaya. **(a, c)** Life forms of native and alien species. **(b, d)** Patterns in the Bhutan region and Jammu & Kashmir for native and alien species.

The 1,000m peak is mainly attributable to native trees and associated epiphytes, with a small additional contribution from shrubs. Herbs show a plateau from approximately 1,000m to 3,500m (Fig. 2.6a), which reflects their gradual replacement of trees and shrubs, against a backdrop of a general decline in all species. Consistent with other partitions of the data, alien naturalised species all show the monotonic decline, which again steepens abruptly beyond 2,000m (Fig. 2.6c).

2.3.3 Elevational richness patterns within regions

The above analysis gives a crude representation because it combines data across the entire Himalaya. I compare the Bhutan region in the east with Jammu & Kashmir in the northwest, because these regions are relatively well documented. However, elevational patterns for these four regions are consistent with those shown for the Bhutan region and Jammu & Kashmir. For natives, the Bhutan region shows a peak at 1,000m, whereas the pattern in Jammu & Kashmir is more of a plateau from the lowest elevations right up to 3,000m (Fig. 2.6b). Naturalized alien species in the Bhutan region show a slight decline up to about 2,000m, which then steepens, whereas naturalised aliens in Kashmir show a plateau up to 2,000m (Fig. 2.6d). Hence, the steep decline in aliens with elevation when integrated across the Himalaya arises because fewer alien species at low elevations are held in common with northwest and east locations, than at higher elevations.

Comparison of nestedness in species composition of native and alien species along the elevational gradient shows that in Bhutan region naturalised aliens are much more nested than the natives (Fig. 2.7a, c). This implies that alien species present at high elevations tend to be a subset of those found at low elevations. However, in Jammu & Kashmir the nestedness patterns of aliens and natives are quite similar (Fig. 2.7b,d). The results of nestedness for Bhutan region are consistent with directional ecological filtering hypothesis. The competition of aliens with natives for establishment has played a significant role, and only species with broad climatic tolerance were able to reach the higher elevations in tropical Bhutan region. However, in the temperate region of Jammu & Kashmir, the alien species were more successful in reaching higher elevations. One possibility for this could be higher rates of human-mediated introductions since higher altitudes in Jammu & Kashmir are more densely populated with humans in comparison to eastern Himalayan regions.

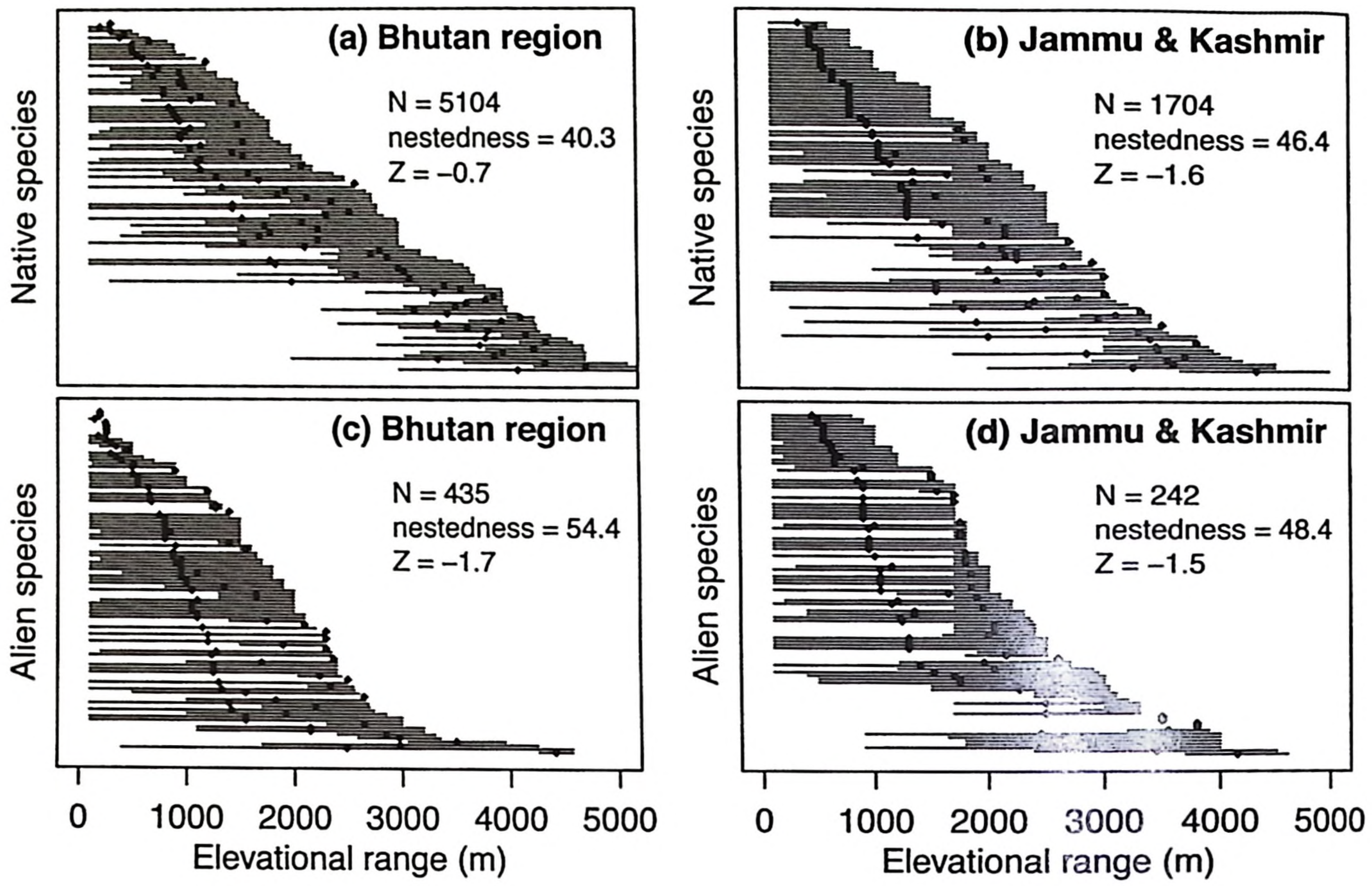

Figure 2.7 Representation of nestedness values for native and alien species in Bhutan region in east and Jammu & Kashmir in northwest Himalaya. Lines represent elevational ranges, and points represent mean elevational range of 100 randomly drawn species.

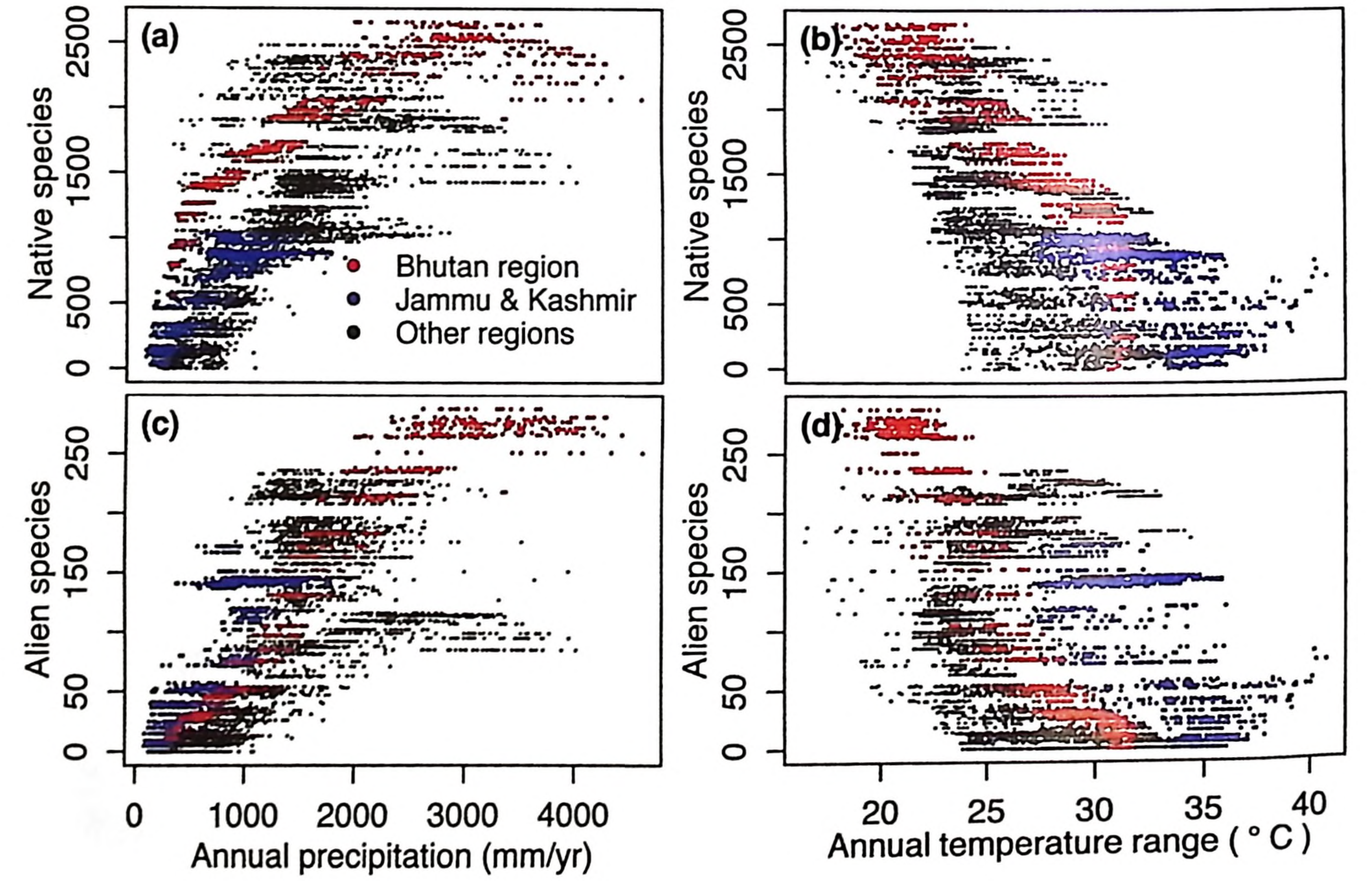

Figure 2.8 Scatter plot of species richness versus annual precipitation and annual temperature range for native and alien species. Red points represent Bhutan region, blue points represent Jammu & Kashmir, and black points represent other sub-regions.

2.3.4 Geographical richness patterns

The species richness map across the whole Himalayan region shows a noticeable decline in species number both across the latitudes and elevations (Fig. 2.1); note that Arunachal Pradesh certainly has more species that remain to be documented. The Bhutan region has 3x more native plants than Jammu & Kashmir (5,735 vs 1,872), but just twice the number of aliens (549 vs 275), and only 1.5x the number of naturalised aliens (311 vs 212). Hence, the latitudinal gradient of alien species is shallower than that of natives. Comparing biogeographic affinities, in the Bhutan region, 48% of the natives and 50% of the naturalised aliens are tropical, whereas in Jammu & Kashmir the corresponding figures are 31% and 30%.

Annual precipitation and seasonality correlate strongly with species richness (Fig. 2.8), for the 6,000 pixels assessed, annual precipitation (natives; r = 0.74, naturalised aliens r = 0.71) and annual temperature range (natives; r = -0.71, naturalised aliens; r = -0.41). The two climate variables are correlated (r = -0.75) and only 3% more variation is explained when the temperature range is added to precipitation in a linear model. Elevational and regional patterns of annual precipitation match species richness well except, more so for aliens than natives. Among natives (1) the lowest elevations in Bhutan may experience the highest precipitation but have fewer native species that are found at 1,000m and (2) precipitation is similar above 3,000m in Bhutan and Jammu & Kashmir but there are many fewer native species at these elevations in Jammu & Kashmir than Bhutan. Plausibly this is because Jammu & Kashmir is more seasonal (Fig. 2.1) and colder, with the consequence that productivity, as measured by actual evapotranspiration (AET), is lower in northwest Himalaya.

2.4 Discussion

The above data has presented a rigorous compilation of our current state of knowledge of plant species richness across the Himalaya, from Arunachal Pradesh in the east to Jammu & Kashmir in the northwest. This is the first assessment for any mountain chain of how regional pools correlate with both elevational and geographical distributions. Given the different sources, timescales, and modes of introduction and aliens often introduced into disturbed habitats; Turbelin *et al.* (2017), a comparison of richness patterns between natives and aliens illuminates the role for dispersal limitation and local conditions on community assembly. I first consider data reliability, before implications of the findings.

All biogeographic studies depend on an accurate assessment of not only distributions of known species, but on all species having been described. For example, Arunachal Pradesh is particularly understudied and at present has fewer species recorded than the neighbouring Bhutan region, despite being larger. In fact, many species probably remain to be described from the Himalaya (Joppa *et al*., 2011), and many described species probably remain to be documented as present in the Himalaya. I base these statements on the presence of only 3% of the accepted names on The Plant List (2013) in the Himalaya (9,375 natives out of the 305,523 world seed plants). That figure contrasts with better-known groups: more than 7% of the world's bird species are native to the region (Price *et al*., 2014). Even among the described plant species, ~10% do not have elevational ranges recorded at all, and some species are documented from only one or a few specimens. Therefore, more study will lead to an increase in elevational ranges for many species. More study will also increase geographical ranges, particularly into Arunachal Pradesh. However, Bhutan and Jammu & Kashmir's floras are now relatively well known, particularly if augmented by plains floras, which I have done here. Further, my field sampling of the trees (Chapter-4) in these specific regions gives results concordant with those based on the literature survey reported. The patterns are also based on a considerable sample size, and it would take a substantial bias in the sampling to overturn them. Finally, the highest number of naturalised alien species come from the north and south America (Khuroo *et al*., 2012; Pandit, 2017), whereas the highest number of native species are shared with Africa, Europe and Australia. It is possible that the relatively few aliens from Africa and Australia are partly a consequence of misclassification of aliens as natives, given the long time the human exchange has been ongoing between these continents and India. However, the difference in numbers seems too high to account for the disparity between native and alien sources. Hence, I consider the primary results to be robust to further research.

In many respects, native and alien species show similar patterns; (1) species richness is similarly correlated with climatic variables, declining from east to west and towards higher elevations. (2) the fraction of species showing tropical and temperate affinities is similar in both groups and differs in the same way between the east and west. (3) in both groups, richness only starts to decline steeply above 2000m, which is about the elevation at which substantial freezing regularly occurs (the freezing line is at about 1500m-1800m based on Worldclim data). (4) in both groups in the west, richness patterns follow a rough plateau from the lowest elevations up to 2,000m. (5) in both groups, species held in common with

Europe peak in richness at 2000m, whereas species held in common with Africa, Australia, and the Americas show monotonic declines in richness with elevation.

In several respects patterns differ; (1) species richness declines threefold from east to northwest in natives, but the decline is half of this in naturalised aliens. (2) in the east, alien species show a monotonic decline with elevation, whereas natives show a richness peak at about 1,000m, a pattern which applies especially to trees and epiphytes. (3) in Bhutan, high elevation aliens show a greater nestedness within the lower elevation aliens than the natives do. (4) Native species with temperate affinities have the highest richness at 3,000m, whereas alien species with temperate affinities are actually more frequent below 2,000m than above 2,000m. (5) At low precipitation levels more natives are present in Bhutan than Jammu & Kashmir, but more aliens in Jammu & Kashmir than Bhutan. Plausibly all these differences can be explained as a result of most introduction pressures of aliens coming largely from the plains of India. Differences in nestedness along elevation and total richness in east Himalaya is most simply explained in terms of a preponderance of introductions occurring at the lowest elevations, followed by climate filtering (the so-called directional ecological filtering hypothesis; Haider *et al*., 2010; Alexander *et al*., 2011; Steyn *et al*., 2017). Elevations with low precipitation in Bhutan are much higher than those in Jammu & Kashmir. Directional ecological filtering is also consistent with the similarity of native and introduced species patterns in the northwest up to 2000m, because there is a large populated and cultivated area that forms the Vale of Kashmir, extending 1500-2000m, and likely experiencing many introductions. Finally, I suggest the relatively shallow latitudinal gradient in alien species richness from east to northwest reflects many introductions across the entire plains of India.

Among the Himalayan natives, 77% species are not endemic to the region I studied. Although some of the sharing may represent expansions of ranges out of the Himalaya, as suggested for connections of temperate species with Europe (Kadereit *et al*., 2008), the implication is that many species are likely to have colonised the Himalaya from elsewhere. It is particularly remarkable that >1000 native species are shared with other continents (although this number may be reduced if molecular work results in the splitting of taxa). Sharing of many natives with other regions suggests that dispersal has been relatively recent, and gene flow is ongoing.

If differences between aliens and natives are attributable to a recent introduction from the plains, it is possible that the strong correspondences also reflect introductions from the plains for natives. Native species show strong affinities with tropical flora, suggesting like aliens, that many have also been sourced from the lowlands. These leaves open the question of why the richness patterns of natives do not monotonically decline with elevation. Notably, in the east, native richness peaks at 1,000m or follows a low elevation plateau, depending on the life form. A richness peak in the Himalaya has been explained in terms of local conditions (a quadratic influence of temperature on species richness; Kluge *et al.*, 2017) and source pool access. With respect to source pools, Oommen & Shanker (2005) suggest a mixing of temperate and tropical floras creates the peak. However, my extensive compilation implies the peak is too low for this explanation, but is instead present for species with tropical affinities. A second dispersal-based explanation is based on the observation that on a bounded domain dispersal leads to a build-up of species at intermediate elevations (Grytnes, 2003), more generally modelled in terms of geometric constraints (Colwell *et al.*, 2016; Feng *et al.*, 2016). This model appears the most promising at present, with the failure of aliens to follow it reflecting relative recency of establishment.

If I assume differences between naturalised alien and native patterns are set by the recency of introduction of aliens, then over time the alien patterns should come to more closely match those of the natives, reflecting processes happening within the mountain chain. Given that many patterns that are similar already, I suggest that local conditions have already operated to filter alien species. Aliens broadly follow large-scale patterns of natives (e.g. showing a decline from east to the northwest) suggesting that climatic controls on species numbers operate over relatively short timescales, perhaps a result of niche-based processes, and given aliens and natives are sourced from different regions, this process can operate independently of species identity. Large-scale diversity gradients in aliens have been noted before and similarly attributed to climatic influences (Sax, 2001; Pyšek & Richardson, 2006; Feng *et al.*, 2011). This gives some justification to the approach of Adhikari *et al.* (2015) who identified susceptibility of regions across India to the invasion, based on correlations of climatic niche in India with potential source regions, but it is worth noting that disparities between distribution of natives and alien indicate that this can only give an approximate guide.

Although I have focused on assembly into the Himalaya, species richness patterns may depend not only on dispersal and establishment but also diversification within the Himalaya (speciation-extinction). Approximately one-quarter of all native species are endemic, and hence many of these may have formed within the Himalaya. Endemics are mainly species-rich at mid-elevations in the east (the number of Himalayan endemics declines more steeply from east to west than the native species, by about fivefold, with 966 species in the Bhutan region and 193 species in Jammu & Kashmir). The mid elevations have an excessive number of barriers (White, 2016), which creates optimal conditions for speciation and limits dispersal once new species have formed and the east has greater historical climatic stability, which should decrease extinction rates in the east. Recently Xing & Ree (2017) concluded that speciation rates were relatively low in the Himalaya when compared to the mountains of southern China. However, given that many species remain to be documented in the far east (Arunachal Pradesh), which is the area that is inferred to have been climatically more stable than other parts of the Himalaya (Ray & Adams, 2001), it may well be that the eastern region continues to accumulate species. The eastern Himalaya assemblage is a consequence of both assembly across a large variety of climates, and location with relatively high speciation and low extinctions.

This discussion more generally bears on the question of whether tropical regions have more species than temperate ones because of non-equilibrium dynamics (e.g. age and area correlating with net diversification; (Wiens & Donoghue 1994; Harmon & Harrison 2015) or because they can accommodate more species at equilibrium (Rabosky & Hurlbert 2015; Tomasovych *et al.*, 2016). The alternatives are hard to tease apart (Tomasovych *et al.*, 2016). The fact that introduced species augment local richness (Sax, 2001; Pyšek & Richardson, 2006) may be regarded as support for non-equilibrium conditions. However, the large turnover between regions (< 10% of alien species are shared between Bhutan and Jammu & Kashmir) and along elevational gradients suggest strong local controls on the number of species that can establish. For example, the fraction of species showing tropical and temperate affinities are similar in both natives and aliens and differs in the same way between the east and west, which suggests considerable sorting, and that many species with both tropical and temperate fail to establish when others are present. Consistent latitudinal and elevational patterns of species in natives and aliens strengthen the support for the role of local climatic controls not only of what species are present but also of species numbers.

CHAPTER 3

Phylogenetic affinities of the Himalayan flora

CHAPTER 3

Phylogenetic affinities of the Himalayan flora

3.1 Introduction

Understanding the process of species assembly of a region requires analysis of not only present day and local-scale ecological interactions but also the integration of evolutionary histories of the species pools (Donoghue, 2008; Thorpe *et al.*, 2011; Swenson, 2013; Gerhold *et al.*, 2015). Increasing availability of well-supported phylogenies has greatly facilitated a better understanding of the ecological and evolutionary processes that underlie spatial variation in community composition. Integration of phylogenetic information into the ecology of local species pools had now become a promising way to explore the process of species assembly (Graham & Fine, 2008; Cavender-Bares *et al.*, 2009). Phylogenetic signals of species within a community are used to evaluate how species interactions and relatedness are associated with the composition (Webb *et al.*, 2002). Analysis of phylogenetic structure reveals the relative importance of the processes like habitat filtering and competitive exclusion in a community (Cavender-Bares *et al.*, 2009). Various measures like phylogenetic diversity (Faith, 1992), net relatedness index, nearest taxon index (Webb *et al.*, 2002), phylogenetic beta diversity (Leprieur *et al.*, 2012) etc. have been devised to evaluate the phylogenetic structure of community compositions. Thus, a variety of community phylogenetic measures can be assessed in comparison to null models of random sampling from a species pool, for testing phylogenetic richness, divergence and turnover in species assemblages (Tucker *et al.*, 2016).

Plant communities in temperate regions of high latitudes and altitudes have been assembled from tropical low-land floras through different evolutionary pathways, i.e. niche conservatism and niche convergence (Qian & Ricklefs, 2016). Two hypotheses providing contrasting explanations for the anomaly in tropical-temperate species richness have been proposed, i.e. Tropical Niche Conservatism hypothesis (Wiens & Donoghue, 2004) and Out of the Tropics hypothesis (Jablonski *et al.*, 2006). Tropical niche conservatism, i.e. the tendency of lineages to retain their niche-related traits through speciation events, has been demonstrated by most of the studies as a major cause for variation in species richness across gradients (Wiens & Graham, 2005; Crisp *et al.*, 2009; Wiens *et al.*, 2010; Crisp & Cook, 2012). On the other hand, alternative hypothesis, i.e. Out of Tropics, predicts that high extinction rates due to abiotic environmental constraints and colonisation hindrances in temperate zones causes low diversity (Jablonski *et al.*, 2006; Jablonski *et al.*, 2013).

Tropical environments, due to their large extent together with higher climatic stability, have promoted speciation and reduced extinction rates, resulting in higher diversity in tropics and decreasing diversity towards poles (Hawkins *et al.*, 2011; Brown, 2013; Romdal *et al.*, 2013; Fine, 2015). Patterns of phylogenetic clustering are expected in communities when conserved traits are retained, whereas overdispersion is expected when traits are convergent in response to environmental filtering (Webb, 2000; Cavender-Bares *et al.*, 2009). For example, regional assemblages of woody plants in the northern and southern temperate zones of earth show less phylogenetic diversity than expected based on their species richness (Kerkhoff *et al.*, 2014). That is because lineages with temperate affinities are younger and nested within older tropical lineages (Kerkhoff *et al.*, 2014). Studies on latitudinal gradients have found significant support for tropical niche conservatism, however, along elevational gradients support for the hypothesis is currently weak (Kluge & Kessler, 2011; Culmsee & Leuschner, 2013; Tiede *et al.*, 2016; Zhang *et al.*, 2016; Chun & Li, 2017).

Phylogenetic turnover in plant communities has been employed for understanding the relative roles of ecological mechanisms like environmental filtering, dispersal, competition and evolutionary processes such as speciation and niche evolution (Hardy *et al.*, 2012; Swenson *et al.*, 2012; Zhang *et al.*, 2013). Phylogenetic beta diversity quantifies phylogenetic relatedness of communities across environmental and spatial gradients thus provide a framework for understanding the evolutionary response of biota to biogeographic histories of regional species pools (Graham & Fine, 2008; Swenson 2011; Leprieur *et al.*, 2012; Qian *et al.*, 2013). Thus, phylogenetic beta diversity provides a promising analytical technique for identification of biologically distinct regions for conservation prioritisation. For example, phylogenetic beta diversity in hyperdiverse Amazon forests has recently been implied by Guevara-Andino *et al.* (2017) for delimitation of floristic units and their application in conservation prioritisation of the region. Kreft & Jetz (2010) proposed a framework for global biogeographical regionalisation based on ordination and clustering of beta diversity at taxonomic and geographical scale. This framework has been used at global as well as regional level analyses and across taxa for delineation of distinct biogeographic regions (Holt *et al.*, 2013; Hattab *et al.*, 2015; He *et al.*, 2017).

Plant communities being very diverse, well-resolved phylogenies including all species in a region are rare, thus studies have commonly used super-tree method to generate phylogenetic hypotheses (e.g. Webb, 2000; Hawkins *et al.*, 2011; Qian *et al.*, 2013; Erickson *et al.*, 2014; Kerkhoff *et al.*, 2014; Chun & Lee, 2017). For example, Phylomatic (www.phylodiversity.net/phylomatic) is the popularly used supertree for plants community analyses. Phylomatic is an online phylogenetic query tool where users submit a list of taxa, to obtain phylogenetic hypothesis for the relationships among the focal species (Webb & Donghue, 2005). However, with the generation more phylogenetic data, efforts are being made to create better resolved and bigger phylogenetic trees (mega-phylogeny). For example, Zanne *et al.* (2014) published a dated molecular mega-phylogeny including 32,223 species of globally distributed land plants. Qian & Jin (2016) updated this mega-phylogeny with a critical evaluation on taxonomic inconsistencies and developed a R function "S.PhyloMaker" which can be employed for generating regional phylogenetic hypothesis for a target species pool. Similarly, Harris & Davies, (2016) has published the most updated fossil-calibrated phylogeny of all seed plant families which can be used for testing the regional phylogenetic hypothesis. These mega-phylogeny approaches thus provide useful resources for testing phylogenetic hypotheses and have been utilised in the evaluation of the relative roles of ecological and evolutionary processes in the assembly of regional species pools (Li, 2016; Zhang *et al.*, 2016; Liu *et al.* 2017; Qian *et al.*, 2017).

In this Chapter, I employ the complementary use of phylogenetic community structure and phylogenetic beta diversity metrics at family, genera and species level to investigate and describe floristic patterns in Himalaya. I evaluate the tropical niche conservatism hypothesis for the variability in species richness from tropical east to the temperate northwest and along the elevational gradient of the Himalaya. Further, the phylogenetic beta diversity of families and genera is used to classify the phylogenetically distinct floristic regions of the Himalaya.

3.2 Methods

3.2.1 Species occurrence data

I compiled information on the total number of species and genera in 214 families of native seed plants present in the Himalaya, using the database of 10,503 species described in Chapter-1. For global level estimates of genera and species in these 214 families, information was obtained from The Plant List (2013) www.theplantlist.org (these estimates were also used by Harris & Davies, 2016). All families and genera were broadly categorised into three climatic affinities, i.e. tropical, temperate and cosmopolitan based on their different areal types (Wu, 1991; Wu *et al.*, 2003). The number of species in every family was calculated for six sub-regions of Himalaya, i.e. Arunachal Pradesh, Bhutan & Sikkim (including parts of Northern West Bengal), Nepal, Uttarakhand, Himachal Pradesh and Jammu & Kashmir. Elevational distributions of families, genera and species in six sub-regions across the Himalaya was used for evaluating climatic and phylogenetic patterns across latitudinal and elevational gradients.

3.2.2 Phylogenetic data

I used a time-calibrated phylogeny based on four gene regions (i.e. *rbcL*, *matK*, *atpB* and *18S rRNA*) of 425 global seed plant families and pruned the tree for the 214 families of native species present in Himalaya using R package “ape” (Paradis *et al.*, 2004). I further, reconstructed a species level phylogenetic tree by grafting the native species present in Himalaya, onto a backbone phylogenetic hypothesis (Qian & Jin, 2016). The backbone of this mega-phylogeny was updated version of the largest and time-calibrated species-level phylogeny of seed plants published by Zanne *et al.* (2014). This mega-phylogeny uses seven gene regions (i.e. 18S rDNA, 26S rDNA, ITS, *matK*, *rbcL*, *atpB* and *trnL-F*) and 39 fossil calibrations. I excluded aliens and currently unresolved species leaving behind a total of 8066 native seed plant species of Himalaya. Among these species, 1967 matched directly to those sampled by Zanne *et al.* (2014), and the remainder were added as polytomies at the root node for their genus membership using the function “S.PhyloMaker” (Qian & Jin, 2015) in R package “phytools” (Revell, 2012). This function produce phylogenies with three scenarios, and I used Scenario-3 phylogeny which follows the same approach as implemented in Phylomatic (Webb *et al.*, 2008) and BLADJ (Wikstrom *et al.*, 2001).

3.2.3 Data analysis

The phylogenetic trees of 214 families and 8066 native seed plants were visualised using Figtree v1.4.3 and taxa were classified into seven historical lineages, i.e. gymnosperms and six distinct angiosperm groups as per AGP-IV (2016). These lineages are shown in the same colour on nodes of phylogenies and include gymnosperms, early angiosperms, magnoliids, monocots, eudicots, superrosids and superasterids. Families with tropical, temperate and cosmopolitan affinities are shown with the same colour on tips of family-level phylogeny. To test the null hypothesis that climatic affinities of clades in each historical lineage of seed plants have evolved independent of the age of lineage, I conducted Chi-square analysis on the contingency table of families and genera. Species to genus ratio in all Himalayan families is calculated simply as the average of the number of species per genus in a given family in Himalaya and across the globe. Because clade age and species richness show a highly skewed distribution, correlations among them were evaluated using non-parametric Spearman's rank tests. I conducted a Principal Component Analysis (PCA) to evaluate the relationship of species composition in different sub-region with the climatic affinities of the given family.

As a test for tropical niche conservatism, I quantified phylogenetic richness and divergence measures (Tucker *et al.*, 2016) of plant assemblages in six sub-regions along the latitude and along the elevational gradient across Himalaya. I calculated Faith's (Faith, 1992) phylogenetic diversity (PD), mean pairwise distance (MPD), mean nearest taxon distance (MNTD), in R package "picante" (Kembel *et al.*, 2010). Net relatedness index (NRI) and nearest taxon index (NTI) were calculated as -1 times standardised effect size of MPD and MNTD respectively (Webb *et al.*, 2002; Ghosh-Harihar, 2014). These indices describe whether taxa within sub-regions are more or less closely related than random assemblages of similar species richness drawn from species pool of the Himalaya. Specifically, PD measures the minimum total length of all the phylogenetic branches, NRI measures the average degree of relatedness among all members of the community and NTI measures average distance between closest relatives in each assemblage. To control for the observed species occupancy rates and species richness of each sub-region and elevation zone, I chose 'taxa-labels' null model and ran the analyses for 999 iterations. Positive ~~Negative~~ values of NRI and NTI indicate phylogenetic clustering whereas negative ~~positive~~ values indicate phylogenetic overdispersion within the community (Webb *et al.*, 2002).

I applied the quantitative framework based on clustering and ordination techniques proposed by Kreft & Jetz (2010) to characterise taxonomically distinct floristic regions in the Himalaya. First, I generated equal-size grid cells of 0.2° × 0.2° degrees resolution across Himalaya (1145 cells). Occurrence data of 214 families and 1800 genera was provided to each grid using the elevational information of grids and species range within a sub-region. I computed phylogenetic beta diversity ($p\beta_{jtu}$), the measure that calculates lineage turnover (Leprieur *et al.*, 2012). This index measures the evolutionary dissimilarity between communities by comparing the shared and unique branches of the phylogeny across all pairwise grid combinations. This index is similar to β_{jtu} except that in this instance the shared and unique branches of the overall phylogeny were used rather than species. Turnover component of Jaccard dissimilarity β_{jtu} (Baselga, 2012) is expressed as follows:

$$\beta_{jtu} = 2\min(b,c)/\ a+2\min(b,c),$$

where *a* refers to the number of common species between grid *i* and *j*, *b* is the number of species found in grid *i* but not grid *j* and *c* is the number of species found in grid *j* but not grid *i*. The β_{jtu} index measures the proportion of species that would be replaced between assemblages if both had the same number of species and, hence, accounts for species replacement without the influence of differences in richness and is suggested appropriate for bio-regionalisation (Leprieur & Oikonomou, 2014).

I applied the unweighted pair-group method using arithmetic averages (UPGMA) hierarchical clustering to the dissimilarity matrix. UPGMA produces a dendrogram displaying the hierarchical relationships of all grid cells. From the obtained hierarchical trees, I determined the optimal number of floristic regions by applying the Kelley-Gardner-Sutcliffe penalty function (KGS). This function generates minimum value for the optimal number of clusters based on differences between the groups and cohesiveness within the groups (Kelley *et al.*, 1996). A two-way non-metric multidimensional scaling (NMDS) was performed based on a neighbour-joining algorithm to investigate the distinct floristic regions. Stress values which range from 0 to 1, with smaller values indicating better ordination results, were used to assess the fit between the NMDS and the original dissimilarity matrix (Legendre & Legendre, 1998). Grid cells were coloured according to its position in the ordination space based on UPGMA clusters. The ordination results were then plotted and mapped by assigning a colour to each grid cell for the families and genera.

3.3 Results

3.3.1 Phylogenetic and climatic affinities

Himalayan native flora belongs to 214 families which represent half of the 425 global families of seed plants. Among these families, 53% are tropical, 23% are temperate, and 24% are cosmopolitan in distribution (Fig. 3.1). All seven major clades of seeds plants ranging from oldest to newest lineages are represented (Fig. 3.1). These families are classified as gymnosperms and six angiosperm groups, i.e. early angiosperms, magnoliids, monocots, eudicots, superrosids and superasterids as per AGP IV (2016) classification.

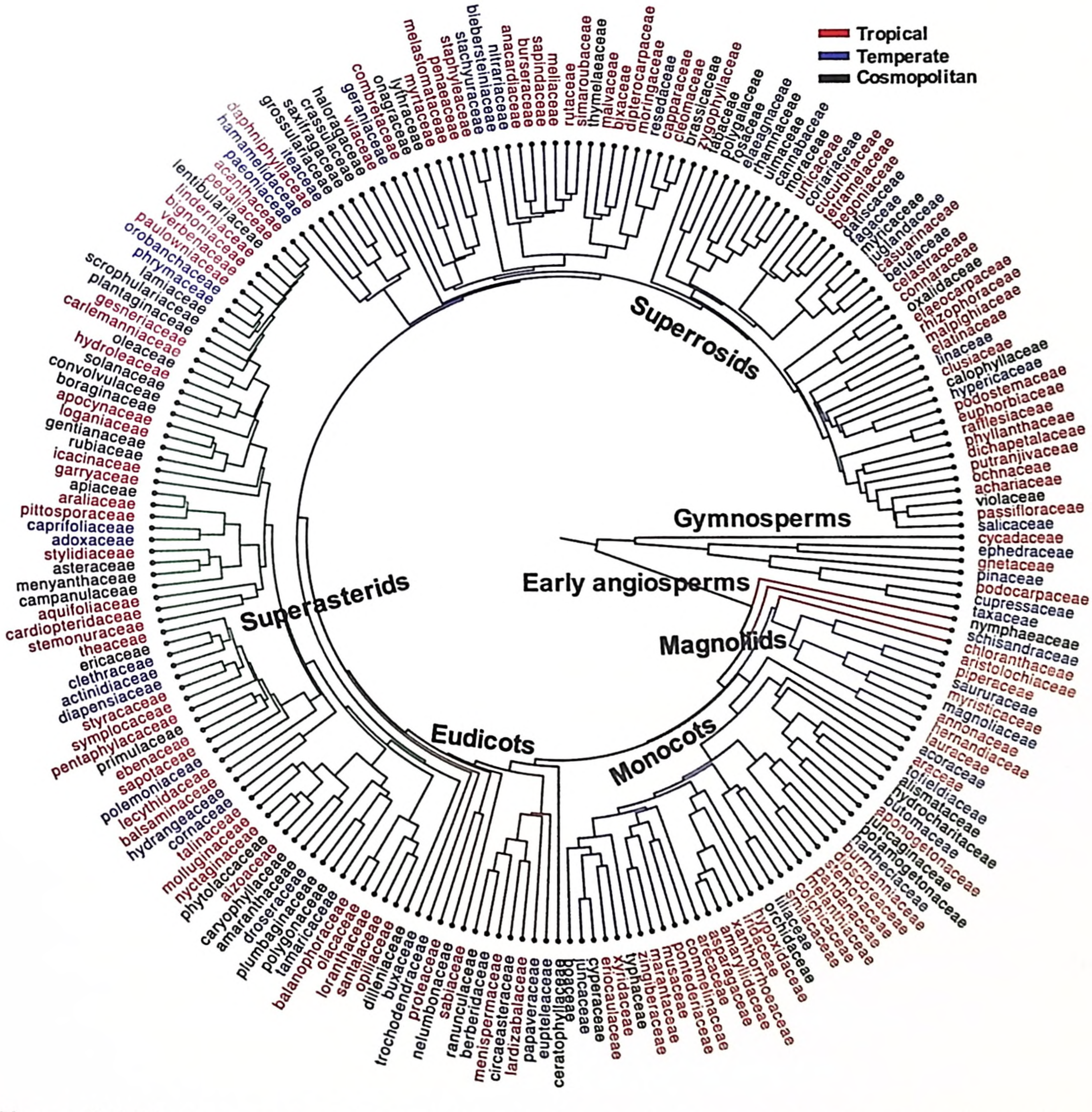

Figure 3.1 Phylogeny for 214 families of native seed plants in Himalaya. Nodes with same colour show families classified into seven major lineages of seed plants. Climatic affinities of families are shown in three different colours.

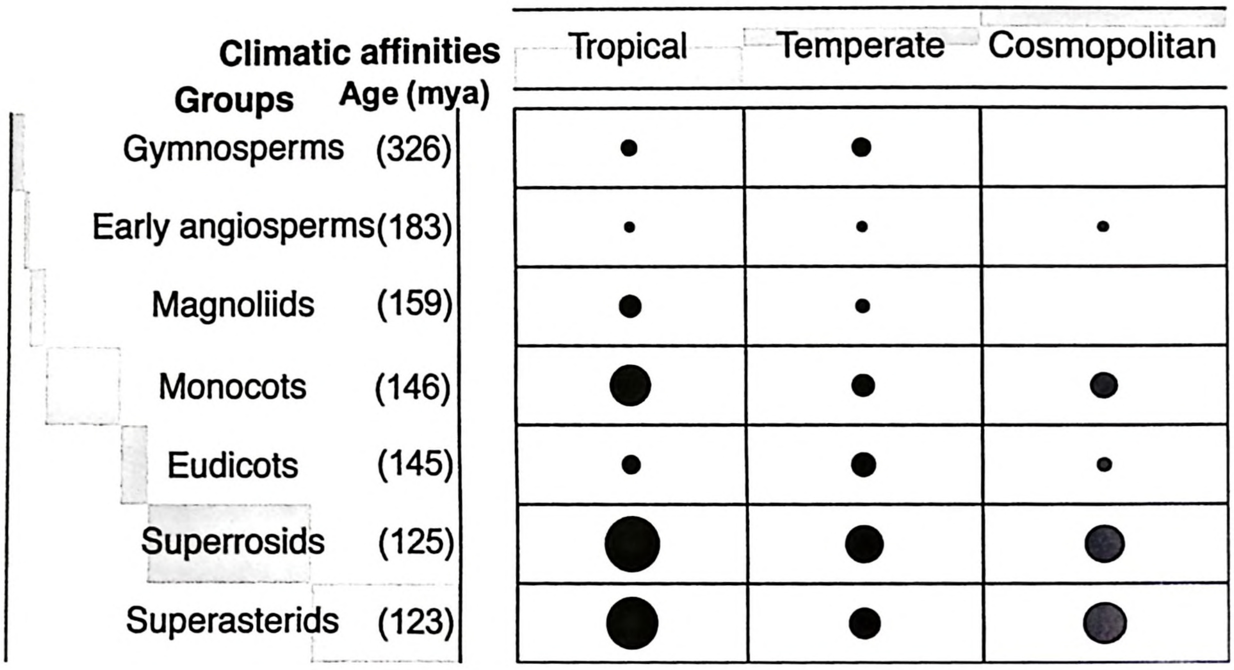

Figure 3.2 Balloon plot showing the clade age of seven lineages of Himalayan seed plants and their proportions of families with climatic affinities. The width of grey blocks in axes represents the proportion of families in each group with respect to all families.

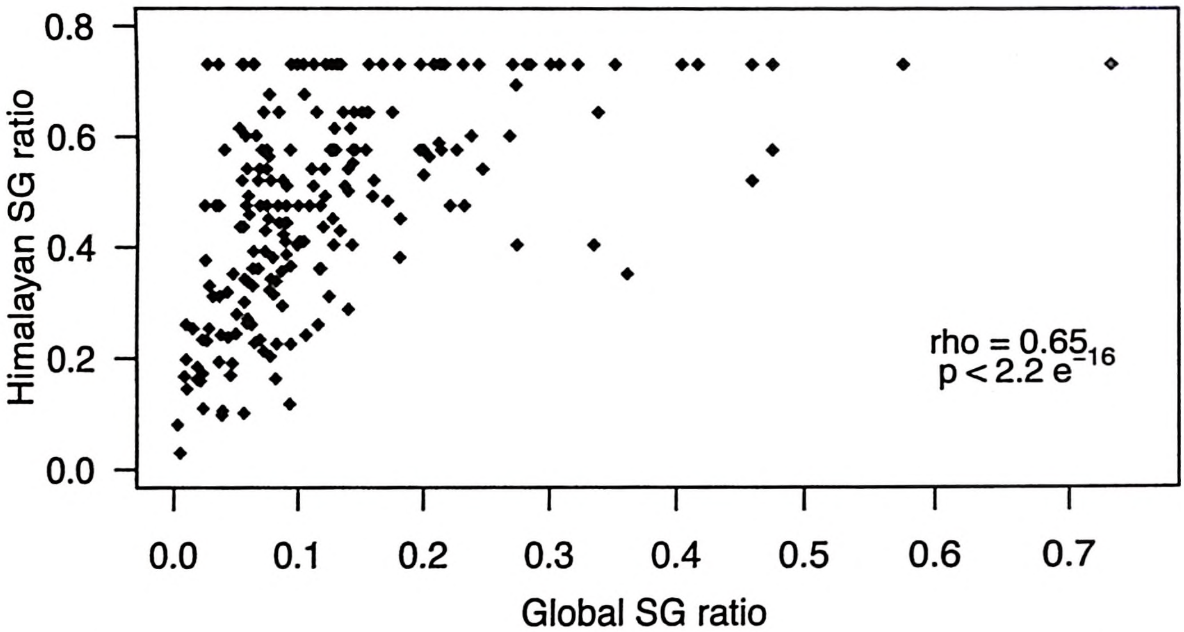

Figure 3.3 A bivariate plot comparing log scale axes of species to genus (SG) ratio between Himalaya and globe for 214 Himalayan seed plant families and Spearman rank correlation between SG ratios.

Chi-square test for families shows that climatic affinities are not significantly distributed among the seven major lineages of plants ($\chi^2 = 19.2$, df= 12, p = 0.08), but genera shows a significant distribution ($\chi^2 = 67.6$, df= 12, p = $8.9e^{-10}$). Proportions of families with different climatic affinities in Figure 3.2 shows that older clades represent lower number of families whereas the younger clades represent most of the families with the dominance of tropical affinities. These results signify the importance of relative roles of speciation and extinction of seed plants during the past geological history. The bivariate plot between species to genus ratio for 214 families in Himalaya and their ratios across the globe show a linear trend (Fig. 3.3). Spearman rank correlation between species to genus ratio in Himalaya and across the globe shows a significant correlation (rho=0.65, $p<2.2e^{-16}$). Comparison of clade ages with the number of species and genera in respective families indicates that older families tend to have fewer taxa as compared the younger families. Spearman rank correlation between family age and number of species or genus in Himalaya is weakly correlated (Fig. 3.4). Similarly, at the global scale, the correlation between family age and number of species or genera is also very weak, indicating an uncertain role of family age on the number of taxa.

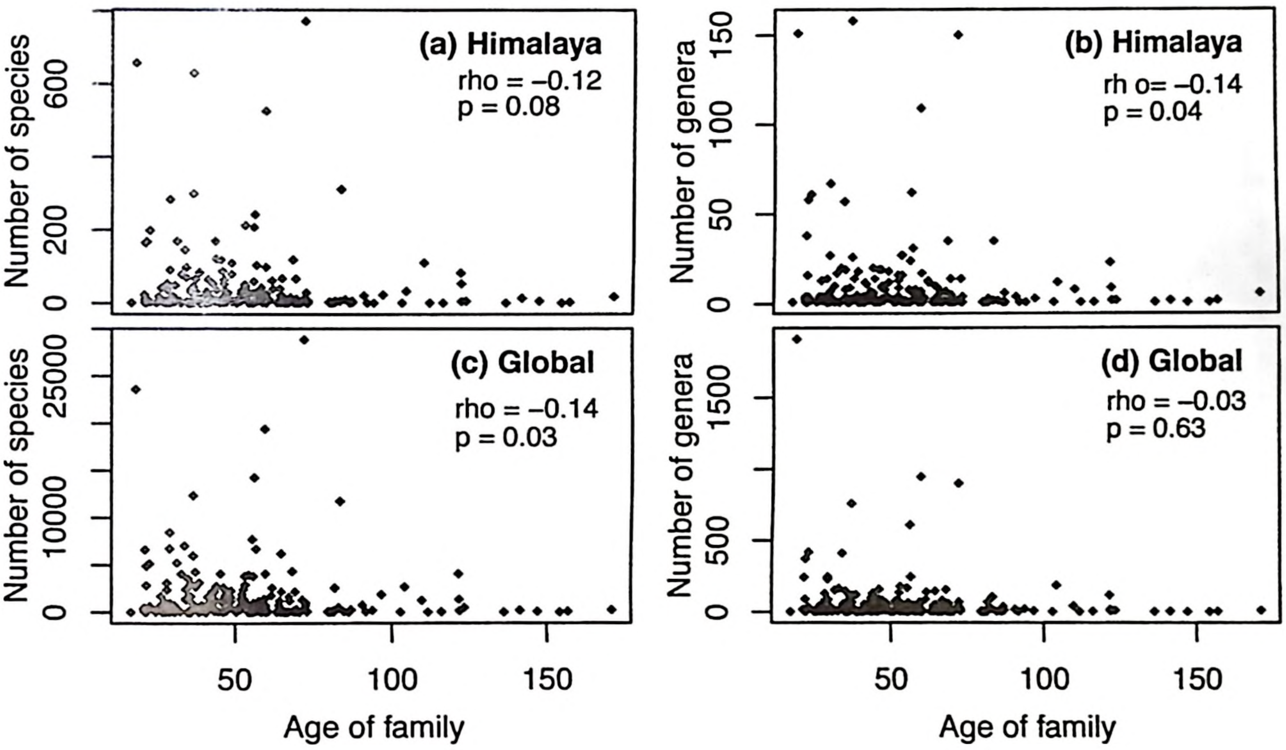

Figure 3.4 Bivariate plot between the number of species and genera and age of 214 families in Himalaya and Spearman rank correlation between them (**a**) Species in the Himalaya (**b**) Genera in the Himalaya (**c**) Species across the globe (**d**) Genera across the globe.

Himalayan climate varies from humid and tropical regions in the east to dry and temperate areas of the northwest. PCA of species richness in families with different climatic affinities shows the dominance of cosmopolitan families in three sub-regions of the northwest Himalaya. Tropical families are dominant only in east whereas temperate families are equally dominant all across Himalaya. These results indicate that dry and temperate regions in lower elevations of northwest Himalaya are more colonised by cosmopolitan clades whereas tropical clades dominate eastern Himalaya. However, since climatic conditions are very similar across high altitudes in Himalaya, temperate clades show identical assemblages from east to northwest Himalaya.

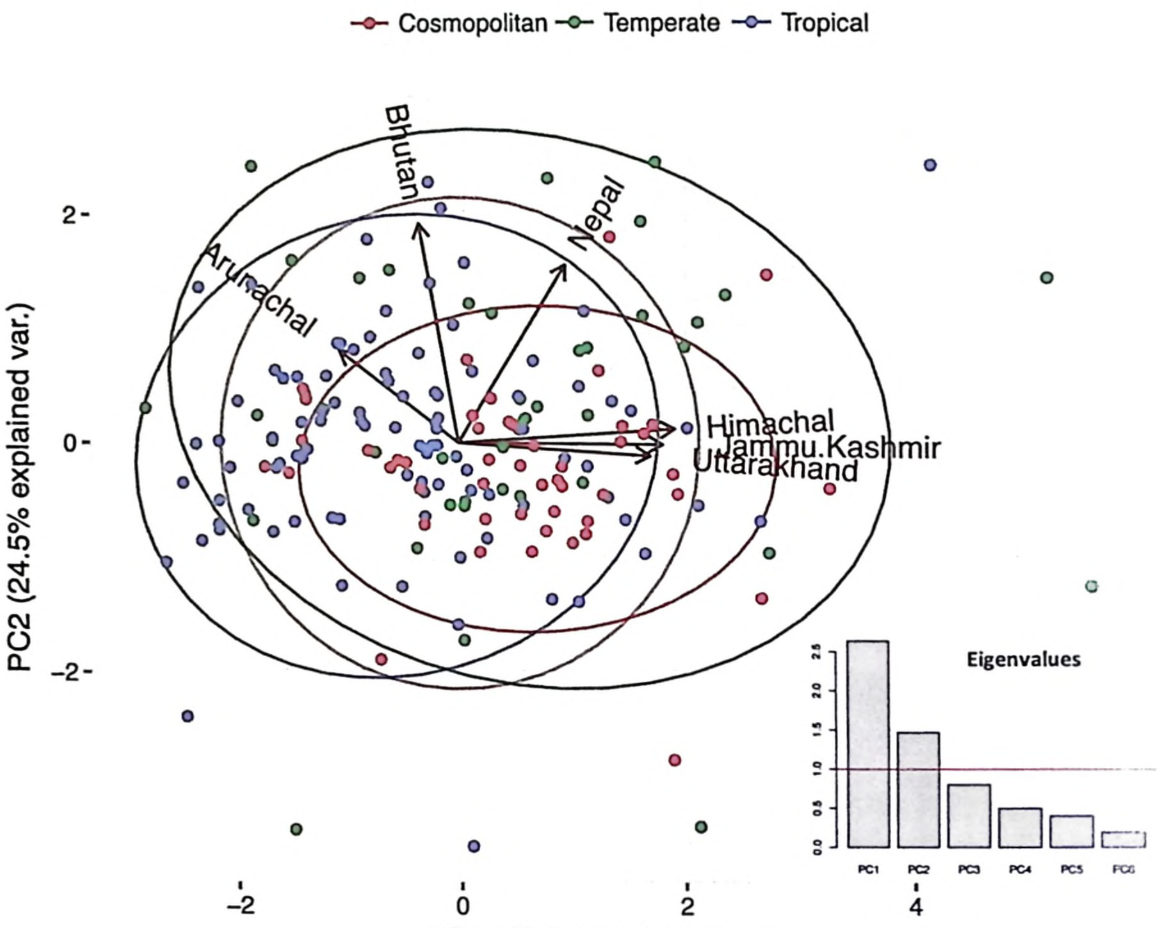

Figure 3.5 Biplot of PCA showing first two principal components describing the relationships of species climatic affinities between six sub-regions across Himalaya.

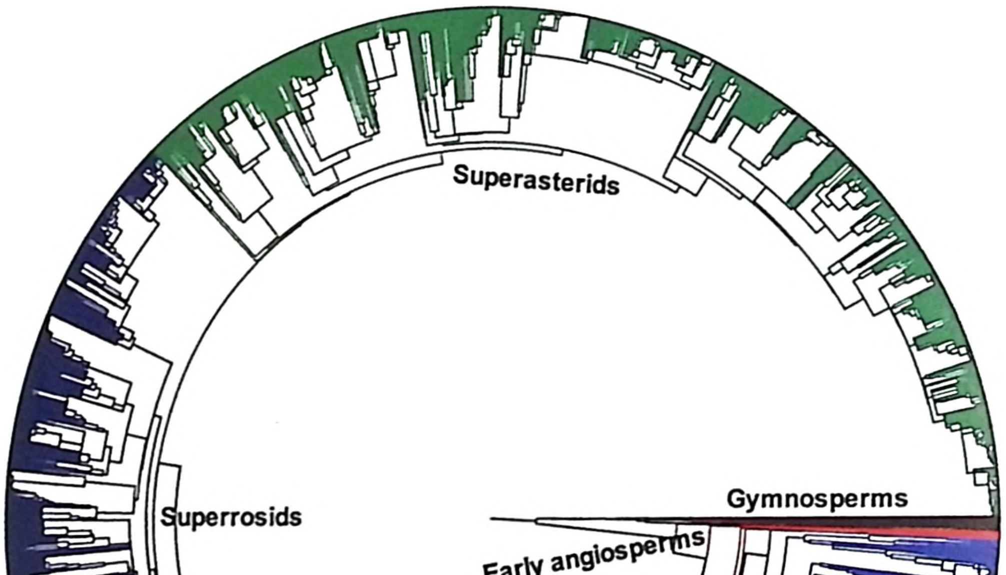

Figure 3.6 Phylogeny for 8,066 species of seed plants in Himalaya. Species representing one of the seven major lineages of seed plants are shown in the same colour.

3.3.2 Patterns of phylogenetic diversity

A total of 8066 native plant species (Fig. 3.6) were used for phylogenetic analysis across six sub-regions along the latitudinal gradient and along the elevational gradient of Himalaya. Along the latitudinal gradient, Faith's phylogenetic diversity (PD) was highest in Bhutan & Sikkim, and PD declines linearly towards northwest Himalaya which is consistent with the taxonomic species richness (Table 3.1). Correlation between PD and SR was highly positive (r = 0.98, p = 0.0002). Comparison of observed phylogenetic diversity with diversity expected under null model sampling from the Himalayan species pool shows significant phylogenetic ~~clustering~~ overdispersion in the eastern Himalaya and an increasing ~~overdispersion~~ clustering towards northwest Himalaya. Both net relatedness index (NRI) and nearest taxon index (NTI) shows a significant phylogenetic ~~clustering~~ overdispersion with highest negative values in tropical Arunachal Pradesh. On the contrary, temperate regions of northwest Himalaya show highest phylogenetic ~~overdispersion~~ clustering. These results are consistent with the tropical niche conservatism theory, that tropical habitat provide a suitable environment for clades invoking evolution of more closely related taxa with conserved traits in comparison to temperate regions.

Table 3.1 Phylogenetic richness and variability indices for plant communities within six sub-regions across Himalaya. (SR: species richness, PD: phylogenetic diversity (*million years*), MPD: mean pairwise distance, MNTD: mean nearest taxon distance, NRI: net relatedness index, NTI: nearest taxon index).

Sub-region	**SR**	**Faith's PD**	**MPD**	**MNTD**	**NRI**	**NTI**
Arunachal Pradesh	3923	112756	302.4	46.2	-7.2	-3.1
Bhutan & Sikkim	5153	137120	296.1	43.9	-1.3	-2.5
Nepal	4586	118435	293.1	42.2	2.3	3.1
Uttarakhand	3773	93677	291.4	39.3	3.5	9.6
Himachal Pradesh	2606	64737	283.3	38.2	8.4	10.8
Jammu & Kashmir	1717	45620	281.5	38.9	7.5	10.3

Along elevational gradient of Himalaya, phylogenetic diversity (PD) again shows a consistent pattern of taxonomic diversity. However, NRI and NTI do not show a consistent pattern along the elevational gradient. NRI shows a weak ~~overdispersion~~ clustering between 100-500m, a weak phylogenetic ~~clustering~~ overdispersion between 1000-2000m and above 2000m shows an increasing ~~overdispersion~~ clustering with increasing elevation. However, NTI exhibits similar ~~overdispersion~~ clustering along the complete elevational gradient of Himalaya. These results thus suggest a weak support for the tropical niche conservatism theory for assembly of the community along the elevational gradient of Himalaya.

Table 3.2 Phylogenetic richness and variability indices for plant communities along the Himalayan elevational gradient. (Abbreviations same as Table 3.1).

Elevation	SR	Faith's PD	MPD	MNTD	NRI	NTI
100 m	2862	79490	293.4	43.4	1.63	4.4
500 m	3099	86073	295.3	43.9	0.17	3.2
1000 m	3356	93254	297.1	44.3	-1.51	2.1
1500 m	3231	88560	296.1	43.6	-0.57	3.3
2000 m	2844	76750	297.0	42.0	-1.17	6.3
2500 m	2396	66170	294.7	42.8	0.51	5.8
3000 m	2149	59920	291.6	44.2	2.46	4.8
3500 m	1810	50125	288.3	44.1	4.03	5.5
4000 m	1413	39966	282.1	44.3	6.58	6.1
4500 m	929	27742	272.2	47.5	8.69	5.1
5000 m	414	14307	266.4	51.8	6.41	5.0

3.3.3 Identification of floristic regions

The UPGMA hierarchical clustering of species assemblages yielded six major distinct floristic regions for families (Fig. 3.7) and five distinct regions for genera (Fig. 3.8). The NMDS ordinations and their resulting maps in both families and genera indicate a biogeographical transition between lower and higher elevations and along latitude across Himalaya. Mainly, two dominant geographical gradients can be identified, the first gradient representing high-elevations is related to the first NMDS axis, and the low-elevations gradient is associated with the second NMDS axis. The KGS function identifies six distinct floristic regions in families, i.e. Low-elevation gradient (east, central and west Himalaya), high-elevation gradient (mid-elevations, east and west high elevations).

However, in case of genera, five distinct regions can be identified, i.e. low-elevation gradient (east and west Himalaya), mid-elevations (east and west Himalaya) and high elevations all across Himalaya. The stress value of 0.21 for families and 0.13 for genera indicate the relatively good projection of the dissimilarity matrix into the two-dimensional ordination space. These phylogenetic beta diversity turnover results are consistent with the phylogenetic richness and variability indices which also identifies east Himalaya very distinct from the western Himalaya.

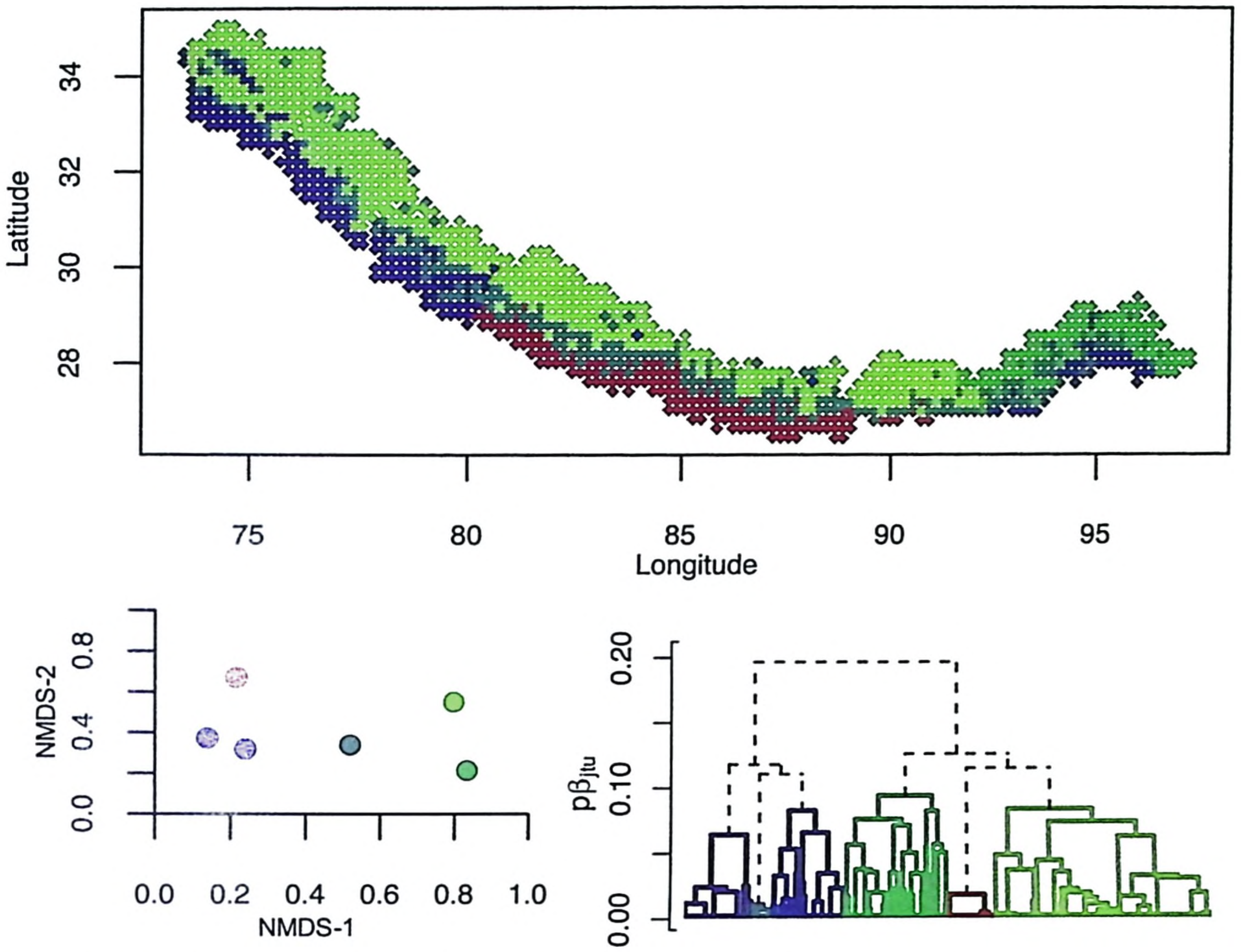

Figure 3.7 Dendrogram, NMDS scores and map resulting from the UPGMA hierarchical clustering of phylogenetic beta diversity turnover ($p\beta_{jtu}$) for 214 seed plant families.

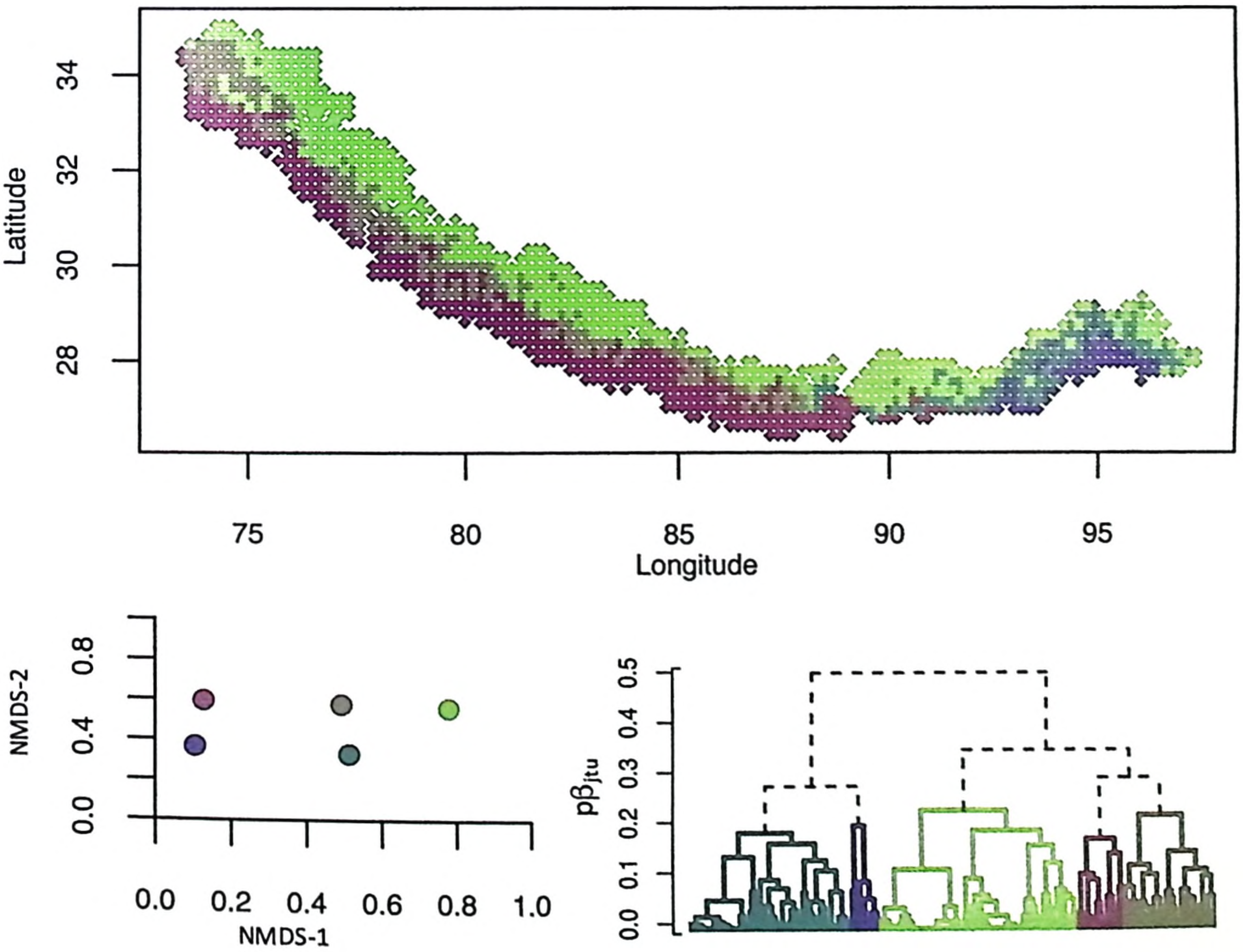

Figure 3.8 Dendrograms, NMDS scores and maps resulting from the UPGMA hierarchical clustering phylogenetic beta diversity turnover ($p\beta_{jtu}$) for 1800 seed plant genera.

3.4 Discussion

Phylogenetic diversity patterns of seed plants communities are significantly different between east and west Himalaya. The differences in phylogenetic signals are consistent with the climatic and geological history of Himalaya during the last glacial maximum (see Wang *et al.*, 2010; Trivedi *et al.*, 2013; Bhattacharyya *et al.*, 2014). Geological and climatic history had a strong role in the evolution of the present day taxa on earth (Wiens & Donoghue, 2004; Ficetola *et al.*, 2017). For example, my analysis shows that ancient lineages of seed plants represent comparatively lesser taxa both at the global scale as well as in Himalaya, which may happen either due to low speciation and/or high extinction rates in ancient clades as compared to younger clades (Harris & Davies, 2016). The correlation of family age with the number of species or genera is also very weak. Species to genus ratios are very skewed across the families both across the globe and in Himalaya. Species to genus ratios within families present in Himalaya are strongly correlated with global ratios, indicating that patterns of diversification in Himalaya are consistent with the global diversification of seed plants. Himalaya shows a wide range of climatic conditions and is thus inhabited by clades of all climatic affinities (Singh & Singh, 1987; White, 2016). Distribution of clades in Himalaya is strongly controlled by the climatic conditions and past geological history. For example, cosmopolitan families are dominant in western Himalaya and tropical families are dominant in eastern Himalaya. Interestingly, temperate families are equally distributed all across the Himalaya which coincides with the similarity of climatic conditions in the high elevations.

Past climatic history invokes the explanation for variability in phylogenetic diversity of plants from east to northwest Himalaya. Western Himalaya is situated comparatively more towards the north and was heavily influenced by the last glacial maximum (Ray & Adam, 2002). Most of the biodiversity may have been eliminated from the region, and the remaining found a refuge in the eastern Himalayan regions and southeast Asia (Bhattacharyya *et al.*, 2014). Thus, recolonisation of species from east to northwest Himalaya may still be an ongoing process (White, 2016). Precipitation pattern, i.e. Asian-monsoon and western disturbances is another factor which strongly influences the climate (Wang *et al.*, 2010). Eastern Himalaya receives fivefold higher rainfall during the summer monsoons and is less seasonal, whereas on contrary northwest Himalaya is heavily influenced by western disturbances during winters making the region very seasonal

(Chapter-2; Fig. 2.7). Thus historical climatic conditions had remained more favourable in the east as compared to the northwest, explaining the variability in the taxonomic and phylogenetic diversity of seed plants across Himalaya.

Along the latitudinal gradient of Himalaya, phylogenetic diversity (PD) was consistent with taxonomic richness with highest values for Bhutan region and declining towards northwest Himalaya. However, NRI and NTI show a significant phylogenetic overdispersion ~~clustering~~ for plant community in east Himalaya (Arunachal Pradesh), and significant phylogenetic clustering ~~overdispersion~~ for northwestern Himalaya (Himachal Pradesh, Jammu & Kashmir). Phylogenetic overdispersion ~~clustering~~ in the tropical region of east Himalaya indicates tropical niche conservatism in the plant community. However, plant communities of temperate northwest Himalaya show significant phylogenetic clustering ~~overdispersion~~ indicating the strong role of environmental filtering, enabling evolution or colonisation of species with convergent traits (Webb, 2000; Cavender-Bares *et al.*, 2009). These results are thus consistent with tropical niche conservatism theory (Wiens & Donoghue, 2004; Wiens & Graham, 2005; Wiens *et al.*, 2010; Brown, 2012; Crisp & Cook, 2012) and suggest a strong role of niche conservatism in shaping the plant richness along the latitudinal gradient of Himalaya. However, considering the impact of last glacial maximum, possibility of the alternative hypothesis that low diversity in temperate zones is caused by high extinction rates hindering colonisation of these regions (Jablonski *et al.*, 2006), may also be applicable for Himalayan plant communities. Given the historical loss of lineages during last glacial maximum only a subset of taxa from east Himalaya with suitable niches in the northwest were successful in recolonisation.

On the contrary, along elevational gradient both NTI and NRI shows a weak support for tropical niche conservatism theory. In contrast to predictions of tropical niche conservatism, plant communities in the low elevation of Himalaya do not show phylogenetic overdispersion ~~clustering~~. Assemblages in higher elevations show clustering ~~overdispersion~~ in NRI but NTI vary less along the elevational gradient of Himalaya. Many other studies have also reported the net relatedness of plant communities along different elevational gradients and have gained little support for tropical niche conservatism (Kluge & Kessler, 2011; Culmsee & Leuschner, 2013; Tiede *et al.*, 2016; Zhang *et al.*, 2016; Chun & Li, 2017). These results are thus consistent with the out of tropics hypothesis, indicating that older taxa from low-lands have colonised at the higher elevations. Similar results from tropical Asia and tropical America suggests that mean family age of angiosperm woody plants increases with elevation and phylogenetic relatedness decreases with elevation (Culmsee & Leuschner, 2013; Qian, 2014). These contrasting patterns along latitudes and elevations indicate that phylogenetic relatedness within plant assemblages across latitudes are driven by niche conservatism, whereas elevational gradients reflects a strong role of niche convergence (Qian & Ricklefs, 2016).

Phylogenetic beta diversity ($p\beta_{jtu}$) of seed plant families and genera also identifies phylogenetically distinct floristic regions in east and northwest Himalaya. The ordination and hierarchical clustering of phylogenetic beta diversity separate distinct floristic groups both across latitudinal and elevational gradients of Himalaya. Comparison of the geographical distance along latitude and elevation will suggest a higher rate of phylogenetic turnover along the elevational gradient. That may be a result of substantial differences in temperature along elevation over short distances, which is expected to increase beta diversity (e.g. McKnight *et al.*, 2007). The ordination and hierarchical clustering approach using beta diversity turnover has recently been identified as powerful quantitative technique for identification of taxonomically and phylogenetically distinct biogeographic regions both at global level (Kreft & Jets, 2010; Holt *et al.*, 2013) as well as at regional levels (Hattab *et al.*, 2015; He *et al.*, 2017). Eastern and western Himalayan regions are taxonomically, and evolutionarily distinct floristic regions thus have unique values for conservation priorities and planning.

CHAPTER 4

Latitudinal and elevational richness of trees along the Himalaya

CHAPTER 4

Latitudinal and elevational richness of trees along the Himalaya

4.1 Introduction

One of the fascinating facts about biodiversity on earth is that species diversity varies from place to place. Investigation of variability in species diversity across the globe has identified some general patterns including latitudinal and elevational diversity gradients (Pianka, 1966; Janzen, 1967; Stevens, 1989,1992). Along the latitudinal gradient across the globe, species diversity is highest in tropics and the diversity declines with increasing latitude (Hillebrand, 2004). Along elevational gradients it was proposed that mimicking latitudes, species richness should decline with increasing elevation as well (Stevens, 1992). However, global reviews of species richness for different taxa revealed that not a single but three dominant patterns of richness exist along elevational gradients (Rahbek, 1995, 2005; Guo *et al.,* 2013; Grytnes & McCain, 2013). These patterns include mid-elevation peaks, a monotonic decline with elevation and a low-elevation plateau in species richness (Grytnes & McCain, 2013).

Various hypotheses have been proposed, explaining the causes of diversity gradients most of which attribute higher diversity to the regions with larger geographic area, longer time for speciation with a relatively stable climate, and higher energy (Rohde, 1992; Willig *et al*., 2003; Grytnes & McCain, 2013; Brown, 2014). The geographic area hypothesis posits that tropics have larger land area thus provide more niches and barriers to gene flow, which enhances speciation and reduces extinction rates (Terborgh, 1973, Rosenzweig, 1995). The niche conservatism hypothesis complements this, by highlighting that tropical species maintain their ancestral niche (Wiens & Donoghue, 2004). Many explanations for diversity gradients are based on energy and productivity which tends to have the inverse relation with latitude (Pianka 1966, Wright 1983) and altitude (McCain, 2007a). For example, fluctuating environments are expected to increase extinction and preclude specialisation, while stable climates promote specialisation, allowing species to have narrow niches, and facilitate speciation (Janzen, 1967; Stevens, 1989). Geometric constraints hypothesis suggests a non-biological explanation for latitudinal and elevational diversity gradients, demonstrating that merely random placement of species ranges within a bounded domain will form a hump of species number towards centre due to under-sampling at the edges (Colwell & Hurtt, 1994, Colwell *et al.,* 2016).

Species richness of trees on the earth ranges from over 250 species a hectare in Amazon to rarely more than 20 species a hectare in the eastern United States and even zero species in some temperate and alpine regions (Leigh *et al.*, 2004). A general review on tropical tree diversity shows that species richness tends to increase with precipitation, forest stature, soil fertility, the rate of canopy turnover and time since catastrophic disturbance, and tends to decrease with seasonality, latitude, altitude (Givnish, 1999). Studies on causes of latitudinal diversity gradients in trees show significant support for age-area hypothesis (Fine & Ree, 2006), and tropical niche conservatism hypothesis (Kerkhoff *et al.*, 2014). However, support for both these hypotheses along elevational gradients is weaker (McCain, 2007b, Tiede *et al.,* 2016). Energy-diversity hypothesis on tree species richness was first proposed by Currie & Paquin (1987), who reported that realised annual evapotranspiration (which is correlated to primary production and thus a measure of available energy) explains the variability in tree species richness. However, this hypothesis has been contested in favour of historical hypotheses. Past climatic and geological upheavals have been suggested to have a strong influence on regional ecology effecting diversification and extinction rates and thus shaping species richness from regional to continental and latitudinal scale (Adams & Woodward, 1989; Latham & Ricklefs, 1993; Ricklefs *et al.*, 1999; Ricklefs & He, 2016).

Contemporary climate regimes act as a surrogate for the total of past climatic states and their effects on diversity, and hence the strong regional climate correlations with tree diversity (McGlone, 1996; Fine & Ree, 2006). The most recent climatic upheaval during last glacial period had also played an important role in shaping current diversity patterns. For example, pollen records suggest that elimination of many species from Europe during the last glacial period and their failure to recolonise has resulted in fewer species in Europe than eastern North America and eastern Asia (Adams & Woodward, 1989; Svenning & Flem, 2007). The Himalayan region was also influenced heavily by last Pleistocene glacial maximum and northwest was much cooler and drier in comparison to east Himalaya (see; Ray & Adams, 2001). These climatic upheavals probably resulted in the reduction of forest habitats in northwest Himalaya (Trivedi *et al*., 2013) and most of the biodiversity found refuge in the climatically stable southeastern forests (see Bhattacharyya *et al*., 2014).

Both as a result of these climatic fluctuations and being closer to tropics the east Himalaya is richer than the west Himalaya and considered to be a biodiversity hotspot (Myers *et al.,* 2000, Kreft & Jetz, 2007; Jenkins *et al.*, 2013). On contrary western parts of the Himalaya are situated further north and harbour less biodiversity (Singh & Singh, 1987; Kreft & Jetz, 2007). Studies on elevational diversity patterns of trees in various parts of Himalaya have reported a prominent pattern of mid-elevation peaks (Carpenter, 2005; Oommen & Shankar, 2005; Bhattarai & Vetaas, 2006; Bhera & Kushwaha, 2007; Acharya *et al*., 2011; Khuroo *et al*., 2011). However, both latitudinal and elevational patterns across the entire Himalayan regions and the role of climate in shaping such patterns have not been addressed so far. Given the changes in the historical climate of Himalaya and recolonisation of species in the northwest from an eastern refuge, it is important to evaluate the species range size and nestedness along latitude and elevation to understand the historical processes shaping species richness across Himalaya.

In this chapter, I evaluate tree species richness patterns across Himalaya based on a review of all published floras. Species richness patterns are compared from the published literature with field sampling methods along two elevational gradients, i.e. a more tropical region of North Bengal and Sikkim in the east and a temperate region of Jammu & Kashmir in northwest Himalaya. In both the literature survey and the field sampling, efforts were made to reduce sampling biases highlighted in Chapter-1. For example, I asked if species reported from the Himalaya also occurred in the floras from the Indian plains and if they did, lower limits of species were accordingly adjusted to plains level. For adequate field sampling, I used species accumulation curves to estimate the alpha diversity of trees.

4.2 Methods

4.2.1 Range Interpolation

From the database of 10,503 species of Himalayan plants in Chapter-1 reported in 31 published floras (Appendix-1), I utilised the subset of all tree species reported from Himalaya. For understanding the elevational and latitudinal distribution of tree species, I divided Himalaya into eight sub-regions, i.e. Arunachal Pradesh, Bhutan & Sikkim (including parts of Northern West Bengal), eastern Nepal, central Nepal, western Nepal, Uttarakhand, Himachal Pradesh and Jammu & Kashmir. Information on elevational ranges of all tree species reported from each sub-region was used to interpolate the elevational richness and latitudinal patterns of trees along the Himalaya. Lower elevation ranges of underestimated species were corrected based on the presence of species in the Indian plains (see methods in Chapter-2). A total of 1,382 tree species are presently recorded as growing somewhere in the Himalaya. Of these, 259 species are either native but cultivated or are aliens and thus are not included in the analysis. That excludes 1,123 species which are growing naturally in Himalaya. Elevational richness was calculated based on the number of overlapping ranges in every 100m elevational band within a sub-region. Latitudinal species richness was calculated based on the number of species reported from the floras within each sub-region from east to northwest Himalaya.

4.2.2 Field sampling

I sampled trees along two elevational gradients, one each in the eastern and northwestern Himalaya. In east Himalaya, trees were sampled in northern West Bengal and Sikkim in comparatively undisturbed forests inside protected areas at eight elevational zones in Chapramari Wildlife Sanctuary, Neora Valley National Park and Khangchendzonga National Park. In northwest Himalaya, trees were sampled in relatively undisturbed forests at seven elevation zones in Ramnagar Wildlife Sanctuary, Udhampur, Batote and Kishtwar forest division in Jammu & Kashmir. The elevational bands for sampling were selected after every 500m elevation both in east and northwest Himalaya (Fig 1.1). Multiple plots (n = 50 in east and n = 30 in northwest) at each elevation zone were sampled, each of size 0.1 ha (31.65 x 31.65 m). Because of the steep Himalayan terrain, it is not possible to study a single large plot, so I decided to enumerate trees in small plots at each elevation for a total of 5ha area in east and 3ha area in the northwest. The first plot was selected as near to the indicated elevation as possible. To maximise counts of tree species at each elevation, I then traversed horizontally and set the next plot upon encountering a previously unrecorded tree species, or after 100 meters, whichever came first. The altitudinal location of all plots was restricted to a band ±100m of each designated elevational, with most clustering close to the designated elevation. I recorded GPS information (latitude, longitude and elevation) of every plot and girth at breast height (gbh) of every tree > 30 cm in girth.

Because peaks in plant diversity have been reported at mid-elevations, I conducted additional surveys at four locations, one each at foothills (200m in the east, 450m in the northwest) and 2000m both in the east and northwest Himalaya. At all these four elevations, I found a sufficiently flat location that I could survey a contiguous 5ha grid (200 × 250 m). In these plots all trees >30 cm in girth size have now been numbered with tree-tags; every tree has been identified, and girth at breast height measured. Trees were identified on site using floras (Plounin & Stainton, 1984; Grierson & Long, 1983-2001; Ghosh & Mallick, 2014). I photographed all species, preferably during the flowering or fruiting stage to confirm identification. If the identity of a tree was uncertain, a pressed specimen was taken for identification at Wildlife Institute of India, Dehradun herbarium. At present ten species included in the dataset remain unidentified, but single individuals represent 8 of these. The complete dataset is shown in Appendix-2,3.

4.2.3 Data analysis

Latitudinal species richness was evaluated based on the number of species reported in each of the eight sub-regions, whereas elevational richness was calculated from range interpolation and species encountered in field sampling. From the digital elevation model (DEM), I resampled the Himalayan region into 1145 grids of size 0.2×0.2 degrees each. Species richness was assigned to each grid using its elevational information and number of species ranges overlapping at that elevation in each of the sub-regions. A species richness map for trees was obtained across the Himalaya using the inverse distance weight interpolation (kriging) method in the R package "gstat" (Gräler *et al.*, 2016).

I calculated beta diversity based on the presence/absence of species in different sub-regions using the formula: $\beta = (b+c)/(2*a+b+c)$ where a = species common between sub-regions, b = species unique to the first sub-region and c = species unique to the second sub-region. Beta diversity and its turnover component along the sub-regions was calculated using R package "betapart" (Baselga *et al.,* 2017). Nestedness value for tree species between different sub-regions was calculated using a nestedness metric based on overlap and decreasing fill (NODF) by Almeida-Neto *et al.* (2008) in the R package "vegan" (Oksanen *et al.*, 2016).

To test the range sizes of tree species along latitudinal and elevational gradients, I used Steven's method (Steven, 1989). I averaged the elevational ranges of all species in the eight sub-regions along the latitudinal gradient across Himalaya. Along elevational gradients, I averaged the elevational ranges of all tree species in every 100m elevational band of Himalaya. To compare the differences in mean range size between tropical east and temperate northwest, I averaged the elevational ranges separately for species present in Arunachal Pradesh and Jammu & Kashmir.

4.3 Results

4.3.1 Latitudinal diversity gradient

Tree species richness decline fivefold from east to northwest Himalaya (Fig. 4.1). The highest number of 793 species (excluding cultivated and aliens) are reported from Bhutan & Sikkim sub-region in the east whereas the lowest number of 159 species are reported from Jammu & Kashmir in the northwest. The decreasing species richness from east to northwest Himalaya is consistent with the popular hypothesis of latitudinal diversity gradient (Hillebrand, 2004) explicating declines in species richness with increasing latitude. However, Arunachal Pradesh in the easternmost region of Himalaya is an exception from this pattern. Comparatively fewer species are reported from Arunachal Pradesh which may be a result of under-exploration in the region. Species richness map based on the overlapping of ranges in every 100m elevation band across eight sub-regions of Himalaya shows a decline in species number both along the elevation as well as from east to northwest Himalaya (Fig. 4.2).

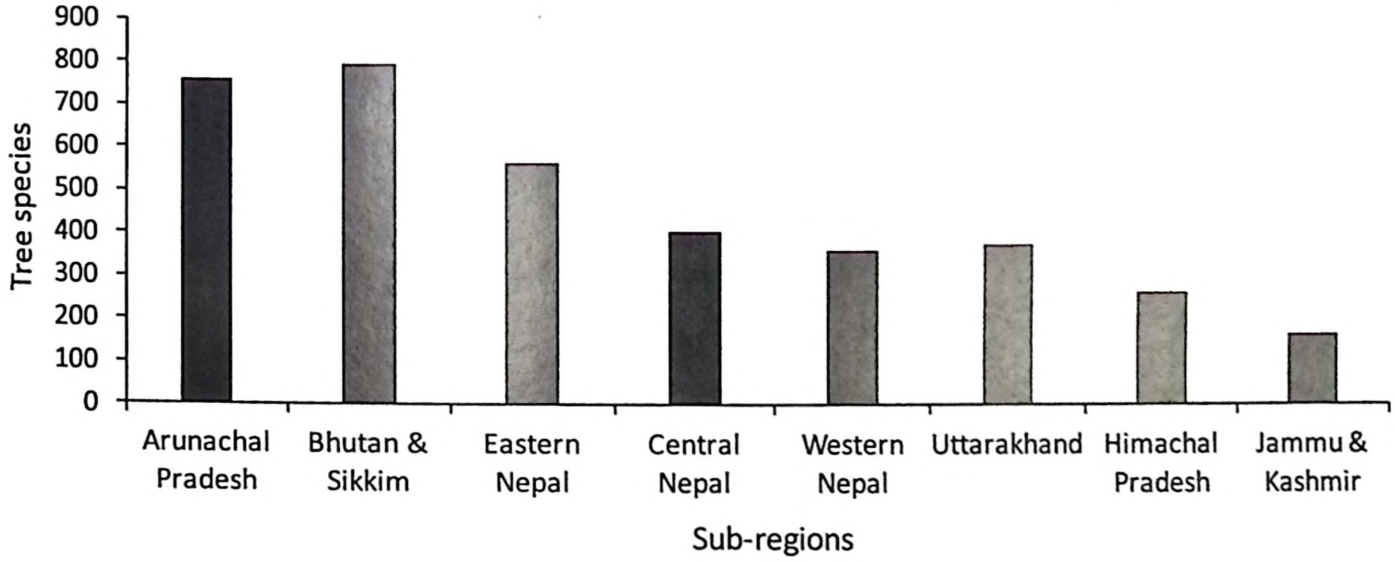

Figure 4.1 Tree species richness (excluding cultivated and aliens) in eight different sub-regions shows a fivefold decline in species number from east to northwest Himalaya.

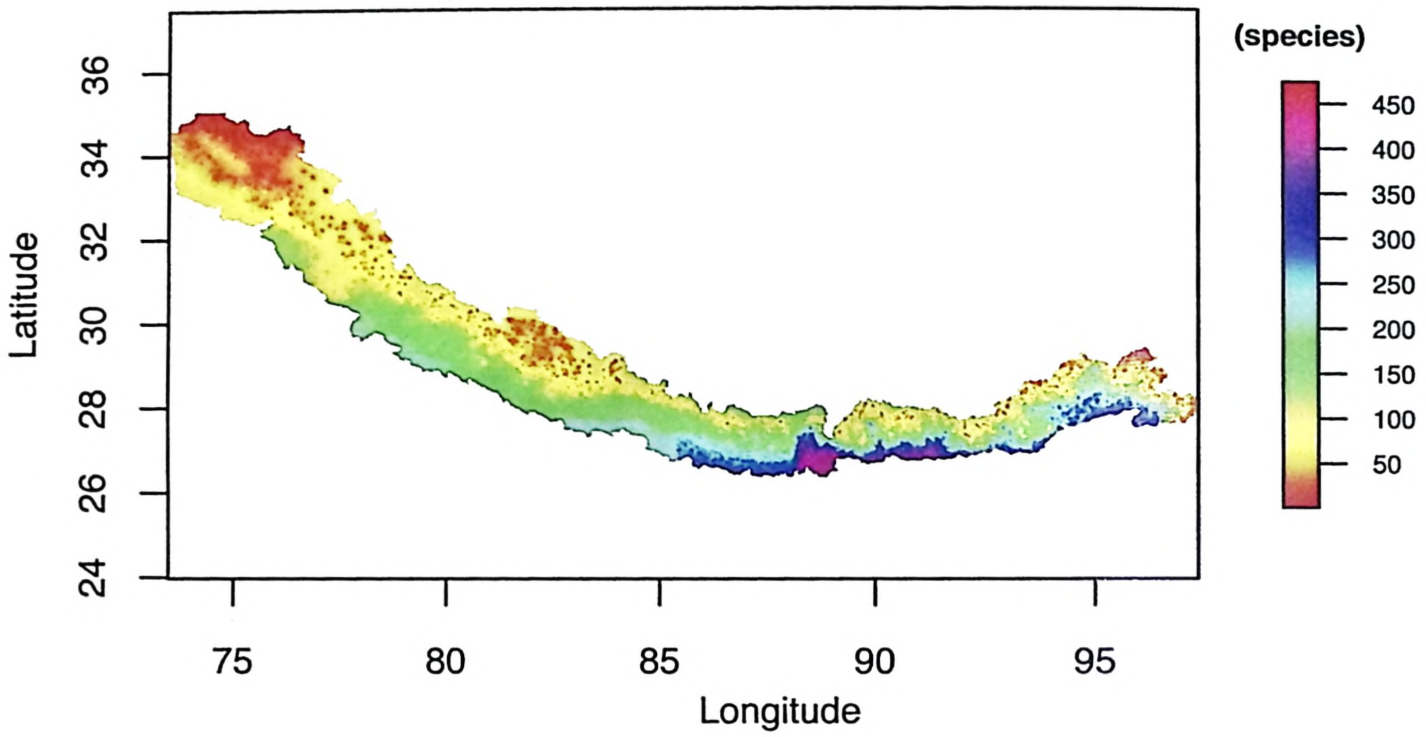

Figure 4.2 Tree species richness map based on range interpolation of species shows a decline in species richness along latitudinal and elevational gradients of the Himalaya.

4.3.2 Latitudinal beta diversity and nestedness

Beta diversity of tree species shows two turnover zones along the latitudinal gradient of Himalaya. Highest beta diversity is between Eastern Nepal and Central Nepal followed by Uttarakhand and Himachal Pradesh (Fig. 4.3a). Thus beta diversity divides the Himalayan region into three distinct floristic regions, i.e. eastern, central and western Himalaya. However, the turnover component of beta diversity (Fig. 4.3b) clusters the sub-regions into three groups, i.e. Arunachal Pradesh in eastern, Bhutan to West Nepal in central and Uttarakhand to Jammu & Kashmir in the western Himalaya.

Figure 4.4 shows latitudinal nested distribution patterns of tree species across sub-regions from east to northwest Himalaya. Latitudinal distribution of trees shows that most of the species in northwestern Himalaya are nested subset of the eastern Himalaya. A total of 90 species are distributed across all eight sub-regions which constitute ~57% of species in Jammu & Kashmir in the northwest but only ~12% species of Arunachal Pradesh in the easternmost region of the Himalaya. However, considering Arunachal Pradesh as data deficient, 117 species are distributed from Bhutan region to Jammu & Kashmir which shows even higher sharing of species between east and northwest Himalaya. East Himalayan sub-regions also show the highest number of unique species as compared to the northwest.

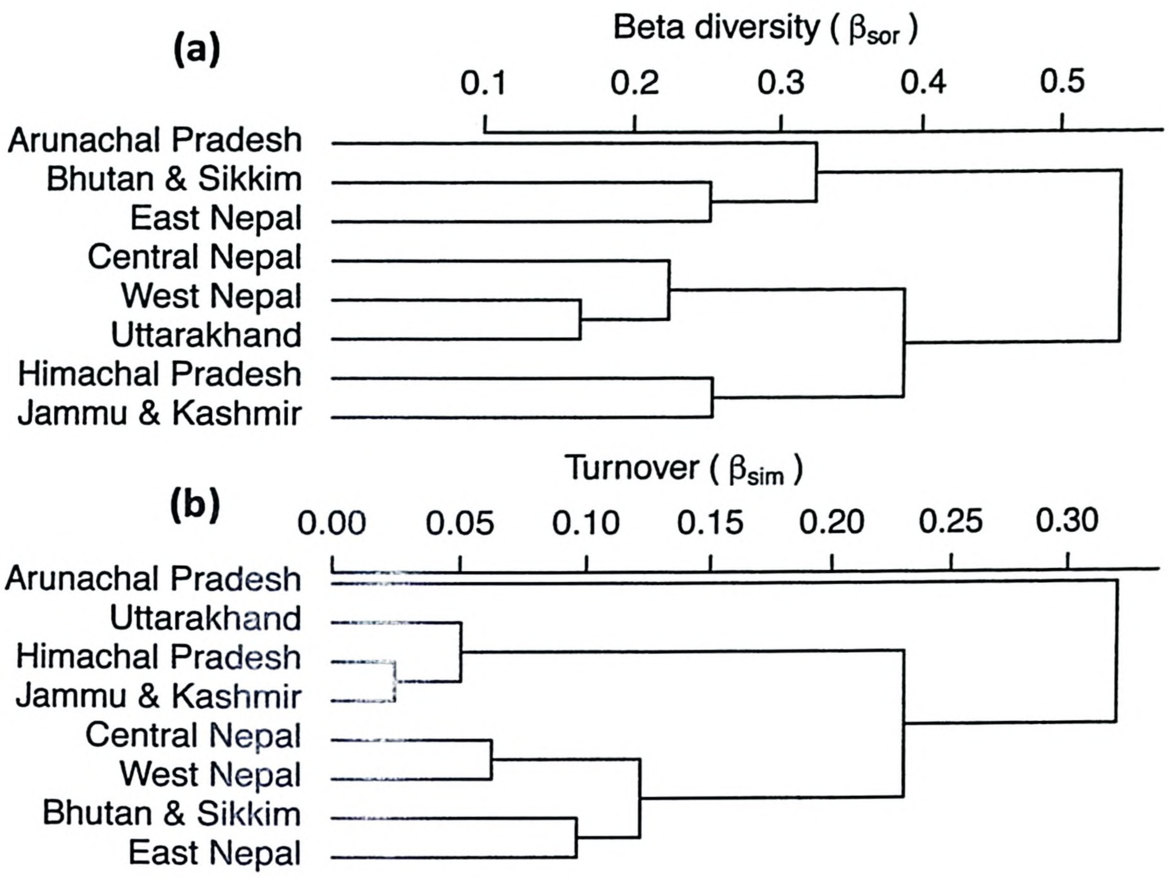

Figure 4.3 Beta diversity of trees species from east to northwest Himalaya **(a)** Beta diversity **(b)** turnover component of beta diversity.

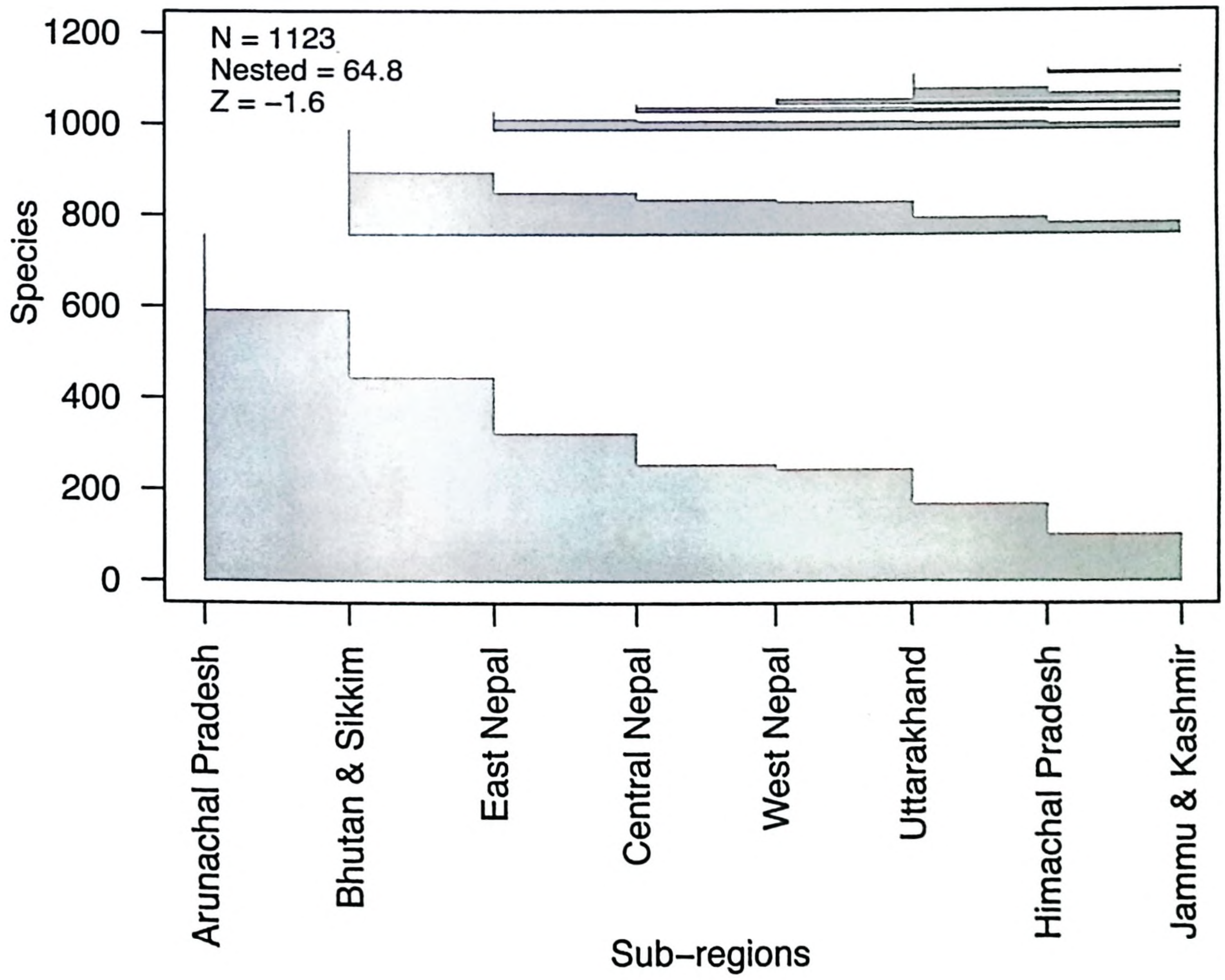

Figure 4.4 Nested distribution pattern of latitudinal ranges of tree species in Himalaya. Y-axis represents individual species, and the grey bars represent its latitudinal extent along the x-axis.

4.3.3 Elevational range sizes across latitude

Along the latitudinal gradient, the mean elevational range of trees was least in easternmost sub-region of Arunachal Pradesh, and the range size increases consistently from east to northwest Himalaya (Fig. 4.5). Along the elevational gradient of whole Himalaya, mean range size of species again increase with increasing elevation (Fig. 4.6). When compared, mean elevational range size in tropical Arunachal Pradesh is much smaller than temperate Jammu & Kashmir in low elevations. However, at the higher elevation, the difference in range size is very less between Arunachal Pradesh and Jammu & Kashmir. These results are consistent with the tropical niche conservatism hypothesis that species in tropical climates tend to have smaller niche size as compared to the more temperate region where species tends to have broader niches with large range sizes. Both the latitude and the altitude affect the niche width of the species (elevational ranges) similarly.

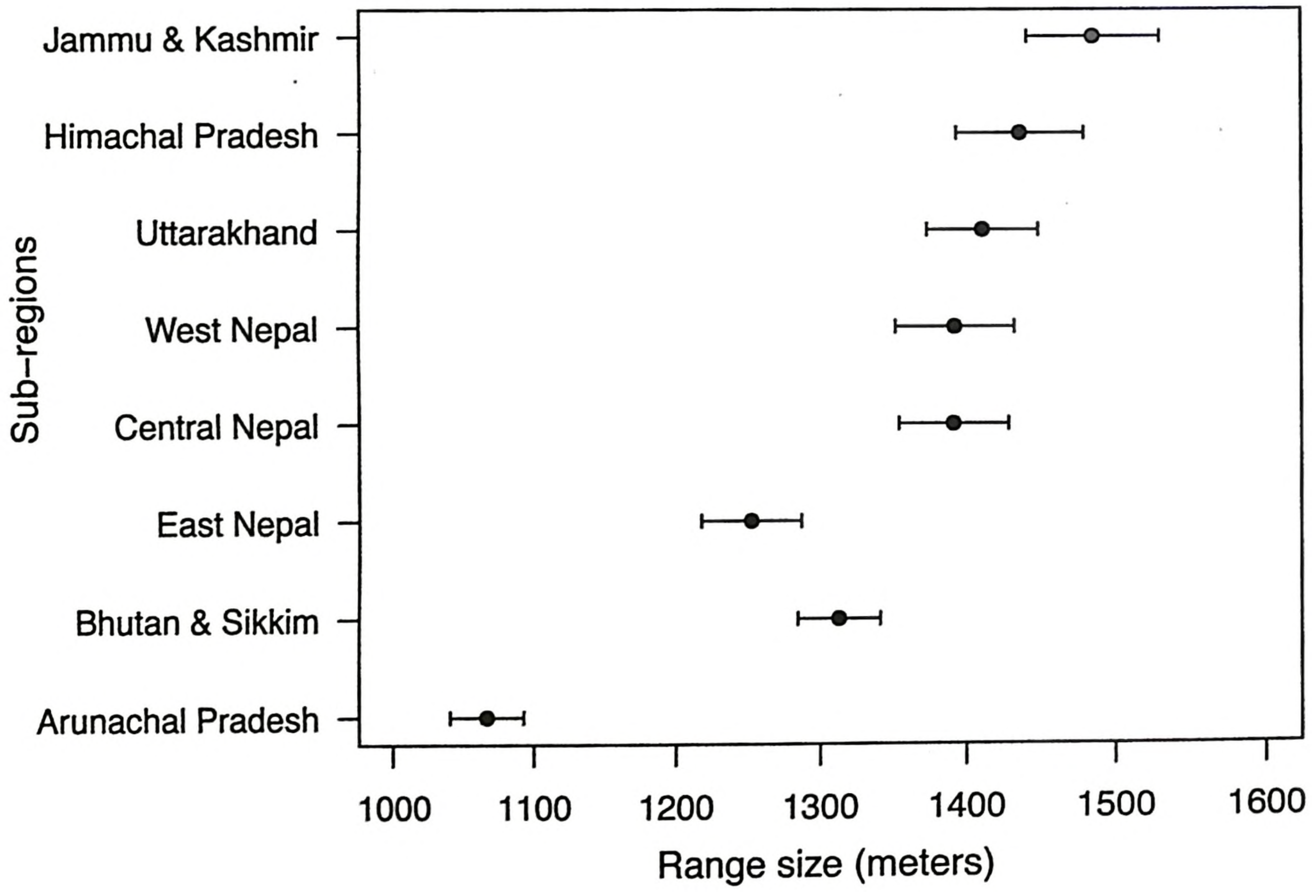

Figure 4.5 Mean elevational range size of trees across different sub-regions is lowest in the east and increases towards northwest Himalaya. Bars show mean values with standard errors.

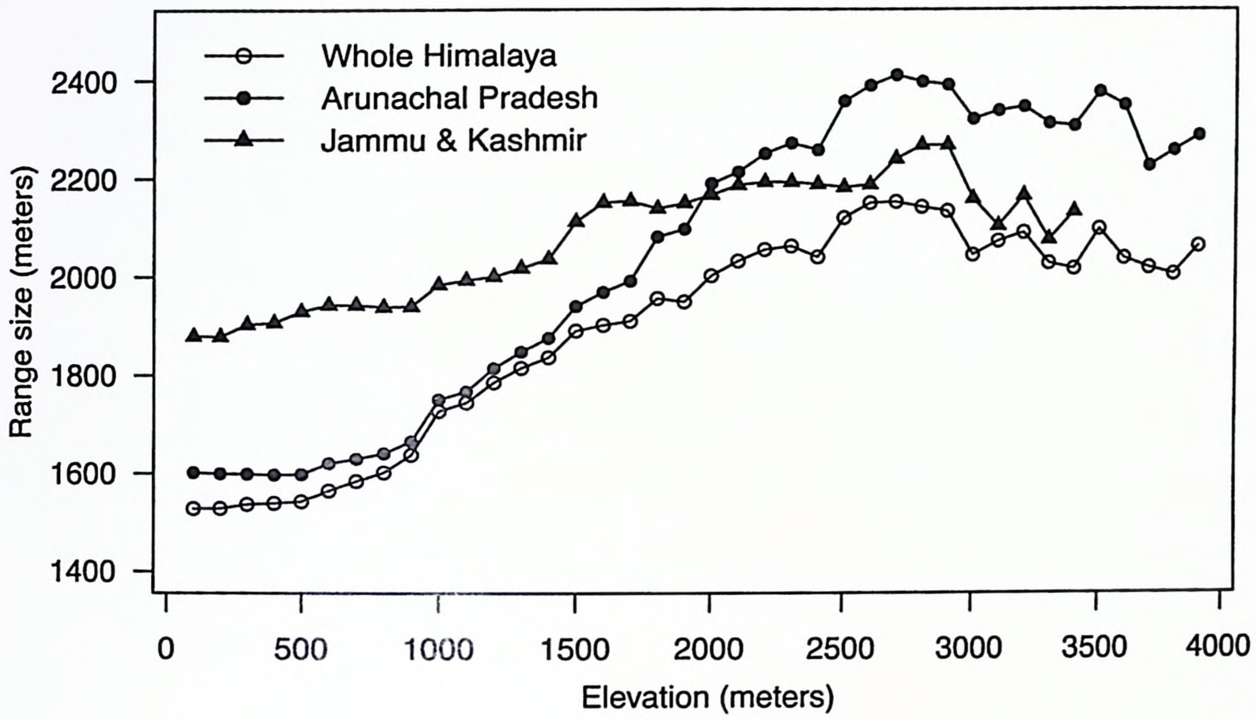

Figure 4.6 Mean elevational range of tree species along the elevational gradient for the whole Himalaya, tropical Arunachal Pradesh and temperate Jammu & Kashmir.

4.3.4 Elevational richness patterns

Across the whole Himalaya combined, interpolation of elevational ranges of 1,123 species with available range limits in Himalayan floras, shows a low-elevation peak in tree species richness at 500-1000m (Fig. 4.7a). The bias of range underestimation for foothill species was addressed by cross-checking the distribution of all Himalayan species in the Indian plains, which showed 318 species with underestimated lowest limits. After modification of lower bounds of underestimated species, the number of species at foothills is increased, but the peak in species richness at 500-1000m is still retained. Species were divided into genera with tropical and temperate affinities following Wu (1991). Richness curves for species belonging to tropical affinities show a similar low-elevation peak, whereas those with temperate affinities shows a mid-elevation peak. The tropical and temperate species merge at approximately 2000m. This indicates that mixing of tropical-temperate species does not generate species richness peak along the Himalayan elevational gradient (Fig 4.7b).

Elevational species richness patterns of trees based on range interpolation in the sub-regions shows a species richness peak in the eastern Himalaya, e.g. Arunachal Pradesh, Bhutan & Sikkim, Nepal, whereas the peak disappears towards northwest (Fig. 4.8). These results suggest that the mid-elevation peak is present only in tropical regions of eastern Himalaya.

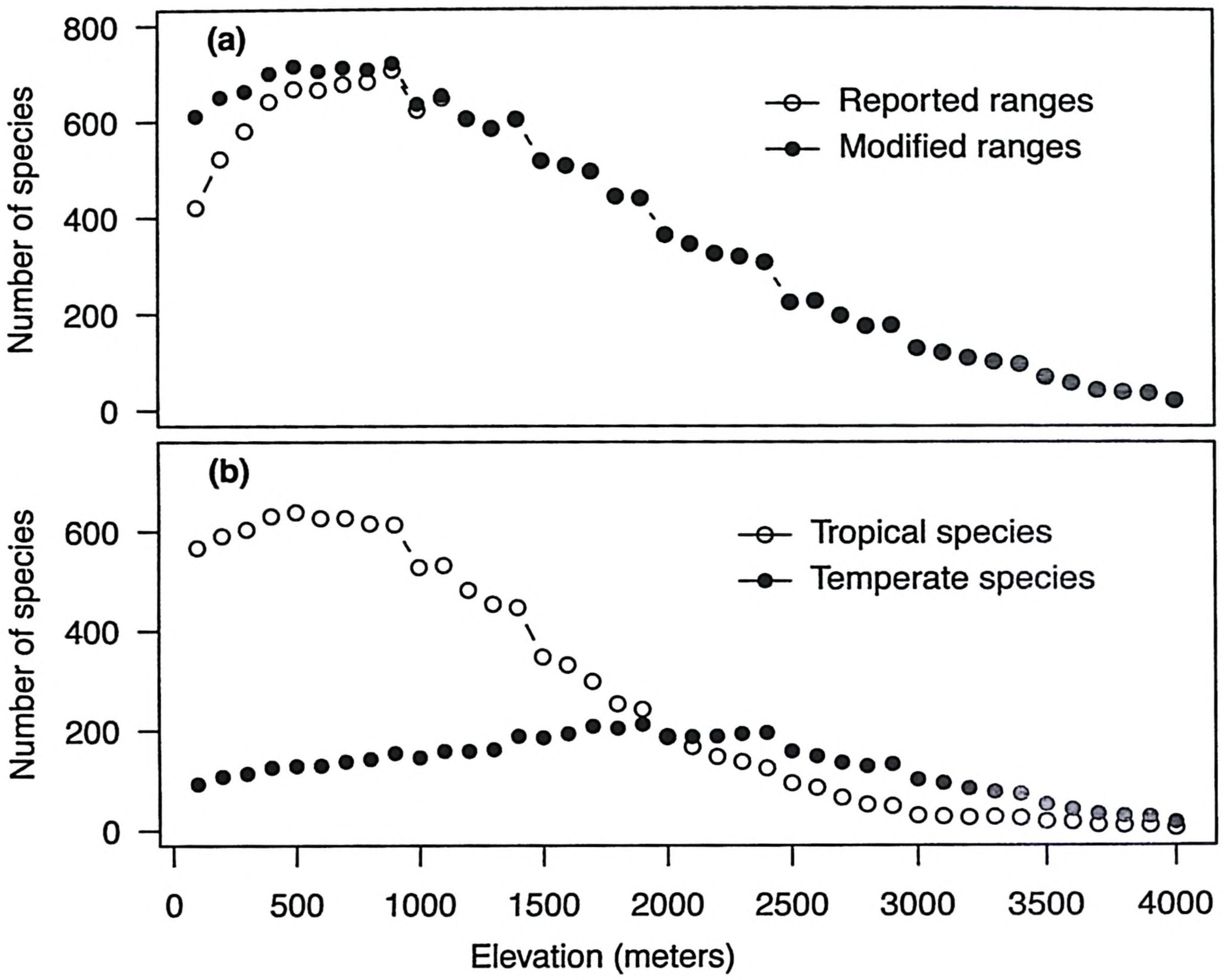

Figure 4.7 Elevational richness patterns of tree species in Himalaya **(a)** Comparison of species richness obtained from elevational ranges reported in the floras (dark circles) and modified ranges for species present in Indian plains (open circles). **(b)** Elevational richness patterns of species belonging to tropical and temperate affinities.

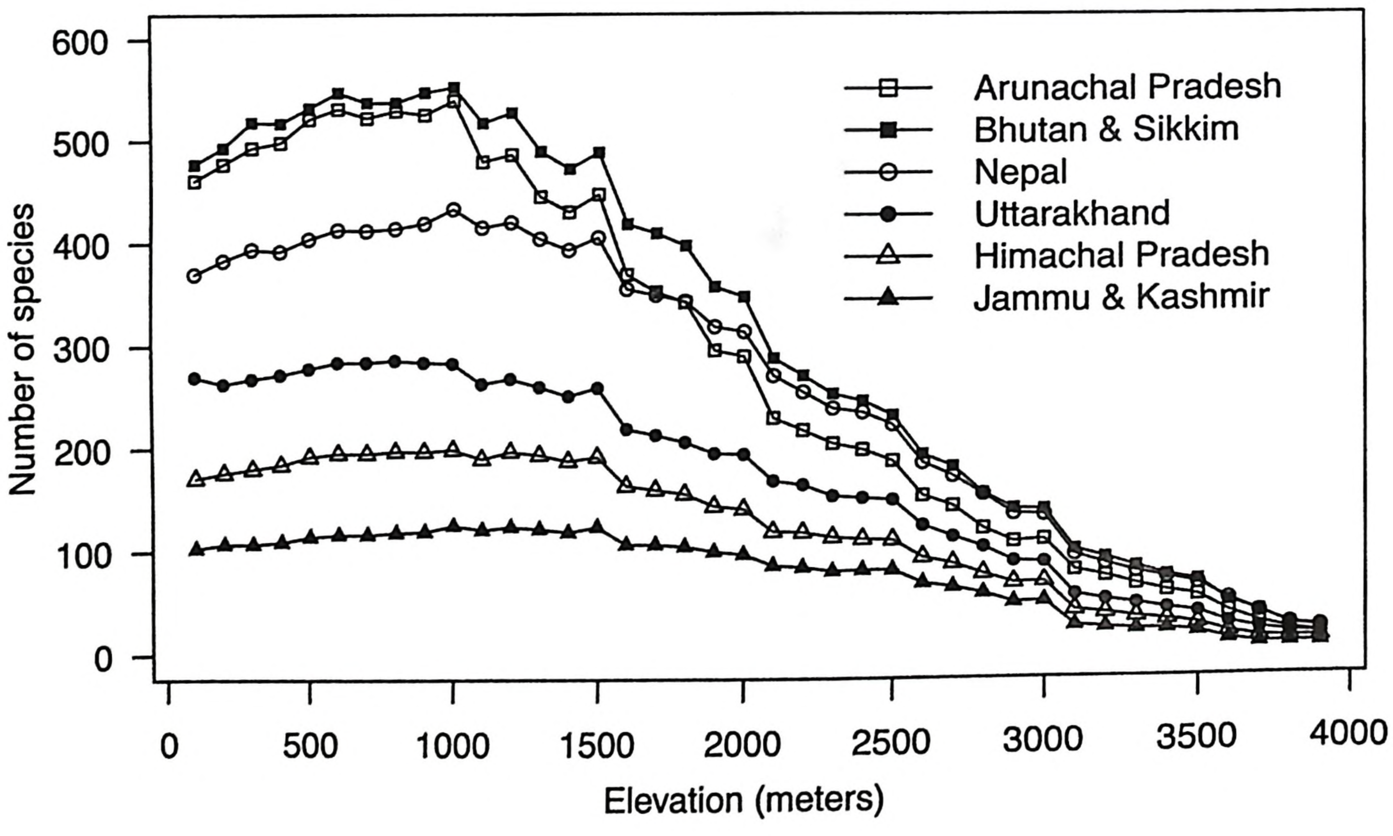

Figure 4.8 Elevational richness of tree species in six sub-regions extending from east to northwest Himalaya. East show a peak in richness which disappears in northwest Himalaya.

4.3.5 Comparison of sampling methods

Elevational richness patterns based on range interpolation and field sampling along the two elevational gradients are more or less consistent. Species richness along the northwest Himalayan elevational gradient in Jammu & Kashmir shows a monotonic decline with elevation in both sampling methods (Fig. 4.9a). However, species richness along the east Himalayan elevational gradient in North Bengal & Sikkim shows a peak between 500-1000m by range interpolation and a peak at 500m by field sampling method (Fig 4.9b). Overall species richness is higher at all elevations in the east than northwest by both sampling method.

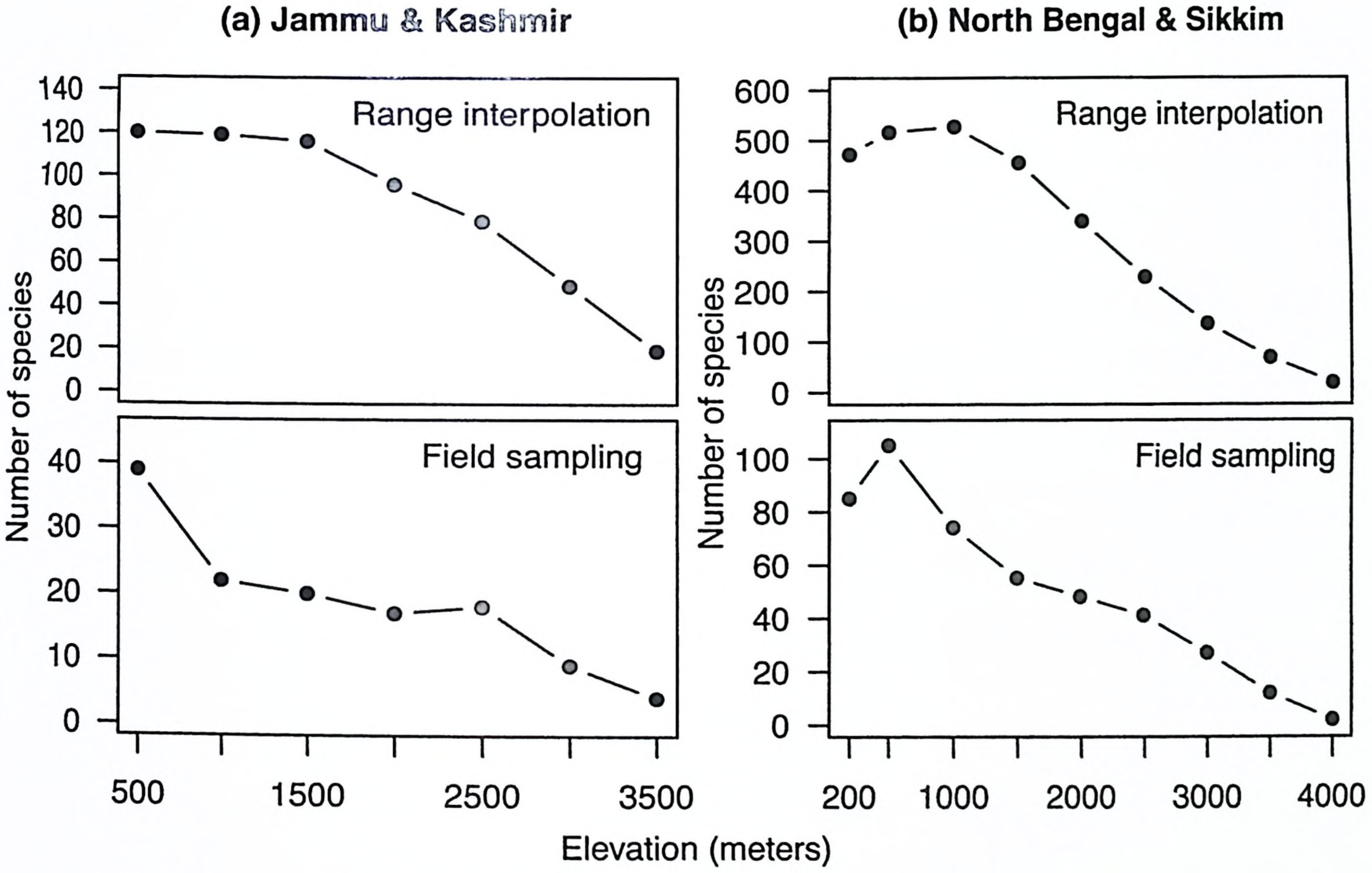

Figure 4.9 Comparison of tree species richness for different sampling methods along the elevational gradients of North Bengal & Sikkim in east and Jammu & Kashmir in northwest Himalaya.

4.3.6 Tree densities and girth size

Tree density and girth size do not vary in a consistent manner along the elevational gradient both in the east and the northwest Himalaya. Tree density is highest in the 1000m and 2000m elevation zones in the east and at 500m in the northwest Himalaya (Fig. 4.10). Tree girth is an important attribute as it provides information on biomass accumulation in the community. Girth size of trees is smallest at the edges of elevational gradients, i.e. at

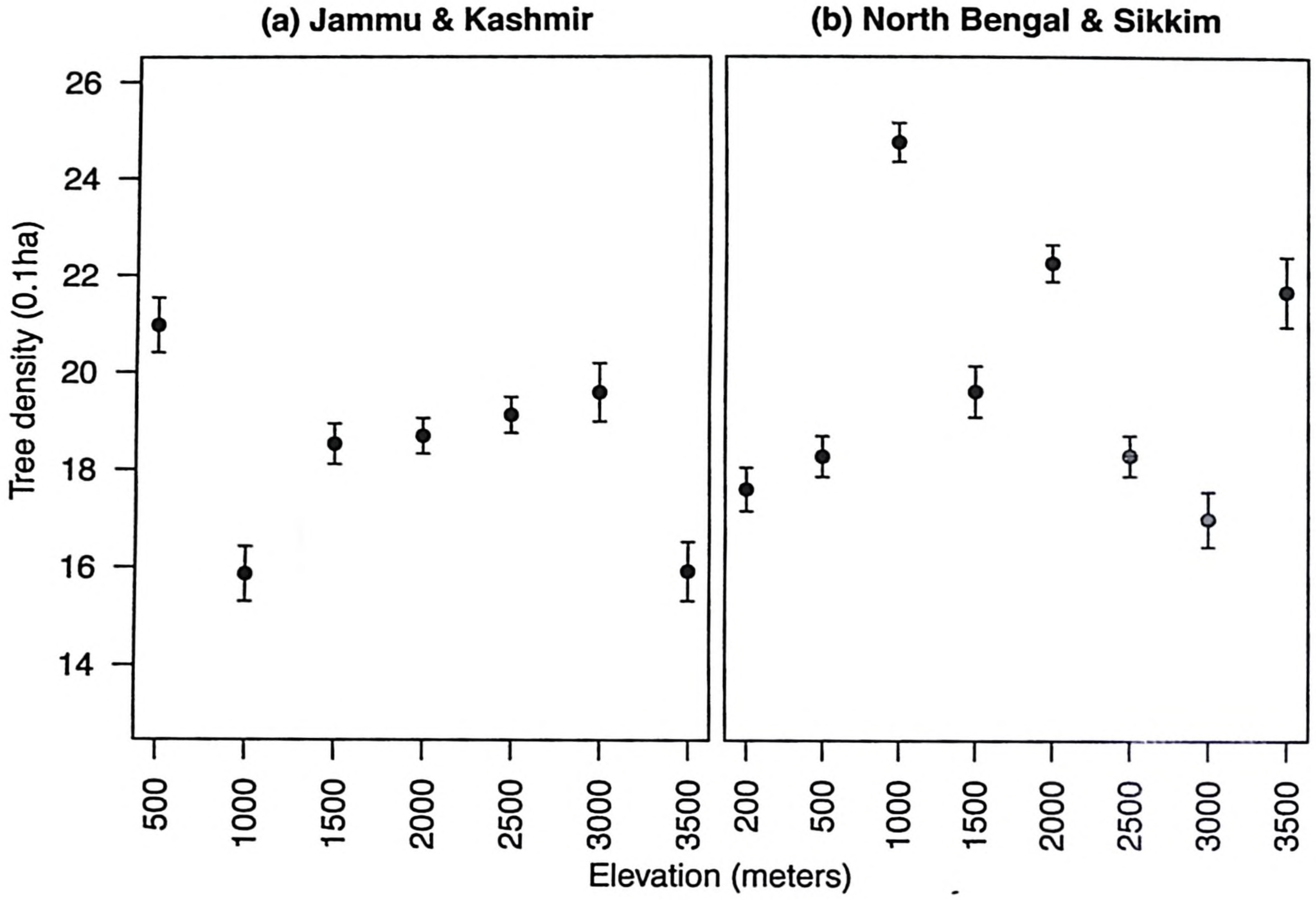

Figure 4.10 Comparison of average tree densities with the standard error along the elevational gradients of North Bengal & Sikkim in east and Jammu & Kashmir in northwest Himalaya.

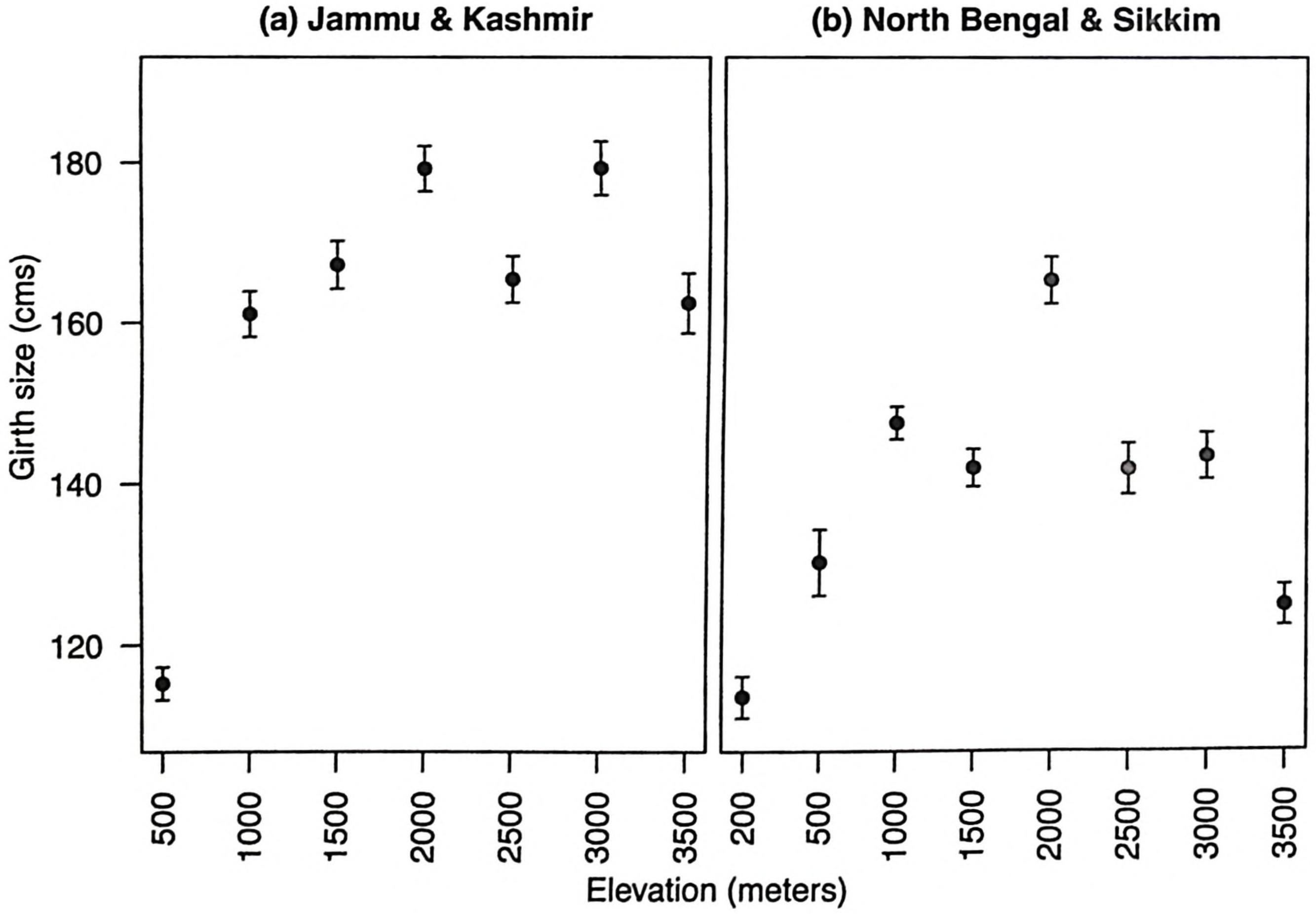

Figure 4.11 Comparison of the average tree girth size with the standard error along the elevational gradients of North Bengal & Sikkim in east and Jammu & Kashmir in northwest Himalaya.

foothill and treeline and largest at the mid-elevations in both the east and northwest Himalaya (Fig. 4.11). Notably, mid-elevations, which have the largest girth sizes, are prominently covered by temperate oaks forests in the eastern Himalaya and conifer forests in northwest Himalaya. These results suggest some climatic control on the metabolism of species resulting in more accumulation of biomass at those elevations.

4.3.7 Additional sampling at foothills and mid-elevations.

Four grids of size 5ha were also sampled one each at foothills and mid-elevation both in the east and the northwest Himalaya. Results show a much higher number of species in the foothills as compared to mid-elevation both in the east and northwest Himalaya. In the east, more species in total are encountered across the smaller sampling units (0.1ha plots) than in the larger grid, although the density and basal area were higher at the single large plot. In northwest also the results were similar with higher species richness in small plots. Overall the density and basal area tends to be higher at the mid-elevation zones both in east and northwest Himalaya. Sharing of species between the two sampling methods in east is lesser in foothills (50.4 %) than 2000m (67 %) presumably because of the larger total number of species (105 in the foothills, 52 at 2000m). In northwest Himalaya, sharing of species between the single and multiple plots was 58% at foothills and 40% at 2000m. These results again confirm that foothills are more diverse than the mid-elevations of both east and northwest Himalaya, and the species richness peak in east is present at elevations adjacent to the foothills.

Table 4.1 Comparison of results obtained from sampling of a single 5ha grid and multiple small (0.1ha) plots with a total sampling area of 5ha in the east and northwest Himalaya.

Elevation (meters)	**Single grid (5 ha)**			**50 plots of size 0.1ha**			**Total species**	**Species sharing (%)**
	Species	**Density** trees/ha	**BA** m^2/ha	**Species**	**Density** trees/ha	**BA** m^2/ha		
200 east	71	247	31.37	87	177	26.25	105	50.4
2000 east	38	327	47.26	47	223	65.49	52	67.3
450 west	33	202	23.12	41	210	26.39	48	58.0
2000 west	6	263	55.63	15	187	54.57	15	40.1

Abbreviations: BA; Basal area, Ha, Hectare, m^2; meter square

4.4 Discussion

Along the latitudinal gradient of Himalaya, tree species richness is fivefold higher in the east as compared to the northwest. These results are consistent with the global patterns of latitudinal diversity gradients in trees (Givnish, 1999; Leigh *et al.*, 2004; Kreft & Jetz, 2007). As shown in Chapter-2, Himalaya shows a similar climatic gradient with approximately fivefold higher precipitation and considerably less seasonality in the east as compared to northwest Himalaya. Tree species richness shows a strong positive correlation (r = 0.89) with annual precipitation and a strong negative correlation with temperature seasonality (r = -0.8) across the Himalaya. These results are consistent with the energy-diversity hypothesis elucidating that environments with higher available energy are richer in species (Currie & Paquin, 1987; Kreft & Jetz, 2007).

Beta diversity and nestedness analysis shows that majority of north-western tree species are a nested subset of species from east Himalaya and turnover show two distinct zones. The climate has been reported as a major driver of beta diversity along the latitudinal gradient (Davidar *et al.*, 2007). Mean species range size was smaller in the tropical east and low elevations as compared to the temperate northwest and higher elevations. These results are consistent with Rapaport's rule (Stevens, 1989) that species ranges are comparatively smaller in tropical regions with more favourable climate in east Himalaya than the harsh temperate regions in northwest Himalaya. Overall, these findings point to the larger body of research which highlights the importance of water-energy variables as an important determinant of plant distribution and richness at broad spatial scales (O'Brien *et al.*, 2000, Hawkins *et al.*, 2003, Kreft & Jetz, 2007).

Studies on Himalayan bird assemblages also show similar gradients with twice the number of species in the east as compared to the northwest (Price *et al.*, 2011; White, 2016). These studies showed that eastern Himalaya acted as potential refuge for avifauna during glacial maximum, and northerly range limits of the recolonizing Himalayan avifauna are strongly controlled by climate (Price *et al.*, 2011), but other ecological factors like inter-specific interaction, dispersal propensity, topography also play an important role in setting species ranges (Srinivasan *et al.*, 2014; White, 2016). This could be true in case of plants in general and trees in particular, but so far, no such studies have been conducted on plants.

I evaluate the richness patterns of trees which show even higher (fivefold) decline of species as compared to the avifauna from east to northwest Himalaya. These differences may be a consequence of variation in dispersal ability, e.g. birds are highly mobile flying animals, but plants disperse by propagules, which in turn will be influenced more strongly by the above-mentioned factors. Investigation of the role of ecological factors like dispersal modes in shaping such diversity gradients of trees in Himalaya is crucial. However, basic data on dispersal syndromes for most of the Himalayan tree species is still missing and it is necessary to conduct more studies for generation of such data. Evaluating the role of climate and ecological interactions like dispersal, competition, topography etc. on the latitudinal range limits of species will help in disentangling the relative roles of these factors for shaping latitudinal gradients of trees in Himalaya.

Along elevational gradients, a unimodal peak at low-elevation is present in the east Himalaya however the peak flattens and turns into a low-elevation plateau or monotonic decline with elevation in the northwest Himalaya. Passerines in Himalaya also show similar pattern with a mid-elevation peak in east and low-elevation plateau in northwest with the exception that the elevation of peak is much higher in birds than plants (Price *et al.,* 2011). These elevational richness patterns in trees are also consistent with both the methods, i.e. range interpolation and field sampling. Previous studies have also reported tree species richness peaks from different sub-regions across Himalaya, but the position of the richness peak is not consistent. For example, studies based on field sampling of trees have reported richness peaks at comparable elevation in the Himalaya, e.g. at 600-800m in south-eastern Nepal (Bhattarai & Vetaas, 2003), at 750-1000m in eastern Nepal (Carpenter, 2005) and 600-1000m in Arunachal Pradesh (Behera & Kushwaha, 2007). However, Acharya *et al.* (2011) reported a peak in trees richness at 1500m in Sikkim. Possible explanations for anomalous results of Acharya *et al.* (2011) is relatively small samples at each elevation and/or study in more disturbed locations. Similarly, based on range interpolation a similar peak has been reported at 1000m in Nepal (Bhattarai & Vetaas, 2006).

Addition of 5ha sampling area in a single grid at foothills and 2000m elevation shows a much higher increase in species at foothills, indicating that low-elevations are more diverse than that of 2000m elevation in Himalaya. However, unlike species richness, tree density and girth size does not show any consistent pattern along elevational gradient both in the east and northwest Himalaya. The largest girth size was at mid-elevations both in east and northwest, whereas highest density was at foothills in the northwest and 1000m in east Himalaya. These results are consistent with the facts that world's temperate forests have highest biomass density as compared to tropical and boreal forests (Keith *et al.*, 2009). Community structure and dynamics of trees is mainly controlled by metabolism and bio-mechanistic processes (Norberg, 1988; West *et al.*, 2009), whereas species establishment in a forest community could be the first step which is primarily controlled by local climatic conditions like temperature and precipitation (Loranger *et al.*, 2016).

Competition for resources controls various metrics like tree density, girth size, tree heights, canopy structure etc. which have a strict relationship with each other (Norberg, 1988; Stephenson *et al.*, 2014). For example, size class and spatial separation of trees is a function of water and nutrients uptake from a substrate (West *et al.*, 2009), and mass growth rate in a majority of tree species increases continuously with increase in overall tree size (Stephenson *et al.*, 2014). As shown by Keith *et al.* (2009), my results also indicate that relatively cold temperatures and moderately high precipitation at temperate mid-elevations may have resulted in fast growth but slow decomposition, thus show larger girth sizes. It may also be that these temperate multilayered forests with minimal human disturbance have accumulated more biomass than the low-elevation forests which are prone to higher levels of anthropogenic disturbance.

Like the latitudinal diversity gradients, various hypothesis based on climate, niche conservatism, source-sink dynamics, mid-domain effect etc. have been proposed for elevational richness patterns (Grytnes & McCain, 2013), but currently, the reasons are not fully resolved. Previous studies have attempted to correlate climate with elevational richness patterns in Himalaya (e.g. Acharya *et al.*, 2011; Li & Feng, 2015: Kluge *et al.*, 2017). However, the results are not consistent partly because of the associated biases in the sampling methods and given the relatively few climate stations in the region. Comparison of climate data from different sources also varies. For example, my data on precipitation and temperature extracted from worldclim.org (Hijmans *et al.*, 2005) and actual evapotranspiration data from CGIAR (Trabucco & Zomer, 2010), shows a linear decline with increasing elevations in the study area. Similarly, Acharya *et al.*, (2011) reported a linear decline in precipitation and temperature with elevation between 700m and 4200m in Sikkim. On the other hand, remote sensing (Bookhagen & Burbank, 2010) and models based on measured atmospheric pressure and topography (Gerlitz *et al.*, 2015) suggest a peak in precipitation at low-elevations.

So far, climate (O'Brien *et al.*, 2000, Kreft & Jetz, 2007) and dispersal (Gryntes, 2003; Grytnes *et al.*, 2008) based explanations provide little evidence for the mechanism of elevational richness patterns in Himalaya. Thus, it is very important to collect more accurate climatic data with temporal and spatial coverage across Himalaya for a better understanding of the relationship of species richness with the climate. However, other hypotheses like niche conservatism, species-area relationship, geometric constrains etc. do not provide sufficient evidences to explain the elevational richness patterns across Himalaya. More details on the role of climate and dispersal for the setting position and causes of tree species richness peak along elevational gradient in the eastern Himalaya are discussed in Chapter-5.

CHAPTER 5

Position and causes of elevational richness peak in eastern Himalaya

CHAPTER 5

Position and causes of elevational richness peak in eastern Himalaya

5.1 Introduction

It is an appreciated fact that as one proceeds from low elevations to mountain peaks, species richness in many clades does not show a monotonic decline (Grytnes & McCain, 2013; Guo *et al.*, 2013; Colwell *et al.*, 2016). Grytnes & McCain (2013) in their global review on elevational diversity described three different patterns including a monotonic decline but also a low-elevation plateau and a unimodal mid-elevational peak. Mid-elevation peaks have been reported to be the most familiar pattern along the elevational gradients (Rahbek 1995, 2005; Kessler *et al.*, 2011; Grytnes & McCain, 2013; Guo *et al.*, 2013). A number of explanations have been proposed for the presence of peaks at mid-elevations. These include climate (notably high productivity at mid-elevations), a null model mid-domain effect based on the idea of geometric constraints, habitat heterogeneity, source-sink dynamics, species-area relationships, historical differences in diversification rate at different elevations with climatic niche conservatism limiting dispersal, mixing of different floras, and competition from groups that show a linear decline with elevation (Lomolino, 2001; Kozak & Wiens, 2010; Grytnes & McCain, 2013; Price *et al.*, 2014; Colwell *et al.*, 2016). In this chapter, I evaluate elevational correlates of tree species richness in the eastern Himalaya. Although no general review has specifically focused on trees, Guo *et al.* (2013) concluded that across the globe tree richness peaked at mid-elevations (on average 1400m).

The eastern Himalaya is thought to be one of the most species-rich places in the world in general (Myers *et al.*, 2000; Jenkins *et al.*, 2013), as well as specifically for vascular plants (Kreft & Jetz, 2007). Several studies in Nepal, Sikkim and Bhutan have described elevational patterns for various plant groups, including all seed plants (Grytnes & Vetaas, 2002; Kluge *et al.*, 2017; Manish *et al.* 2017), trees specifically (Carpenter, 2005; Bhattarai & Vetaas, 2006; Behera & Kushwaha, 2007; Acharya *et al.*, 2011) and ferns and bryophytes (Bhattarai *et al.*, 2004; Grau *et al.*, 2007; see Table 1.1). They (and studies of elevational gradients more generally) have primarily used two methods. First, species elevational ranges are interpolated from secondary literature sources (*range interpolation*) where a species is assumed present everywhere between its highest and lowest record (Grytnes & Vetaas, 2002;

Bhattarai *et al.*, 2004; Bhattarai & Vetaas, 2006; Grau *et al.*, 2007; Kluge *et al.*, 2017; Manish *et al.*, 2017). Second, limited *field sampling* has been used to estimate local richness at selected sites (Bhattarai & Vetaas, 2003; Carpenter, 2005; Behera & Kushwaha, 2007; Acharya *et al.*, 2011). All studies show a mid-elevation peak in species richness, but the position of the peak varies with the method. Notably, studies based on range interpolation from the secondary literature tend to have a higher peak in species richness than estimates of local richness from field samples (Table 1.1).

As highlighted in Chapter-1 both methods are prone to the risk of deviation from actual patterns of richness. Range interpolation may result in underestimation of the higher and lower limits, with a consequent accumulation of species at mid-elevations (Grytnes & Vetaas, 2002). On the other hand, field sampling circumvents these problems, but results in only a small fraction of the total richness being recorded, and raises issues of how to ascertain true richness at a location (Lomolino, 2001; Gotelli & Colwell, 2001; Slik *et al.*, 2015). For example, on a New Caledonian elevational gradient, Ibanez *et al.* (2016) show that same area plots with large trees tend to contain fewer individuals and have fewer species than plots with small trees, and this can obscure elevational trends. Given the different problems associated with each method, concordant results would provide supporting evidence that the patterns are real.

I use both range interpolation and field sampling methods in a detailed study of tree species richness along an elevational gradient in eastern Himalaya. I show that a comprehensive survey of the literature reduces the magnitude of the richness peak in comparison to previous studies, and that field sampling results are concordant with the literature survey. Having confirmed the presence of a peak at 500-1000m, I examine underlying causes, by asking how species richness is associated with diversity, turnover (beta diversity), abundance distributions, and climatic variables.

Climate has been thought to be a particularly important determinant of species richness. The global distribution of vascular plants correlates with various climatic measures, but most notably with actual evapotranspiration (AET; Kreft & Jetz, 2007). Specifically for trees, Ricklefs & He (2016) analysed 47 plots across the world, and they found the temperature during the warmest season and lack of seasonality to be strongly correlated with richness and noted both these measures are correlated with AET. Thus, high tree richness in the east Himalaya may be attributed to a warm, wet climate at the base (~100m), coupled with high turnover as both precipitation and temperature decline and seasonality increases towards higher altitudes, up to treeline at 4000-4200m (Rawat & Tambe, 2011). Indeed, previous studies along the east Himalayan elevational gradients have reported precipitation and temperature (Acharya *et al.*, 2011), precipitation and temperature seasonality (Li & Feng, 2015) and temperature alone (Kluge *et al.*, 2017) as strong correlates of plant richness. Differences among studies result not only from differences in the plant datasets but also the climate information (see Discussion).

In global studies, after climate is controlled for, East Asia is known for having exceptional tree richness (Ricklefs & He, 2016). In this case, a historically stable climate across a topographically diverse area may have resulted in high speciation and low extinction rates, elevating regional diversity, with a corresponding increase in local diversity following dispersal (Ricklefs & He, 2016). Here I ask how this high tree diversity is distributed across the elevational gradient, evaluate the extent to which inferred climatic effects on geography could account for elevational patterns, and suggest how influences often considered in a more regional context, notably source-sink dynamics (Grytnes, 2003), may contribute to the pattern.

5.2 Methods

I define a tree as a woody perennial plant, typically having a single stem growing to a considerable height and bearing lateral branches from above the ground. Trees are the most prominent component of vegetation communities, are most easily surveyed, and are likely to have better information on elevational ranges in the secondary literature than other plant groups. I enumerated all trees >30 cm girth at breast height.

5.2.1 Range Interpolation

I compiled elevational ranges of the trees from floras that list tree species from north Bengal and Sikkim (Dash & Singh, 2011; Ghosh & Mallick, 2014), henceforth "local floras". Lower elevational ranges were determined using these floras as well as two floras that cover the plains of West Bengal and Bihar (Hines, 1978; Prain, 1981). If a Himalayan species is present in the plains, I considered its lower elevational limit to be below 200m, even if the Himalayan floras gave a higher limit. I compare results that do or do not include the plains floras to assess consequences of using the range interpolation method. A total of 850 species are present in the local floras. Of these, 53 species (6.2%) are cultivated, and elevational ranges of 12 species (1.4%) are not reported, so I excluded these from the analysis. Thus, I included 92.4% of the species that are found in the Himalayan region of Bengal and Sikkim according to the floras. I calculate the total number of tree species at each elevation from the lower and upper elevational range limits, assuming the *range interpolation* method.

5.2.2 Field sampling

I sampled trees from eight elevational zones, which apart from the lowest and next zone, were separated by 500m (Fig. 5.1, Table 5.1). I sampled within three protected areas, i.e. Chapramari Wildlife Sanctuary and Neora Valley National Park in northern Bengal and Khangchendzonga National Park in Sikkim. Trees were enumerated in 50 plots of size 0.1 ha (31.65 x 31.65 m), for a total of 5 ha at each elevation zone. The altitudinal location of all plots was restricted to a band ±100m of each designated elevational, with most clustering close to the designated elevation. However, the lowest elevation was in the plains between 100-200m elevation, and sampling was over a narrower elevational range than other locations. I also sampled at 4000m which have few tree species and but here I simply recorded all species present. I recorded GPS information (latitude, longitude and elevation) of every plot and girth at breast height (gbh) of every tree >30 cm in girth. Trees were identified on site using floras (Grierson & Long, 1983-2001; Ghosh & Mallick, 2014). I photographed all species, preferably during the flowering or fruiting stage to confirm identification. If the identity of a tree was uncertain, a pressed specimen was taken for identification at Wildlife Institute of India, Dehradun herbarium. At present ten species included in the dataset remain unidentified, but single individuals represent 8 of these species. The complete dataset is shown in Appendix-1.

5.2.3 Analysis

Field sampling results are presented as the total number of species encountered at each elevational zone. I used species accumulation curves and rarefaction to evaluate the extent to which species richness has been underestimated (Gotelli & Colwell, 2001). As a measure of species evenness I calculated the Shannon index ($H' = -\sum P_i \ln P_i$) and Inverse-Simpson index ($\lambda = 1/\sum P_i^2$) where P_i represents the proportion of individuals found in *i*th species. I also computed Fisher's alpha index (Fisher e*t al.*, 1943), $\alpha = N(1-x)/x)$ where x is estimated from the iterative solution of $S/N = (1-x)/x(-\ln(1-x))$, S = the number of species and N = total individuals (Magurran, 2004). The analysis was conducted using R package "vegan" (Oksanen *et al.* 2016).

I calculated species turnover as beta diversity based on the presence/absence of species at different elevation zones using the formula; $\beta = (b+c)/(2*a+b+c)$ where a = species common at two elevations, b = species unique to the first elevation and c = species unique to the second elevation. Beta diversity includes a component due to nestedness and one due to richness, and I extracted the turnover component (βsim) following the recommendations of Baselga & Leprieur (2015) using the R package "betapart" (Baselga & Orme, 2012).

Various models have been devised to describe species abundance distributions within a community (McGill *et al.*, 2007). I compared log-normal, log-series and geometric distribution models of species abundance with the actual species abundance distribution using the R package "sads" (Prado *et al.*, 2015). The best fit model was identified using Akaike Information Criterion (AIC) values associated with each distribution model. The log-series distribution tends to be more applicable when there are many rare species in the community (McGill *et al.*, 2007; Slik *et al.*, 2015).

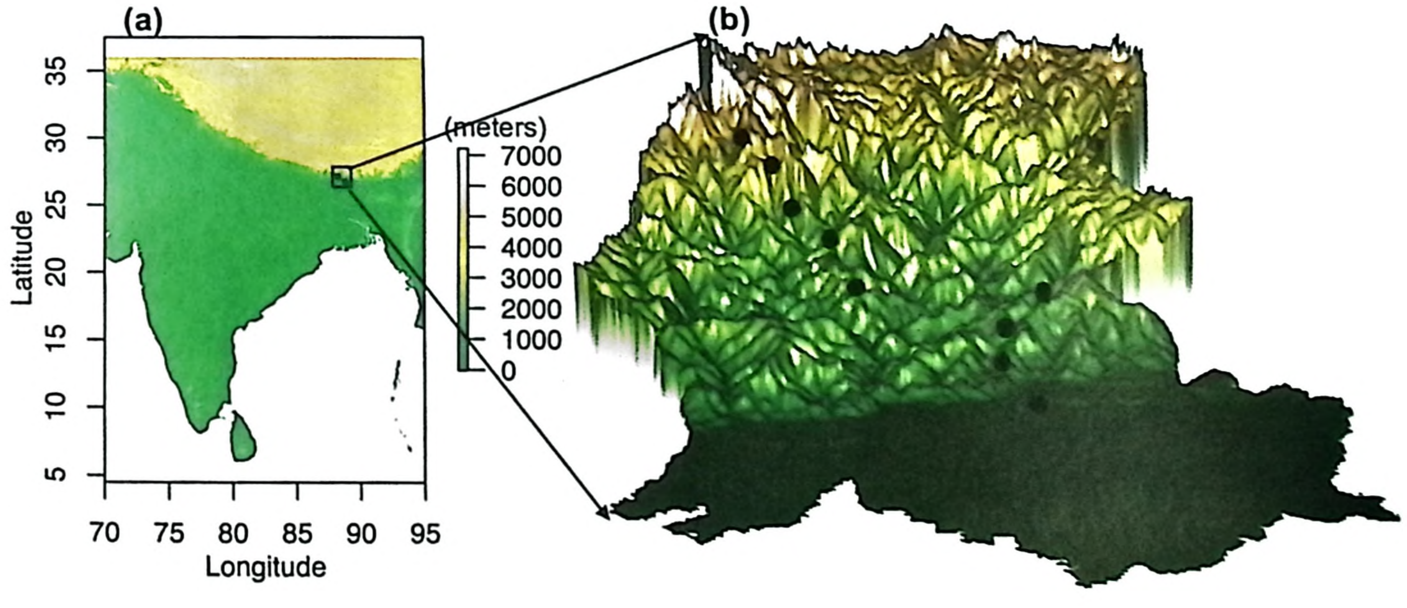

Figure 5.1 Map of the study area showing **(a)** digital elevation model of India with the location of sampling sites **(b)** enlarged 3D plot of study area spanning 9 sampling elevation zones in Northern Bengal and Sikkim, eastern Himalaya available at (Jarvis *et al.*, 2008; www.cgiar-csi.org).

Table 5.1 Elevational sites for field sampling of trees and observed species information in eastern Himalaya (Fig. 5.1).

Elevation (meters)	**Name of location**	**Species sampled**	**Species in literature**	**Total Individuals**	**BA ± sd (m^2/tree)**
200	Chapramari WLS	85	378	894	0.15 ± 0.25
500	Sakam NVNP	106	454	921	0.26 ± 0.81
1000	Mauchuki NVNP	74	467	1235	0.21 ± 0.19
1500	Yuksum KNP	54	402	982	0.20 ± 0.20
2000	Bhotekharka NVNP	49	265	1114	0.29 ± 0.32
2500	Bakhim KNP	41	191	916	0.23 ± 0.33
3000	Tshoka KNP	27	116	851	0.22 ± 0.25
3500	Fidong KNP	12	62	1085	0.18 ± 0.24
4000	Dzongri KNP	5	40	---	

BA: Basal area, WLS: Wildlife Sanctuary, NVNP: Neora Valley National Park, KNP: Khangchendzonga National Park.

Two factors have been previously hypothesized to affect plant species richness. These are climate (Currie, 1991; Kreft & Jetz, 2007) and dispersal (Grytnes *et al.* 2008). I assume climate sets a fixed number of source species unique to each elevation, and a fraction *d* of these disperse between adjacent elevations to produce sink species, only maintained by dispersal. Climatic variables, i.e. actual evapotranspiration, mean annual temperature and annual precipitation declines linearly with elevation across the study area. For climate, I therefore fit a simple prediction model to the data of a linear decline in species richness with elevation. Assumptions include (1) that all shared species between elevations are sink species and (2) that dispersal is equal across species and elevations and (3) dispersal only occurs between adjacent elevations. Results should therefore be considered illustrative of the possible roles of these processes, rather than biologically realistic. However, because so many additional parameters could be envisaged, a more complex model is not justified at present, without greater knowledge of the species biology. I fit the three parameters (intercept and slope for productivity, fraction of dispersers from a site) by maximizing the likelihood, assuming normal errors, and evaluated alternatives using AIC values.

5.3 Results

5.3.1 Species richness, diversity and abundance

Interpolation of elevational ranges of 785 species from local floras, including the compilations of species recorded from the plains, shows that species richness was relatively high and approximately the same at 500-1000m than at 200m (Fig. 5.2, triangles). Note that if I had not included the floras from the plains the number of species at 200m and 500m would be underestimated (Fig. 5.2, circles). Above 1000m elevation tree species richness declines linearly with elevation.

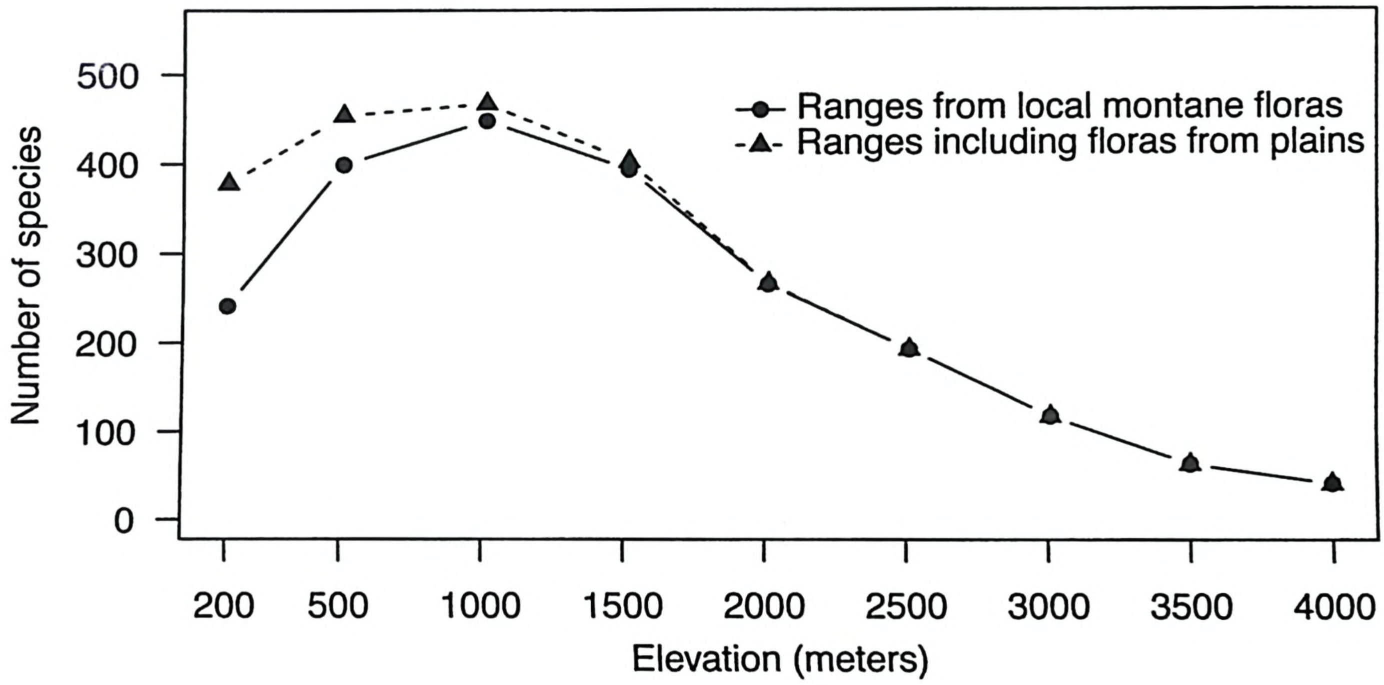

Figure 5.2 Comparison of tree species richness curves along the elevational gradient in eastern Himalaya obtained by interpolation of elevational ranges from local mountain floras and reassigned ranges to species ascending from plains but missing in local floras.

In the field sampling, I encountered a total of 269 tree species (34% of those in the local floras) at the eight elevation zones. Highest number of species were encountered at 500m elevation zone (106 species, Fig. 5.3a). The true number of species at every elevation is underestimated to an unknown degree. However, species rarefaction (Fig. 5.4) implies that the 500m elevation is the least well sampled as compared to other elevation zones; as sample size increases the rate of encounter of new species increases faster at this elevation than higher up. This suggests that the 500m zone indeed has the highest local species richness along the elevational gradient. Fisher's alpha index shows a consistent pattern with species richness. However, Shannon and Inverse-Simpson index shows highest diversity at foothills and a sharp decline at 1000m (Fig. 5.3b,d).

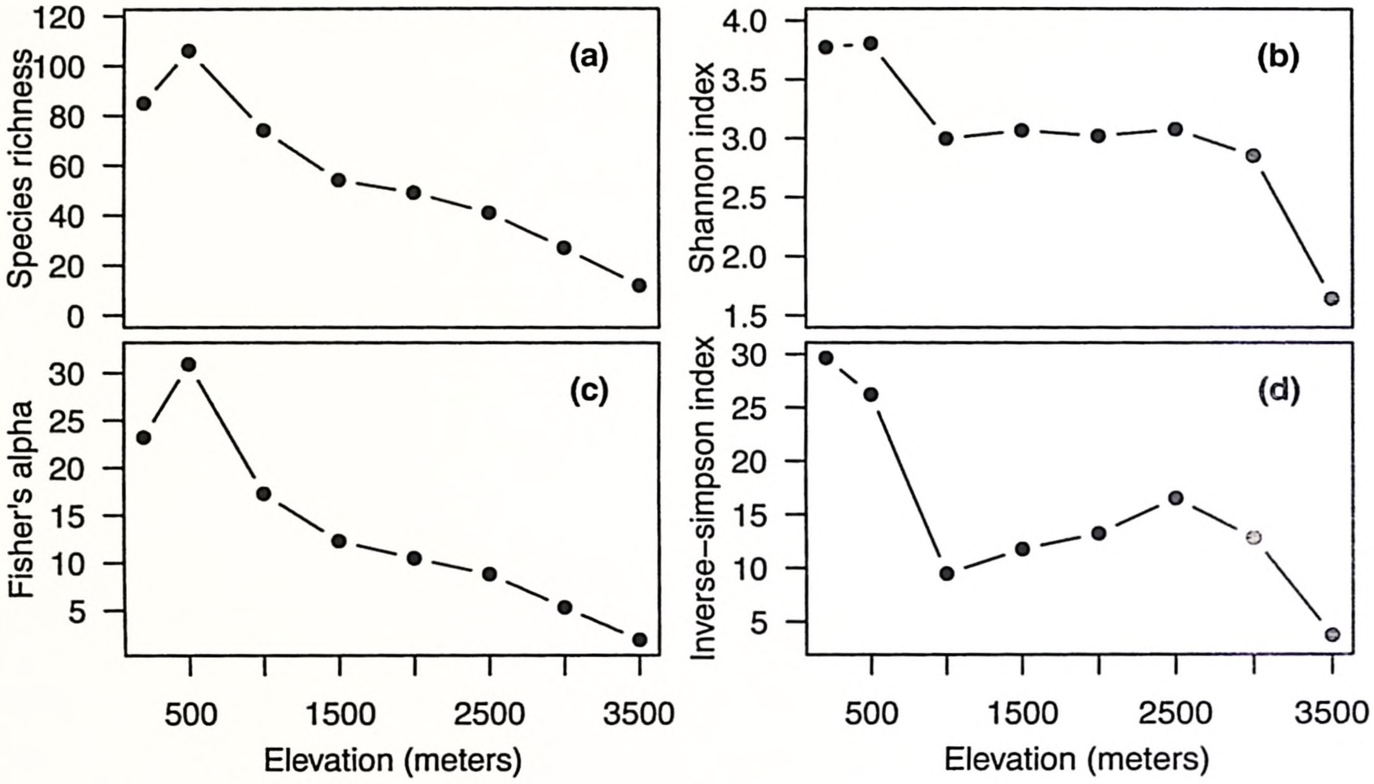

Figure 5.3 Comparison of species richness and diversity indices along the elevational gradient of study area **(a)** Species richness obtained from field sampling **(b)** Shannon index **(c)** Fisher's alpha index **(d)** Inverse Simpson index.

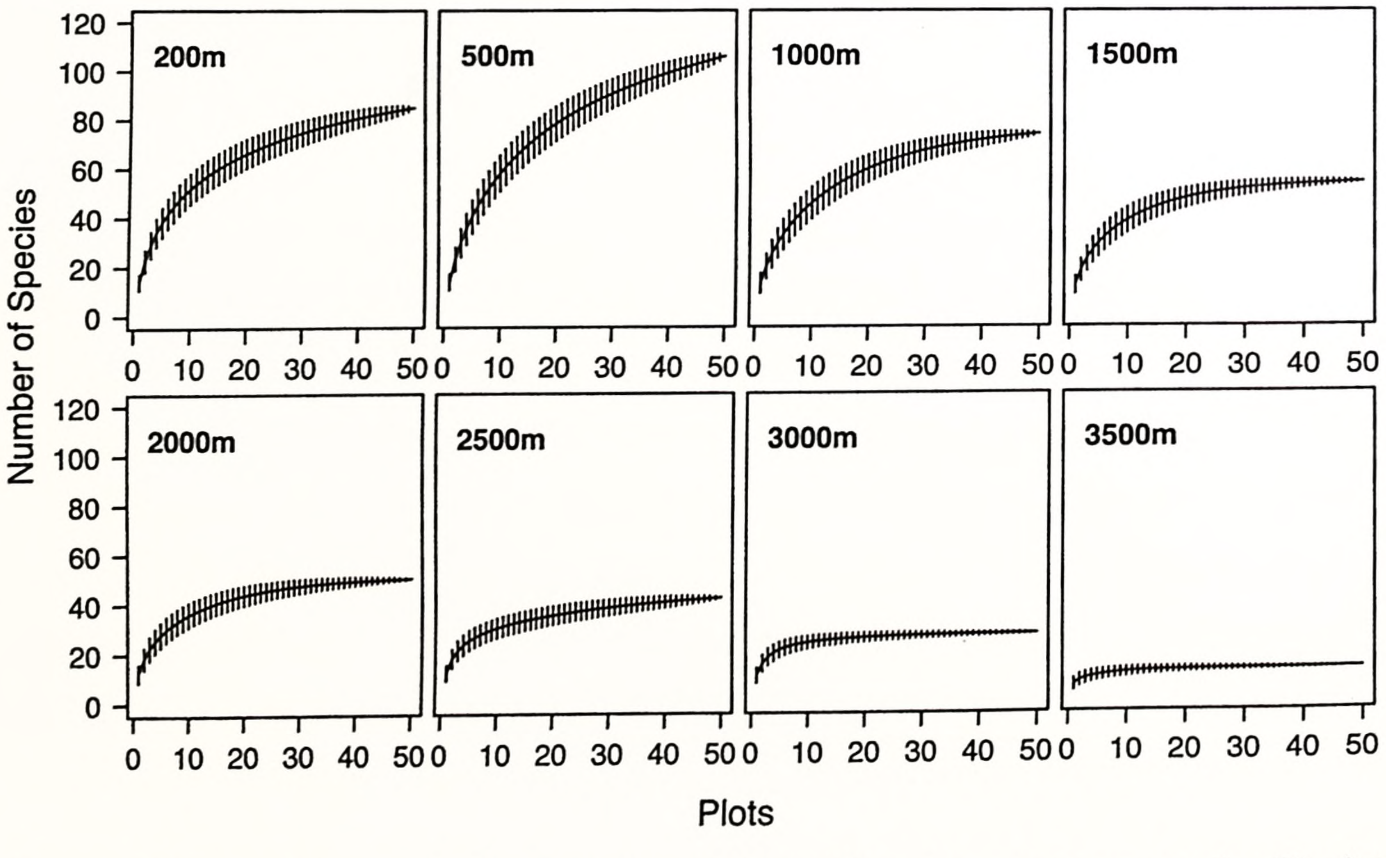

Figure 5.4 Species accumulation curves at different elevation zones across the 50 plots of 0.1ha size at each elevation. The rarefaction curves shows a steepest curve at 500m indicating least saturation of species richness thus is most species-rich zone.

At the 1000m and 1500m elevation zones, Shannon and Simpson index shows an unusually low diversity. Calculation of both these indices takes species evenness into the account (Magurran, 2004), indicating that evenness of species decreases drastically at 1000m elevation zone. On the other hand, Fishers alpha which is least influenced by species evenness show a similar pattern with species richness. Although the number of species encountered at 2000-2500m elevations is less, diversity is higher than at 1000-1500m (Fig. 5.3d). At 1000m three tree species comprise >40% of all individuals and at 1500m three tree species comprise >50% of all individuals (Table 5.2). Whereas, at foothills the highest abundance of top five species ranges only between 5-9 percent.

Table 5.2 Top five commonest tree species (top dominant) at different elevation zones in eastern Himalaya.

Elevation (meters)	**Commonest species in decreasing order of abundance**
200	*Syzygium cumini* (8.17%), *Terminalia bellirica* (6.15%), *Schima wallichii* (5.59%), *Shorea robusta* (5.26%), *Aphanamixis polystachya* (5.1%).
500	*Syzygium claviflorum* (8.9%), *Ailanthus integrifolia* (7.8%), *Crateva unicularis* (6.9%), *Magnolia pterocarpa* (6.1%), *Pterospermum acerifolium* (5.9%).
1000	*Schima wallichii* (24.6%), *Ostodes paniculata* (15.4%), *Terminalia myriocarpa* (10.4%), *Acer hookeri* (5.4%), *Duabanga grandiflora* (4.8%).
1500	*Schima wallichii* (21.3%), *Engelhardia spicata* (10.4%), *Alnus nepalensis* (10.4%), *Ficus racemosa* (8.9%), *Ostodes paniculata* (5.1%).
2000	*Litsea glutinosa* (14.7%), *Machilus duthiei* (12.7%), *Quercus lamellosa* (11.1%), *Symplocos lucida* (10.8%), *Acer campbellii* (6.4%).
2500	*Lithocarpus pachyphyllus* (14%), *Litsea glutinosa* (7.5%), *Symplocos lucida* (7.5%), *Prunus nepalensis* (7.4%), *Machilus duthiei* (6.4%).
3000	*Tsuga dumosa* (18.6%), *Rhododendron arboream* (11.1%), *Rhododendron wightii* (7.6%), *Prunus nepalensis* (7.3%), *Betula utilis* (5.4%).
3500	*Rhododendron hodgsonii* (43.1%), *Abies densa* (24%), *Betula utilis* (14.1%), *Viburnum nervosum* (4.9%), *Rhododendron arboream* (4.7%).

AIC values of species abundance distribution models show a good fit to the log-series distribution at the two lowest elevation (Fig. 5.5). The higher elevations show a good fit a log-normal distribution (except for 2500 m, log-series) and 3000 m (geometric series). Best fits to log-series indicates comparatively higher number of rare species at the foothills. Note that rare species at the low elevations are not colonising from elevations above 2000m. For example, 65 species at 500m were considered rare (represented >5 individuals) and of these only six (9%) extend to 2000m in the field data and ten (15%) in the floras.

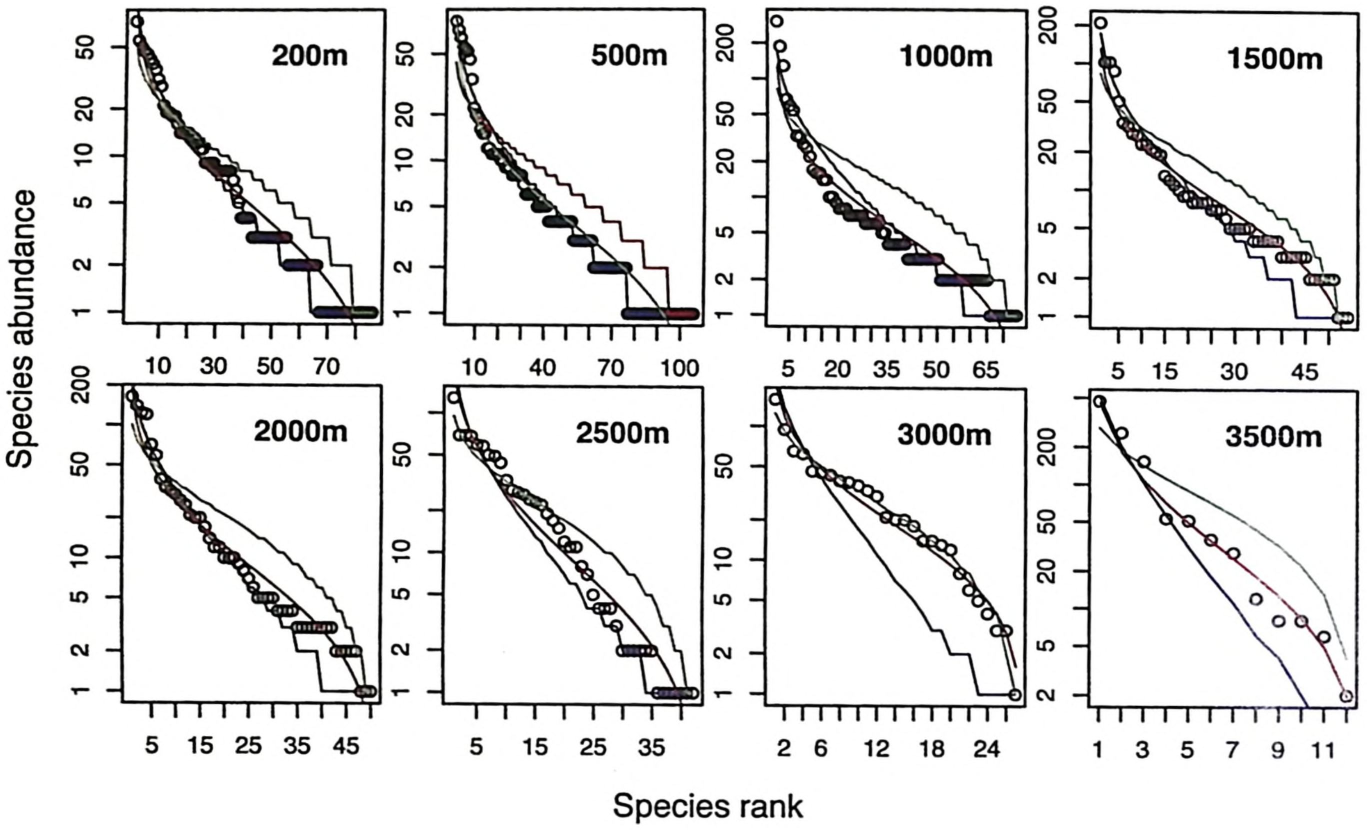

Figure 5.5 Species abundance diagrams for different elevations showing the fit of different species abundance distribution models: observed (black), log series (blue), log normal (red), geometric series (green).

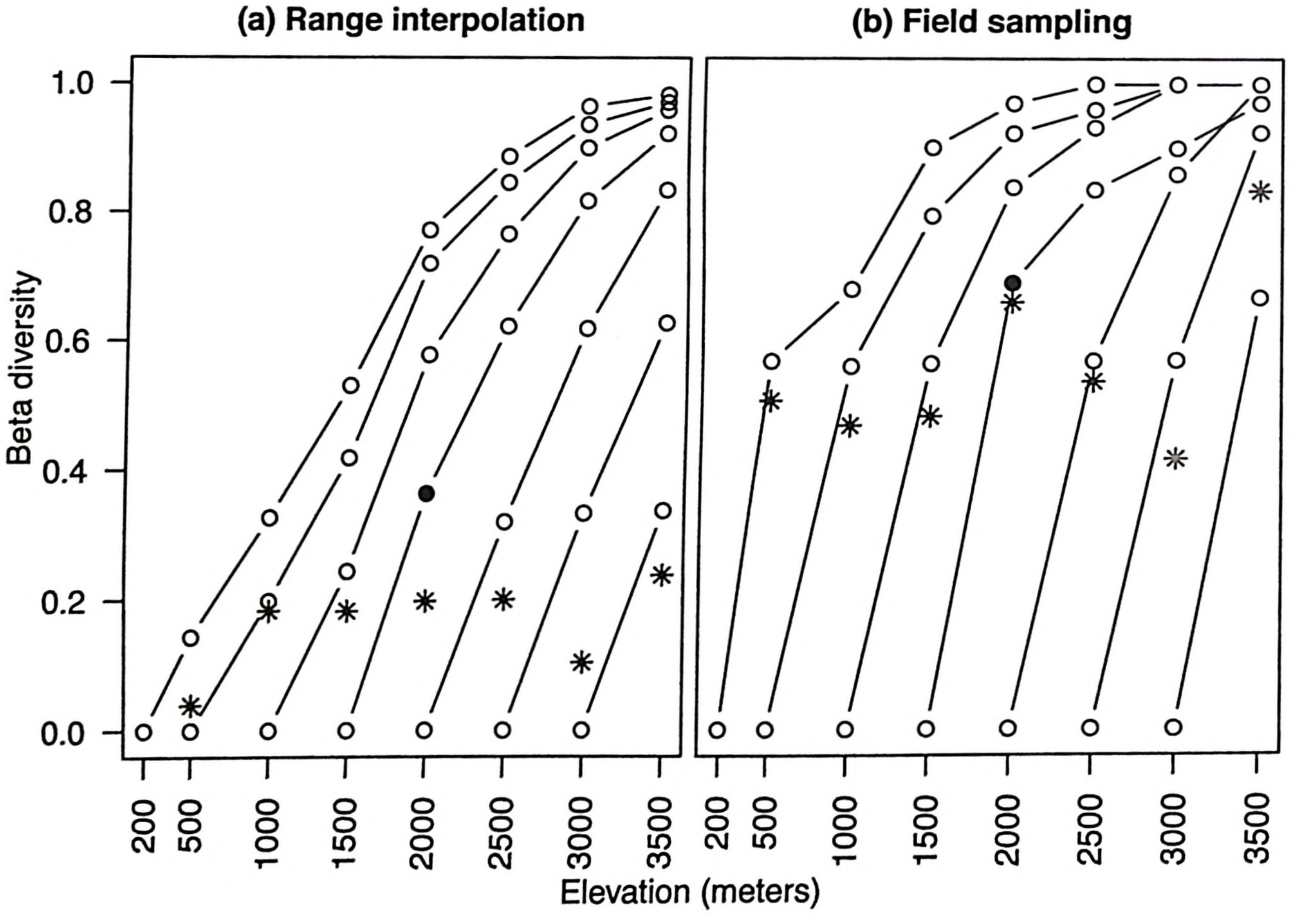

Figure 5.6 Comparison of the beta diversity of trees along the elevational gradient in eastern Himalaya **(a)** Range interpolated **(b)** Field sampling. Points on connecting lines show beta diversity values and asterisks represents turnover component of beta diversity between the adjacent elevational zones.

5.3.2 Beta diversity

The measure of beta diversity is based on presence/absence and does not weight by abundance. I calculated beta diversity between the different elevational zones from both the secondary literature as well as the field samples (Fig. 5.6). Both methods are consistent in indicating the highest beta diversity between 1500-2000m. The number of species encountered is very similar at these two elevations in the field data (54 and 49 respectively, Table 5.1), implying a significant turnover in composition, which is confirmed by a partitioning of beta-diversity into the turnover component (asterisks in Fig. 5.6). These results suggest the 1500-2000m belt is a critical transition zone between sub-tropical and temperate vegetation in the east Himalaya; this also marks the elevation at which freezing regularly occurs (as extracted from worldclim.org; Hijmans *et al.*, 2005).

5.3.3 Climate and dispersal

Patterns of climatic variables along the elevational gradient of the study area shows a linear decline with elevation. Annual mean temperature and annual precipitation values extracted from worlclim data (Hijmans *et al.*, 2005) at 1000 random points along the elevational gradient for the region in Figure 5.1 shows a linear decline in both variables (Fig. 5.7). Similarly, actual evapotranspiration also shows a linear decline along the elevational gradient (Fig. 5.8a).

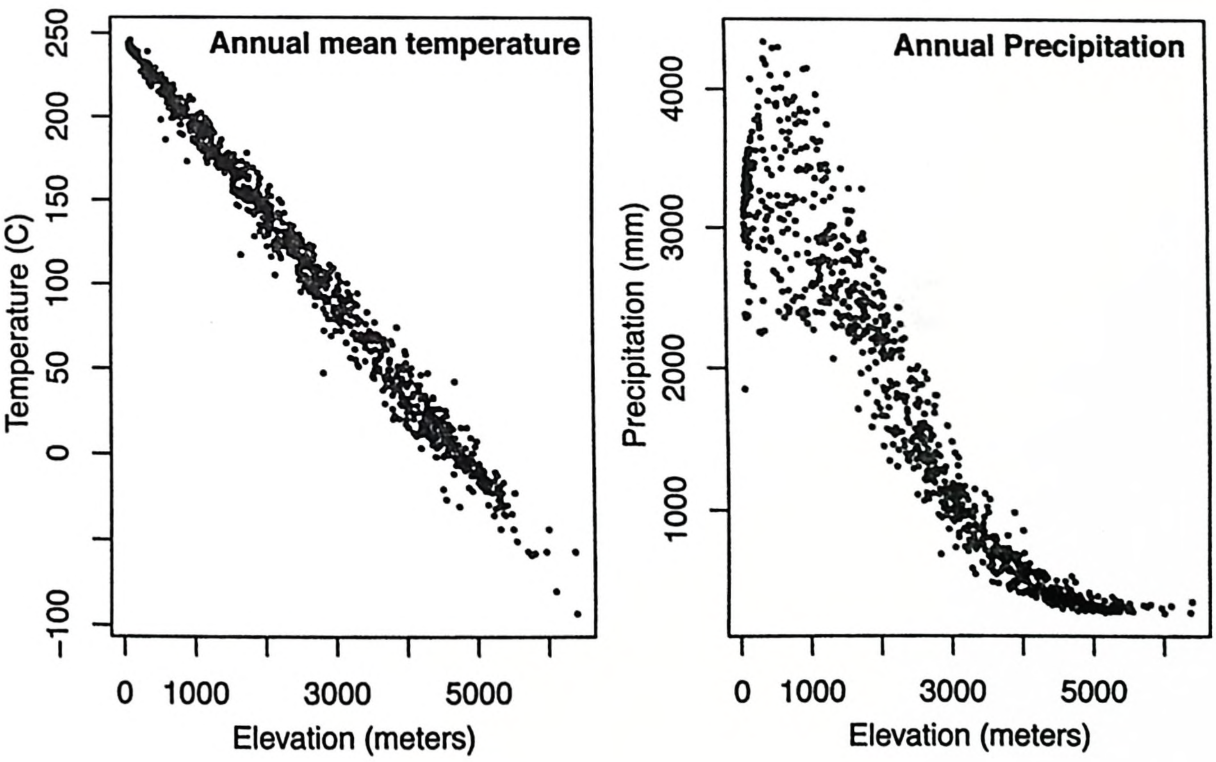

Figure 5.7 Patterns of annual mean temperature and annual precipitation extracted form worldclim data (Hijmans *et al.*, 2005) for 1000 random points of the region in Figure 5.1.

Given that climatic conditions in low elevation plains are more or less uniform and become harsher with increasing elevation (Fig. 5.7), climate is assumed to put constrains on dispersal of species immigrating from low-lands. At the foothills thus, there will be only one-way dispersal of species immigrating from plains, however at the elevations adjacent to foothills species can immigrate both from low-lands as well as from higher elevations. Thus, a two-way dispersal at the elevations adjacent to foothills maintains higher species richness as compared to foothills (Fig. 5.8b). However, at higher elevations an equilibrium will be maintained between species dispersal and climate, resulting in a linear decrease in species richness with increasing elevation.

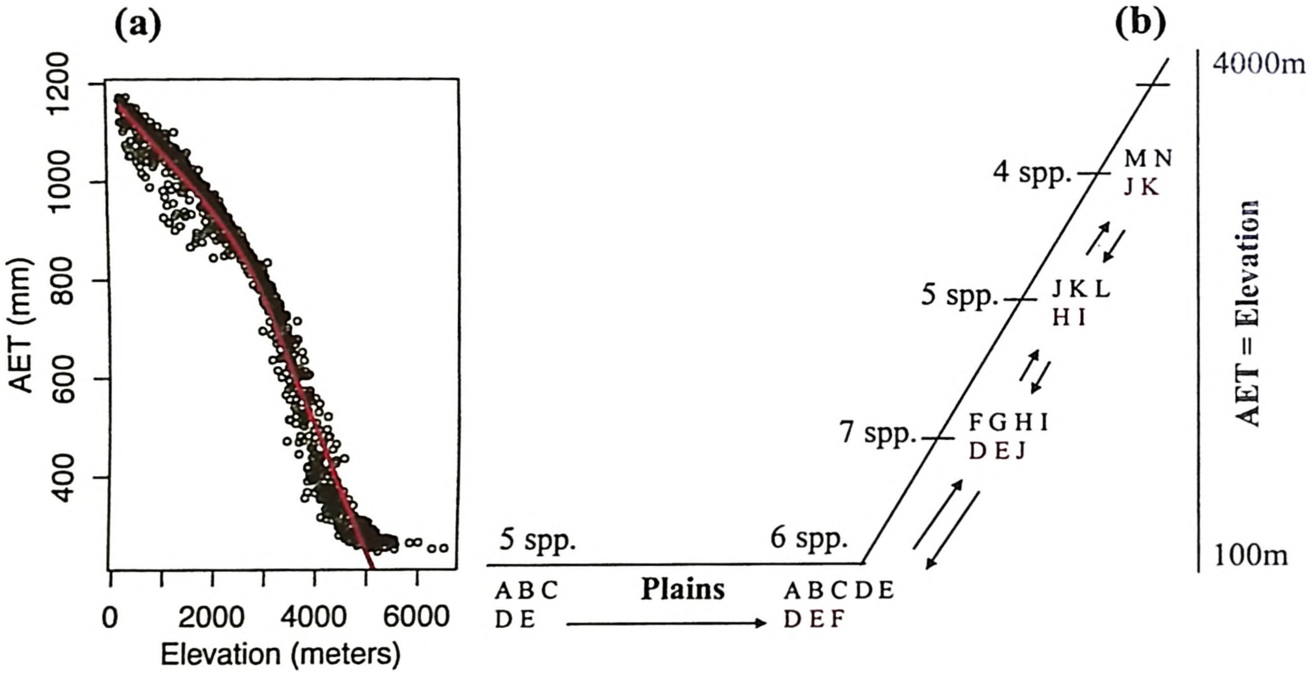

Figure 5.8 **(a)** Modelled AET against elevation for the region in Fig. 5.1 **(b)** A qualitative description for how AET and dispersal together can lead to a richness peak just above the lowest elevations. Source species are in black, and maintained at the locations indicated. They contribute to other locations as sink species (red) and elevate species richness when they differ from the source species at those locations.

In Figure 5.9, I compare the observed species richness patterns obtained from range interpolation and field sampling with those that fit a model of climate and dispersal to the data. In secondary literature data, source species, whose presence is determined by climate follow the equation y = 232 - 0.06 m (elevation), with dispersal $d = 0.75$ of all source species in one location to another. This results in 60% of all species at the lowest elevation being source species, and ~40% at the other locations, with the shared species between locations more or less commensurate with beta diversity patterns (Fig. 5.6). Adding the dispersal term to the linear model results in a highly significant improvement, $\Delta AIC = 6.9$. In field sampling data, source species are given by the equation y = 76 - 0.019 m (elevation), with $d = 0.20$.

Adding a dispersal term to the linear model results in a weak improvement, ΔAIC = 2.0. The best fit results in 84% of all species at the lowest elevation being source species, and ~70% at the other locations and again the shared species between locations are more or less commensurate with beta diversity patterns.

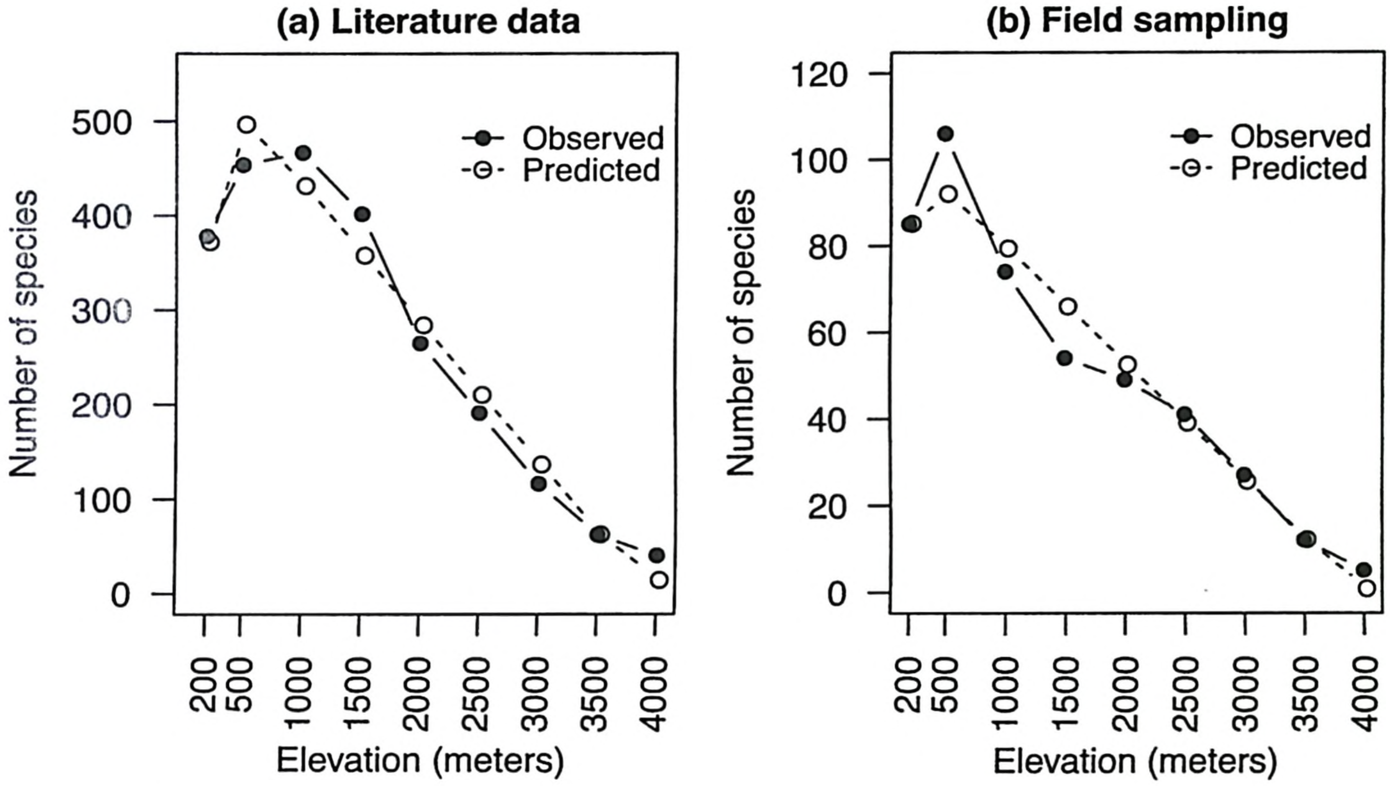

Figure 5.9 Observed species richness compared with the fitted points to a prediction model of productivity and dispersal **(a)** Literature data. **(b)** Field sampling.

5.4 Discussion

Tree species number in east Himalayan peaks at 500m in the field samples and between 500m and 1000m by interpolation of elevational ranges from published data, once species from north Indian plains are included. Diversity in the field samples is much higher at the 200-500m elevation than elsewhere, and a striking result is the dominance of just a few species at 1000-1500m. Notably, *Schima wallichii* dominates other species at two consecutive elevations (1000m and 1500m), where it can form more than 20% of all individuals. Field samples of trees specifically have reported richness peaks at comparable elevation in the Himalaya, e.g. at 600-800m in south-eastern Nepal (Bhattarai & Vetaas, 2003), at 750-1000m in eastern Nepal (Carpenter, 2005) and 600-1000m in Arunachal Pradesh (Behera & Kushwaha, 2007). However, Acharya *et al.* (2011) reported a peak in trees richness at 1500m in Sikkim. Possible explanations for anomalous results of Acharya *et al.* (2011) is relatively small samples at each elevation and/or study in more disturbed locations. Indeed, Acharya *et al.* (2011) noted that tree size was much smaller at 500m than at 2000m, which is contrary to my findings.

Field samples differ from the literature survey in having more species at 500m than at 1000m, and rarefaction suggests that even more species would have been discovered at 500m than at 1000m if I had continued with field sampling. One possible explanation for the discrepancy is that exceptionally rare species are unrecorded in field samples while continuing to appear in the literature surveys up to 1000m. These results emphasise the importance of field studies that estimate abundance, and the subsequent calculation of diversity indices, to which rare species contribute relatively little. While species richness may indeed plateau between 500-1000m, species diversity (and hence likely functional diversity) shows a strong peak at 500m.

Published elevational ranges based on range interpolation are expected to produce a peak at mid-elevations because both the lower and upper elevations are underestimated (Grytnes & Vetaas, 2002). My study demonstrates this point, because although the peak does not disappear when I reassigned ranges based on records from floras of plains, the numbers of species at 500m become commensurate with those at 1000m. The Bhattarai & Vetaas (2006) study from Nepal also used range interpolation method but did not include species from plains. They found the peak at 900-1000m like my results when I did not include information on lower elevational limits gleaned from the plains floras. On the other hand, Kluge *et al.* (2017) studied a floral compilation from Bhutan and found a similar plateau to us, but in this case, the number of trees at each elevation was about 50% less than in my survey from Sikkim and Bengal, suggesting substantial under-sampling in their compilation. Field collections also have sampling issues. Typically, only a fraction of the flora is encountered and even in my rather intensive study I noted only 34% of the total tree species present in the Himalayan floras from Sikkim and northern Bengal (Dash & Singh, 2011; Ghosh & Mallick, 2014). If species abundance distributions vary along the elevational gradient, as they do in my case, real species richness at any one location becomes hard to compare. This issue is particularly important when sampling is low and thought to be one reason why elevational patterns were obscured in the New Caledonian study by Ibanez *et al.*, (2016) (note here I concentrate on richness in the summed 5 ha plot, whereas in their study they focused on 0.04 ha samples).

Because the primary statistical issues associated with field sampling differ from those associated with range interpolations, it is confident that the tree richness peak falls at approximately 500m in this region of the eastern Himalaya, at least after exclusion of very rare species. I ask if these patterns can be related to climate, in a way like that documented across the globe (Ricklefs & He, 2016), as described in the introduction. Previous studies have attempted to correlate climate with richness patterns (e.g. Acharya *et al.*, 2011; Li & Feng, 2015: Kluge *et al.*, 2017). However, the results vary partly because of difficulties in estimating species richness patterns accurately, with many rare species likely included and all the attendant sampling issues, and partly because it is hard to know the climatic pattern, given the relatively few climate stations in the region.

According to data on precipitation and temperature from worldclim.org (Hijmans *et al.*, 2005) and actual evapotranspiration data from CGIAR (Trabucco & Zomer, 2010), these three climatic variables show a linear decline from the lowest elevations. On the other hand, remote sensing (Bookhagen & Burbank, 2010) and models based on measured atmospheric pressure and topography (Gerlitz *et al.*, 2015) suggest a peak in precipitation at 500m. After outliers are excluded, both the remote sensing and the atmospheric pressure models explain a relatively low fraction of precipitation recorded at known climate stations, so I consider a linear decline in AET with elevation to remain plausible. Climate data is available for 7 stations between 700m and 4200m in Sikkim, which does not allow one to separate these alternatives, but confirms a linear decline of precipitation ($r = 0.99$) and temperature ($r = 0.99$) with elevation along this portion of the gradient (Acharya *et al.*, 2011). However, if precipitation indeed peaks at 500m, then strong local climatic controls alone can account for the tree richness peak at 500m because AET is also likely to peak at 500m.

If AET declines linearly with elevation and the number of species maintained at any one location is associated with AET (Currie & Paquin, 1987; Currie, 1991; O'Brien, 1998; Kreft & Jetz, 2007), then local controls should cause a linear decline in species richness with elevation. Still the peak at 500m could potentially be directly driven by local climatic controls because, of necessity, I sampled over a relatively broad elevational range when compared with the 200m elevation, which spans flat terrain in the plains (200m: mean elevation 218 ± 12.6m S.D., 500m: 541 ± 31.9m S.D., N = 50, 0.1ha plots in both locations). I can discount this possibility because the average number of trees within the 0.1ha plots is

20% higher at 500m than 200m (9.86 at 200m, 11.84 at 500m). This is very similar to the difference in the cumulative number at each elevation (23%, 86 vs 106).

In general, geometric constraints of the kind described by Colwell *et al.* (2016) have been thought to affect elevational distributions, and I consider here how this might create a peak just above the lowest elevations. While geometric constraints are usually considered without biological underpinnings, Grytnes (2003) noted that source-sink dynamics could operate to raise abundance of species at intermediate elevations (see also Grytnes *et al.*, 2008; Kessler, 2009). This has been applied to hard boundaries, e.g. coastlines, but it may also apply if a relatively uniform plains flora extends out from the mountains. Dispersal must lead to individuals extending into the range at which death rates exceed birth rates (i.e. sinks) and hence augment species richness, even in locations where species would not normally be maintained.

I suggest that climate (e.g., AET) determines both the kind and number of species maintained at a given site ("source species"), augmented by dispersal from nearby sites ("sink species"). I illustrate 14 hypothetical source species distributed across four sites that shows how dispersal may then produce a peak close to, but not at, the lowest elevations. This is because dispersal from the plains to the lowest elevations introduces no new species, whereas higher elevations can receive new species from both above and below. In this case, the proposition that dispersal from the plains introduces no new species has some support because all the trees reported in a survey of Mahananda Wildlife Sanctuary (26.76°N 88.31°E) ~100 km into the plains (Shankar, 2001) were also present at my lowest site. Note also that for those species that have a maximum abundance at the low point, that lowest point is nearly always at 200m, suggesting that the 200m elevation is more often a source than a sink. A role for dispersal elevating local species richness, even if species are unable to maintain a presence permanently may more generally contribute to regional effects on the local diversity of the kind described by Ricklefs & He (2016).

While turnover in species composition is the same along the elevational gradient, in the field samples it lies above the elevation of maximum richness, i.e., between 1500-2000m. This may correspond to a turnover of subtropical floras and temperate montane floras (Oomen & Shanker, 2005; Li & Feng, 2015; Kluge *et al.* 2017). However, since merging is not a significant contributor to the peak at 500m-1000m, it suggests climatic controls and dispersal are more important than mixing of floras in setting species numbers at the 1500-2000m elevations. Kluge *et al.* (2017) studied all vascular plants in Bhutan and suggested the peak at 1500-2000m was driven by a combination of mixing of floras and a quadratic influence of temperature, but my analysis indicates that it is important to include low elevation floras in the assessment of lower elevational ranges. I have done this for all plants and inferred a plateau in richness from about 1000-2000m.

In summary, in the eastern Himalaya, I have evidence that a peak in tree species richness lies just above the lowest elevations. I argue that relationships of climate with species richness, perhaps combined with simple effects of dispersal leads to a straightforward explanation for the patterns. What is now required is a better understanding of why the species abundance distributions themselves vary along the gradient, and in particular why at some elevations a few tree species are particularly dominant. I suggest this will come from an incorporation of historical analyses, together with detailed studies of individual species.

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Appendix-1

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Appendix-2

Tree species encountered during sampling along the elevational gradient of North Bengal and Sikkim in eastern Himalaya.

Family and botanical name	**Number of trees at different elevations (meters)**									
	200	**200***	**500**	**1000**	**1500**	**2000**	**2000***	**2500**	**3000**	**3500**
Achariaceae										
Gynocardia odorata	3	-	11	26	-	-	-	-	-	-
Actinidiaceae										
Saurauia griffithii	-	-	-	3	-	-	-	-	-	-
Saurauia armata	-	-	-	-	4	-	-	-	-	-
Saurauia roxburghii	1	4	-	-	-	-	-	-	-	-
Adoxaceae										
Viburnum cylindricum	-	-	-	-	-	34	85	1	-	-
Viburnum nervosum	-	-	-	-	-	-	-	7	20	51
Anacardiaceae										
Dendrocnide sinuata	-	-	6	-	-	-	-	-	-	-
Drimycarpus racemosus	-	1	1	-	-	-	-	-	-	-
Lannea coromandelica	4	4	-	-	-	-	-	-	-	-
Mangifera indica	-	1	9	3	-	-	-	-	-	-
Mangifera sylvatica	-	-	4	-	-	-	-	-	-	-
Semecarpus anacardium	-	6	-	2	28	-	-	-	-	-
Spondias pinnata	-	-	2	1	-	-	-	-	-	-
Toxicodendron hookeri	-	-	-	-	-	-	-	2	-	-
Annonaceae										
Polyalthia simiarum	8	1	52	-	-	-	-	-	-	-
Apocynaceae										
Alstonia nerifolia	-	-	3	-	-	-	-	-	-	-
Alstonia scholaris	8	9	15	2	-	-	-	-	-	-
Holarrhena pubescens	36	49	5	7	-	-	-	-	-	-
Tabernaemontana divaricata	-	-	1	-	-	-	-	-	-	-
Wrightia arborea	14	2	-	-	-	-	-	-	-	-
Wrightia sikkimensis	-	-	9	-	-	4	-	-	-	-
Aquifoliaceae										
Ilex dipyrena	-	-	-	-	-	-	-	3	-	-
Ilex godajam	3	9	-	-	-	-	-	-	-	-
Ilex sikkimensis	-	-	-	-	-	-	-	24	20	-
Araliaceae										
Aralia leschenaultii	-	-	-	-	-	3	3	-	-	-
Brassaiopsis hainla	-	-	4	3	-	-	-	-	-	-
Brassaiopsis mitis	-	-	8	1	-	4	7	-	-	-

Family and botanical name	**Number of trees at different elevations (meters)**									
	200	**200***	**500**	**1000**	**1500**	**2000**	**2000***	**2500**	**3000**	**3500**
Macropanax undulatus	-	-	2	-	-	-	-	-	-	-
Trevesia palmata	-	-	-	-	2	10	14	2	1	-
Caryota urens	-	-	1	-	-	-	-	-	-	-
Berberidaceae										
Mahonia napaulensis	-	-	-	-	-	-	-	11	-	-
Betulaceae										
Alnus nepalensis	-	-	1	4	102	-	-	19	-	-
Betula alanoides	-	-	-	14	9	-	-	-	-	-
Betula utilis	-	-	-	-	-	-	-	-	46	153
Carpinus viminea	-	-	-	-	-	7	21	-	-	-
Corylus ferox	-	-	-	-	-	3	-	-	-	-
Bignoniaceae										
Oroxylum indicum	4	5	2	-	-	-	-	-	-	-
Stereospermum chelonoides	12	5	6	-	-	-	-	-	-	-
Boraginaceae										
Ehretia wallichiana	-	5	11	-	-	-	-	-	-	-
Burseraceae										
Garuga floribunda	-	-	-	-	-	59	55	-	-	-
Garuga pinnata	1	1	3	-	-	-	-	-	-	-
Cannabaceae										
Celtis tetrandra	-	10	-	-	5	-	-	-	-	-
Trema orientalis	4	33	-	-	-	-	-	-	-	-
Capparaceae										
Crateva unilocularis	3	2	64	-	-	-	-	-	-	-
Celastraceae										
Microtropis discolor	-	-	-	2	-	-	-	-	-	-
Clusiaceae										
Garcinia cowa	-	-	2	-	-	-	-	-	-	-
Garcinia stipulata	-	-	1	-	-	-	-	-	-	-
Comberetaceae										
Terminalia alata	9	-	-	6	-	-	-	-	-	-
Terminalia bellirica	55	35	-	-	-	-	-	-	-	-
Terminalia chebula	-	1	2	-	-	-	-	-	-	-
Terminalia myriocarpa	9	-	10	128	12	-	-	-	-	-
Cornaceae										
Alangium chinense	1	-	20	-	-	-	-	-	-	-
Toricellia tiliifolia	-	-	-	-	23	-	-	-	-	-
Cupressaceae										
Cryptomeria japonica	-	-	-	8	9	-	-	-	-	-

Family and botanical name	Number of trees at different elevations (meters)									
	200	200*	500	1000	1500	2000	2000*	2500	3000	3500
Cunninghamia lanceolata	-	-	-	2	-	-	-	-	-	-
Cyatheaceae	-	-	-	-	-	-	-	-	-	-
Cyathea spinulosa	-	-	-	2	2	2	1	-	-	-
Daphniphyllaceae										
Daphniphyllum himalayense	-	-	-	-	-	3	33	-	-	-
Dilleniaceae										
Dillenia indica	14	22	-	-	-	-	-	-	-	-
Dillenia pentagyna	42	43	-	-	-	-	-	-	-	-
Dipterocarpaceae										
Shorea robusta	47	113	-	-	-	-	-	-	-	-
Elaeocarpaceae										
Elaeocarpus rugosus	-	-	1	-	-	-	-	-	-	-
Elaeocarpus varunua	1	24	1	-	-	-	-	-	-	-
Ericaceae										
Enkianthus deflexus	-	-	-	-	-	-	-	-	12	-
Lyonia ovalifolia	-	-	-	-	23	-	-	50	6	-
Pieris formosa	-	-	-	-	-	-	-	-	38	-
Rhododendron arboream	-	-	-	-	13	-	-	49	94	36
Rhododendron barbatum	-	-	-	-	-	9	62	2	-	-
Rhododendron falconeri	-	-	-	-	-	-	-	-	33	-
Rhododendron grande	-	-	-	-	-	-	-	44	8	-
Rhododendron griffithianum	-	-	-	-	-	-	-	15	-	-
Rhododendron hodgsonii	-	-	-	-	-	-	-	-	-	468
Rhododendron niveum	-	-	-	-	-	-	-	-	5	-
Rhododendron thomsonii	-	-	-	-	-	-	-	-	-	53
Rhododendron wightii	-	-	-	-	-	-	-	-	65	-
Euphorbiaceae										
Macaranga indica	-	-	-	-	7	-	-	-	-	-
Mallotus nudiflorus	-	-	1	-	-	-	-	-	-	-
Mallotus philippensis	3	-	1	1	-	-	-	-	-	-
Mallotus repandus	2	-	-	-	-	-	-	-	-	-
Ostodes paniculata	-	-	15	187	50	-	-	-	-	-
Fagaceae										
Castanopsis clarkei	-	-	-	-	32	1	-	1	-	-
Castanopsis hystrix	-	3	-	-	-	-	-	-	-	-
Castanopsis indica	20	19	-	-	-	-	-	-	-	-
Castanopsis lancifolia	1	-	16	32	-	-	-	-	-	-
Castanopsis tribuloides	8	14	6	2	34	4	6	-	-	-
Lithocarpus elegans	1	-	7	54	-	-	-	-	-	-

Family and botanical name	Number of trees at different elevations (meters)									
	200	200*	500	1000	1500	2000	2000*	2500	3000	3500
Lithocarpus pachyphyllus	-	-	-	-	-	2	-	-	21	-
Quercus lamellosa	-	-	-	-	-	-	-	58	-	-
Quercus thomsoniana	-	-	-	-	-	35	-	28	-	-
Hamamelidaceae										
Altingia excelsa	2	54	3	-	-	-	-	-	-	-
Hydrangeaceae										
Dichroa febrifuga	-	-	1	-	-	-	-	-	-	-
Hydrangeaceae										
Hydrangea heteromalla	-	-	-	-	-	32	11	-	-	-
Juglandaceae										
Engelhardia spicata	-	-	-	28	102	-	-	-	-	-
Juglans regia	-	-	-	-	27	-	-	-	-	-
Lamiaceae										
Callicarpa arborea	7	2	3	33	3	-	-	-	-	-
Callicarpa vestita	-	-	4	-	-	-	-	-	-	-
Carallia brachiata	-	18	-	-	-	-	-	-	-	-
Gmelina arborea	3	6	1	-	-	-	-	-	-	-
Premna coriacea	13	12	1	-	-	-	-	-	-	-
Premna mollissima	1	-	-	-	-	-	-	-	-	-
Tectona grandis	2	-	-	-	-	-	-	-	-	-
Vitex peduncularis	1	-	-	-	-	-	-	-	-	-
Vitex quinata	1	-	2	2	-	-	-	-	-	-
Lauraceae										
Actinodaphne obovata	13	10	22	7	-	-	-	-	-	-
Beilschmiedia sikkimensis	8	-	3	4	-	21	-	-	-	-
Cinnamomum bejolghota	41	15	4	8	4	2	2	-	-	-
Cinnamomum glaucescens	-	2	3	2	2	-	-	-	-	-
Cinnomum zeylanica	-	-	1	-	-	-	-	-	-	-
Cinomomum tamala	-	-	-	2	5	5	8	-	-	-
Cryptocarya amygdalina	3	-	-	-	-	-	-	-	-	-
Lindera neesiana	-	-	-	-	-	-	89	-	-	-
Lindera obtusiloba	-	-	-	-	-	-	-	1	-	-
Lindera pulcherrima	-	-	-	1	-	10	13	22	-	-
Litsea cubeba	-	-	-	-	5	-	-	-	-	-
Litsea elongata	-	-	-	-	-	10	2	-	-	-
Litsea glutinosa	-	-	-	3	-	-	-	69	-	-
Machilus duthiei	-	-	2	4	-	-	66	59	-	-
Machilus glaucescens	3	2	-	-	-	-	-	-	-	-
Machilus kurzii	-	-	-	-	-	14	21	-	-	-

Family and botanical name	**Number of trees at different elevations (meters)**									
	200	**200***	**500**	**1000**	**1500**	**2000**	**2000***	**2500**	**3000**	**3500**
Neocinnamomum caudatum	-	-	4	-	-	-	-	-	-	-
Ocotea lancifolia	18	21	7	4	-	-	-	-	-	-
Phoebe attenuata	-	-	8	4	-	-	-	-	-	-
Lecythidaceae										
Careya arborea	19	10	-	-	-	-	-	-	-	-
Leguminosae										
Acacia catechu	3	-	1	-	-	-	-	-	-	-
Acrocarpus fraxinifolius	-	-	2	-	-	-	-	-	-	-
Albizia chinensis	-	-	-	3	10	-	-	-	-	-
Albizia gamblei	-	-	2	-	-	-	-	-	-	-
Albizia lucidior	5	-	-	-	-	-	-	-	-	-
Albizia procera	-	1	1	-	3	-	-	-	-	-
Albizzia lebbeck	-	-	-	-	4	-	-	-	-	-
Bauhinia purpurea	8	-	34	2	-	-	-	-	-	-
Bauhinia variegata	-	-	-	-	5	-	-	-	-	-
Cassia fistula	-	-	-	-	-	3	-	-	-	-
Dalbergia sericea	-	-	1	-	-	-	-	-	-	-
Erythrina stricta	-	-	4	7	20	-	-	-	-	-
Millettia pachycarpa	21	1	-	-	-	-	-	-	-	-
Lythraceae										
Duabanga grandiflora	-	1	6	59	-	-	-	-	-	-
Lagerstroemia parviflora	11	12	-	-	-	-	-	-	-	-
Lagerstroemia speciosa	2	-	-	-	-	-	-	-	-	-
Magnoliaceae										
Magnolia campbellii	-	-	-	-	-	3	6	28	36	-
Magnolia champaca	-	-	1	-	-	-	-	-	-	-
Magnolia globosa	-	-	-	-	-	-	-	1	-	-
Magnolia hodgsonii	-	-	5	-	-	-	-	-	-	-
Magnolia pterocarpa	-	-	56	16	5	-	-	-	-	-
Magnolia punduana	-	-	-	-	-	4	-	-	-	-
Magnolia cathcartii	-	-	-	-	-	-	19	27	39	-
Malvaceae										
Bombax ceiba	2	-	3	1	3	-	-	-	-	-
Firmiana fulgens	-	-	-	2	-	-	-	-	-	-
Kydia calycina	-	-	2	-	-	-	-	-	-	-
Pterospermum acerifolium	7	-	54	-	-	-	-	-	-	-
Sterculia villosa	31	12	-	-	-	-	-	-	-	-
Meliaceae										
Aglaia spectabilis	19	91	8	-	-	-	-	-	-	-

Family and botanical name	Number of trees at different elevations (meters)									
	200	200*	500	1000	1500	2000	2000*	2500	3000	3500
Aphanamixis polystachya	45	72	12	7	-	-	-	-	-	-
Azadirachta indica	-	1	-	-	-	-	-	-	-	-
Chisocheton cumingianus	13	9	-	-	-	-	-	-	-	-
Chukrasia tabularis	2	1	4	-	-	-	-	-	-	-
Heynea trijuga	2	-	-	-	-	-	-	-	-	-
Toona ciliata	2	4	1	2	6	-	-	-	-	-
Walsura tabulata	-	-	5	-	-	-	-	-	-	-
Moraceae										
Artocarpus chama	1	-	-	-	-	-	-	-	-	-
Ficus auriculata	-	-	-	3	8	-	-	-	-	-
Ficus benghalensis	-	-	-	-	1	-	-	-	-	-
Ficus benjamina	-	1	-	-	-	-	-	-	-	-
Ficus cyrtophylla	-	-	1	3	-	-	-	-	-	-
Ficus elastica	2	-	-	-	-	-	-	-	-	-
Ficus hirta	-	-	5	1	3	-	-	-	-	-
Ficus hispida	-	-	-	6	-	-	-	-	-	-
Ficus neriifolia	-	-	-	-	8	20	37	-	-	-
Ficus pubigera	-	-	1	-	-	-	-	-	-	-
Ficus racemosa	-	-	4	10	87	-	-	-	-	-
Ficus rumphii	-	-	-	3	-	-	-	-	-	-
Ficus virens	2	-	2	-	-	-	-	-	-	-
Ficus virens	1	-	-	-	-	-	-	-	-	-
Ficus semicordata	-	-	-	5	11	-	-	-	-	-
Morus macroura	-	-	11	-	4	-	-	-	-	-
Myristicaceae										
Knema tenuinervia	-	-	-	1	-	-	-	-	-	-
Myrtaceae										
Eucalyptus tereticornis	-	-	-	4	4	-	-	-	-	-
Syzygium cumini	73	53	-	6	-	-	-	-	-	-
Syzygium formosum	39	35	19	6	-	-	-	-	-	-
Syzygium kurzii	-	-	-	2	-	-	-	-	-	-
Syzygium nervosum	1	15	-	-	-	-	-	-	-	-
Syzygium claviflorum	-	2	82	-	-	-	-	-	-	-
Nyssaceae										
Nyssa javanica	-	9	-	-	1	5	-	-	-	-
Oleaceae										
Fraxinus suaveolens	8	-	-	-	-	-	-	-	-	-
Ligustrum confusum	-	-	-	-	-	-	5	-	-	-
Pandanaceae										

Family and botanical name	**Number of trees at different elevations (meters)**									
	200	**200***	**500**	**1000**	**1500**	**2000**	**2000***	**2500**	**3000**	**3500**
Pandanus furcatus	-	-	9	-	-	-	-	-	-	-
Paulowniaceae										
Wightia speciosissima	-	-	-	6	1	8	-	12	-	-
Pentaphylacaceae	-	-	-	-	-	-	-	-	-	-
Eurya acuminata	4	17	3	2	-	3	2	17	-	-
Eurya cerasifolia	-	-	-	14	-	-	-	-	-	-
Phyllanthaceae										
Antidesma acidum	3	11	-	-	-	-	-	-	-	-
Aporosa octandra	1	-	-	-	-	-	-	-	-	-
Bischofia javanica	3	5	-	-	-	-	-	-	-	-
Bridelia retusa	1	-	-	-	-	-	-	-	-	-
Bridelia tomentosa	-	1	-	-	-	-	-	-	-	-
Glochidion acuminatum	-	-	-	-	-	12	6	-	-	-
Glochidion lanceolarium	-	-	-	6	-	-	-	-	-	-
Glochidion thomsonii	-	9	-	-	-	-	-	-	-	-
Phyllanthus emblica	-	-	2	-	-	-	-	-	-	-
Pinaceae										
Abies densa	-	-	-	-	-	-	-	-	45	260
Larix griffithii	-	-	-	-	-	-	-	-	-	6
Pinus roxburghii	-	-	-	16	8	-	-	-	-	-
Pinus wallichiana	-	-	-	-	-	-	-	-	-	12
Tsuga dumosa	-	-	-	-	-	-	-	11	158	-
Pittosporaceae										
Pittosporum napaulense	-	-	-	7	-	-	-	-	-	-
Primulaceae										
Myrsine semiserrata	-	-	-	-	-	-	-	4	-	-
Maesa chisia	-	-	4	-	-	2	-	-	-	-
Proteaceae										
Helicia nilagirica	-	-	11	10	-	-	-	-	-	-
Putranjivaceae										
Drypetes indica	-	4	-	-	-	-	-	-	-	-
Rosaceae										
Eriobotrya petiolata	-	-	-	-	-	5	5	-	-	-
Photinia glabra	-	-	1	-	-	-	-	-	-	-
Photinia integrifolia	-	-	2	-	-	6	46	1	-	-
Prunus cerasoides	-	-	-	-	8	-	-	-	-	-
Prunus cornuta	-	-	-	-	-	-	-	4	4	-
Prunus nepalensis	-	-	-	-	-	27	15	68	62	-
Prunus rufa	-	-	-	-	-	-	-	-	43	8

Family and botanical name	**Number of trees at different elevations (meters)**									
	200	**200***	**500**	**1000**	**1500**	**2000**	**2000***	**2500**	**3000**	**3500**
Sorbus rhamnoides	-	-	-	-	-	-	-	-	30	28
Sorbus thomsonii	-	-	-	-	-	-	-	-	-	8
Sorbus vestita	-	-	-	-	-	-	-	-	3	-
Rubiaceae										
Aidia cochinchinensis	-	7	4	3	-	-	-	-	-	-
Hyptianthera stricta	1	-	1	-	-	-	-	-	-	-
Neolamarckia cadamba	1	-	1	-	-	-	-	-	-	-
Pitardella sikkimensis	1	-	1	-	-	-	-	-	-	-
Rutaceae										
Tetradium fraxinifolium	-	-	-	5	7	20	7	-	-	-
Zanthoxylum acanthopodium	-	-	-	-	-	1	-	-	-	-
Zanthoxylum armatum	-	-	-	-	-	-	-	4	-	-
Sabiaceae										
Meliosma simplicifolia	11	30	1	-	-	-	-	-	-	-
Salicaceae										
Casearia glomerata	-	-	-	8	2	-	-	-	-	-
Casearia graveolens	14	122	46	-	-	-	-	-	-	-
Populus gamblei	-	-	-	-	19	3	-	-	-	-
Populus glauca	3	1	-	17	-	-	-	-	-	-
Salix wallichiana	-	-	-	-	-	-	-	1	-	-
Santalaceae										
Pyrularia edulis	-	-	-	2	-	-	-	-	-	-
Sapindaceae										
Acer cappadocicum	-	-	-	-	-	25	6	2	-	-
Acer hookeri	-	-	-	67	-	-	-	-	-	-
Acer oblongum	-	-	-	-	3	-	-	-	-	-
Acer osmastonii	-	-	-	-	-	3	-	-	-	-
Acer pectinatum	-	-	-	-	-	-	-	-	18	-
Acer campbellii	-	-	-	-	2	71	46	33	14	-
Acer sterculiaceum	-	-	-	-	-	-	-	26	13	-
Aesculus assamica	-	-	-	-	3	-	-	-	-	-
Schleichera oleosa	16	8	-	-	-	-	-	-	-	-
Sapotaceae										
Mimusops elengi	1	13	-	-	-	-	-	-	-	-
Sarcospermataceae	-	-	-	-	-	-	-	-	-	-
Sarcosperma arboreum	-	-	8	3	-	2	1	-	-	-
Scrophulariaceae										
Buddleja paniculata	-	-	-	-	4	-	-	-	-	-
Simaroubaceae										

Family and botanical name	**Number of trees at different elevations (meters)**									
	200	**200***	**500**	**1000**	**1500**	**2000**	**2000***	**2500**	**3000**	**3500**
Ailanthus integrifolia	9	3	72	22	-	-	-	-	-	-
Staphyleaceae										
Turpinia cochinchinensis	-	-	-	-	2	12	10	-	-	-
Turpinia pomifera	18	18	4	-	-	-	-	-	-	-
Symplocaceae										
Symplocos glomerata	-	-	-	-	-	39	127	8	-	-
Symplocos lucida	-	-	-	-	7	120	262	69	-	-
Symplocos ramosissima	-	-	-	-	-	-	-	2	-	-
Symplocos sumuntia	-	-	-	-	-	-	-	-	14	-
Taxaceae										
Taxus wallichiana	-	-	-	-	-	-	-	-	3	2
Tetramelaceae										
Tetrameles nudiflora	3	2	12	-	-	-	-	-	-	-
Theaceae										
Schima wallichii	50	63	15	304	209	-	-	-	-	-
Thymelaeaceae										
Edgeworthia gardneri	-	-	-	-	-	-	-	2	-	-
Vitaceae										
Leea indica	2	1	6	-	-	-	-	-	-	-
Unidentified	-	-	2	-	-	-	-	-	-	-
Unidentified	-	-	1	-	-	-	-	-	-	-
Unidentified	-	-	1	-	-	-	-	-	-	-
Unidentified	3	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	1	-	-	-	-	-	-
Unidentified	-	-	1	-	-	-	-	-	-	-
Unidentified	-	-	1	-	-	-	-	-	-	-
Unidentified	-	-	-	-	-	1	-	-	-	-
Unidentified	-	-	-	1	-	-	-	-	-	-
Unidentified	-	-	1	-	-	-	-	-	-	-

*represents a single 5ha grid at the denoted elevation zone.

Appendix-3

Tree species encountered during sampling along the elevational gradient of Jammu & Kashmir in northwest Himalaya.

Family and botanical name	**Number of trees at different elevations (meters)**								
	500	**500***	**1000**	**1500**	**2000**	**2000***	**2500**	**3000**	**3500**
Anacardiaceae									
Toxicodendron wallichii	-	-	-	3	-	-	-	-	-
Cotinus coggygria	-	-	-	2	2	-	-	-	-
Lannea coromandelica	84	163	-	-	-	-	-	-	-
Apocynaceae									
Holarrhena pubescens	-	5	-	-	-	-	-	-	-
Wrightia arborea	5	-	-	-	-	-	-	-	-
Betulaceae									
Alnus nitida	-	-	78	14	3	-	6	-	-
Betula utilis	-	-	-	-	-	-	-	37	184
Corylus jacquemontii	-	-	-	-	-	-	6	-	-
Bignoniaceae									
Jacaranda mimosifolia	4	-	-	-	-	-	-	-	-
Oroxylum indicum	2	-	-	-	-	-	-	-	-
Oroxylum indicum	-	2	-	-	-	-	-	-	-
Boraginaceae									
Cordia myxa	19	59	-	-	-	-	-	-	-
Ehretia laevis	-	6	-	-	-	-	-	-	-
Cannabaceae									
Celtis australis	-	-	7	2	7	-	1	-	-
Celastraceae									
Gymnosporia royleana	-	2	-	-	-	-	-	-	-
Combretaceae									
Terminalia arjuna	-	5	-	-	-	-	-	-	-
Ebenaceae						-			
Diospyros cordifolia	6	19	-	-	-	-	-	-	-
Euphorbiaceae									
Mallotus philippensis	39	87	18	-	-	-	-	-	-
Fagaceae						-			
Quercus baloot	-	-	-	2	-	-	127	-	-
Quercus leucotrichophora	-	-	41	97	5	-	-	-	-
Hamamelidaceae									
Parrotiopsis jacquemontiana	-	-	-	-	-	-	11	-	-
Juglandaceae									
Juglans regia	-	-	-	7	-	-	8	-	-

Family and botanical name	Number of trees at different elevations (meters)								
	500	500*	1000	1500	2000	2000*	2500	3000	3500
Lamiaceae									
Callicarpa arborea	-	-	3	-	-	-	-	-	-
Gmelina arborea	24	-	-	-	-	-	-	-	-
Premna barbata	15	-	-	-	-	-	-	-	-
Lauraceae									
Litsea glutinosa	-	-	6	-	-	-	-	-	-
Neolitsea pallens	-	-	-	-	89	407	-	-	-
Leguminosae									
Acacia catechu	32	1	-	-	-	-	-	-	-
Acacia modesta	74	200	12	-	-	-	-	-	-
Acacia nilotica	3	-	25	4	-	-	-	-	-
Albizia lebbeck	22	-	-	-	-	-	-	-	-
Bauhinia variegata	9	5	2	12	-	-	-	-	-
Butea monosperma	1	11	-	-	-	-	-	-	-
Cassia fistula	28	37	-	-	-	-	-	-	-
Cassia glauca	2	2	-	-	-	-	-	-	-
Dalbergia sissoo	15	5	-	-	-	-	-	-	-
Delonix regia	-	7	-	-	-	-	-	-	-
Lythraceae									
Punica granatum	-	-	23	-	-	-	-	-	-
Woodfordia fruticosa	-	3	-	-	-	-	-	-	-
Malvaceae									
Bombax ceiba	13	20	-	-	-	-	-	-	-
Grewia optiva	26	54	7	-	-	-	-	-	-
Grewia tenax	13	-	-	-	-	-	-	-	-
Meliaceae									
Melia azedarach	1	3	3	-	-	-	-	-	-
Toona ciliata	2	-	6	-	-	-	-	-	-
Toona sinensis	-	-	-	-	4	-	-	-	-
Moraceae									
Ficus auriculata	6	4	-	-	-	-	-	-	-
Ficus benghalensis	2	-	-	-	-	-	-	-	-
Ficus carica	-	-	-	3	-	-	-	-	-
Ficus hispida	1	1	-	-	-	-	-	-	-
Ficus palmata	-	-	9	4	-	-	-	-	-
Ficus racemosa	4	1	-	-	-	-	-	-	-
Ficus semicordata	11	-	-	-	-	-	-	-	-
Morus alba	2	-	2	1	-	-	-	-	-
Moringaceae						-			

Family and botanical name	**Number of trees at different elevations (meters)**								
	500	**500***	**1000**	**1500**	**2000**	**2000***	**2500**	**3000**	**3500**
Moringa oleifera	14	5	-	-	-	-	-	-	-
Myrtaceae									
Callistemon citrinus	-	-	1	-	-	-	-	-	-
Eucalyptus tereticornis	-	-	2	-	-	-	-	-	-
Syzygium cumini	9	2	-	-	-	-	-	-	-
Oleaceae									
Fraxinus excelsior	-	-	-	2	13	10	2	-	-
Olea europaea	-	-	22	-	-	-	-	-	-
Phyllanthaceae									
Phyllanthus emblica	7	9	-	-	-	-	-	-	-
Pinaceae									
Abies pindrow	-	-	-	-	-	-	6	149	225
Cedrus deodara	-	-	-	108	264	845	233	21	-
Picea smithiana	-	-	-	-	-	-	29	192	-
Pinus gerardiana	-	-	-	-	-	-	32	-	-
Pinus roxburghii	11	-	174	77	-	-	-	-	-
Pinus wallichiana	-	-	-	190	121	49	9	93	65
Rhamnaceae									
Ziziphus jujuba	63	86	-	-	-	-	-	-	-
Ziziphus oxyphylla	17	5	5	-	-	-	-	-	-
Rosaceae									
Prunus cornuta	-	-	-	-	2	-	9	25	-
Pyrus pashia	-	-	16	3	-	-	-	-	-
Sorbus foliolosa	-	-	-	-	-	-	-	-	4
Sorbus lanata	-	-	-	-	-	-	-	11	-
Rubiaceae									
Hymenodictyon orixense	5	15	-	-	-	-	-	-	-
Mitragyna parvifolia	8	26	-	-	-	-	-	-	-
Rutaceae						-			
Aegle marmelos	14	9	-	-	-	-	-	-	-
Murraya koenigii	12	35	-	-	-	-	-	-	-
Zanthoxylum armatum	-	-	13	-	-	-	-	-	-
Salicaceae									
Flacourtia indica	-	52	-	-	-	-	-	-	-
Populus ciliata	-	-	-	18	26	-	42	-	-
Salix sericocarpa	-	-	-	-	-	-	2	-	-
Sapindaceae									
Acer acuminatum	-	-	-	-	-	-	-	4	-
Acer caesium	-	-	-	-	-	-	8	-	-

Family and botanical name	**Number of trees at different elevations (meters)**								
	500	**500***	**1000**	**1500**	**2000**	**2000***	**2500**	**3000**	**3500**
Acer cappadocicum	-	-	-	-	-	-	17	-	-
Aesculus indica	-	-	-	6	7	7	9	-	-
Simaroubaceae									
Ailanthus altissima	-	-	-	3	8	1	-	-	-
Taxaceae									
Taxus wallichiana	-	-	-	-	1	-	-	57	-
Ulmaceae									
Ulmus wallichiana	-	-	-	-	7	-	16	-	-

*represents a single 5ha grid at the denoted elevation zone.