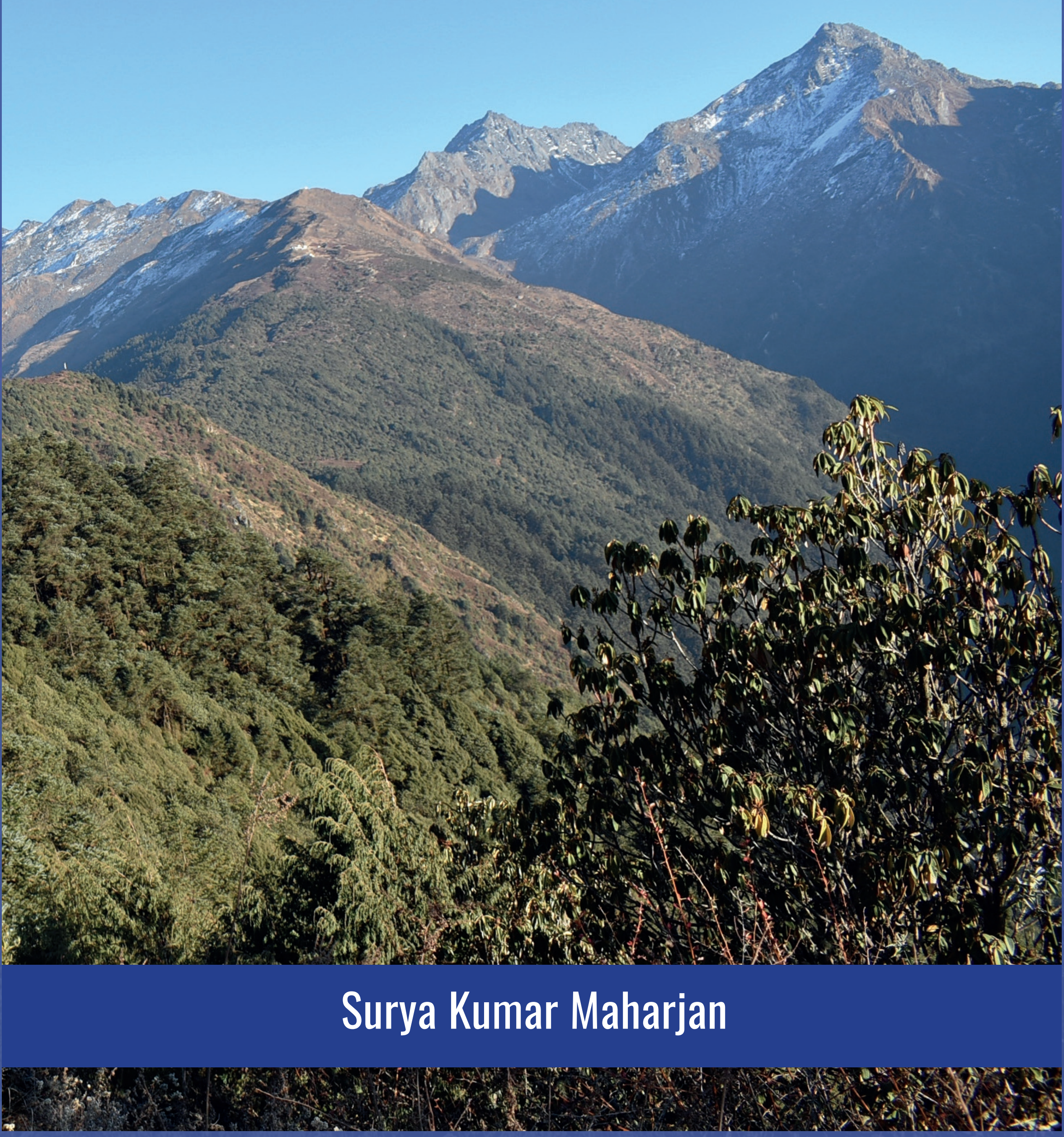
Plant species distribution along an elevational gradient in the Himalayas, Nepal

on drivers, mechanisms and the effects of climate change



Surya Kumar Maharjan

Propositions

1. Stem and branch traits are better predictors of species' elevational distributions than leaf traits.
   (this thesis)

2. The effects of climate change on elevational range shifts of tree species depend not only on changes in temperature and precipitation, but also on local soil conditions.
   (this thesis)

3. In science, beginners look for expected results but veterans look for unexpected results.

4. Ecology and economy are more rivals than friends.

5. Fear of benefitting colleagues prevents many researchers from sharing their data, which is holding back the overall advancement of science and society.

6. International treaties and conventions without proper international institutional support are a burden for the developing world.

Propositions belonging to the thesis, entitled

Plant species distribution along an elevational gradient in the Himalayas, Nepal:
on drivers, mechanisms and the effects of climate change

Surya Kumar Maharjan
Wageningen, 19 November 2021

Plant species distribution along an elevational gradient in the Himalayas, Nepal

on drivers, mechanisms and the effects of climate change

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Surya Kumar Maharjan

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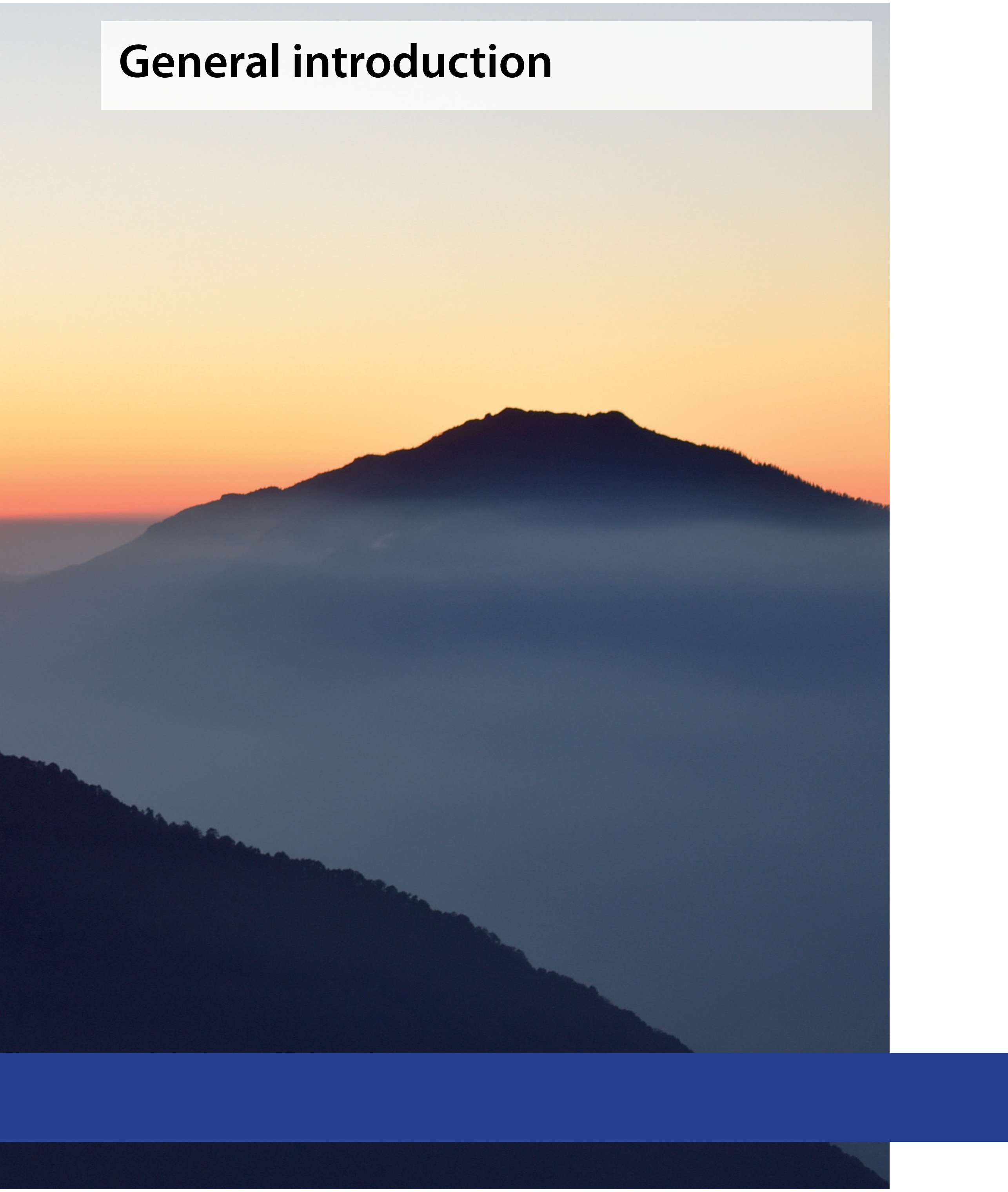
1

General introduction



1.1 Introduction

Tropical montane landscapes are amongst the global hotspots of biodiversity (Mittermeier et al., 2004) because they present highly dynamic ecotones that facilitate speciation, niche partitioning and coexistence. They present, therefore, ideal systems to study one of the central questions in ecology: what determines species distribution patterns? At the same time, these landscapes are threatened by an unprecedented rate of global warming (IPCC, 2014) that forces species to move upward (Bitencourt et al., 2016; Zu et al., 2021). Understanding the mechanisms that shape species distributions along elevational gradients is important for present-day conservation. In addition, it is also needed to predict species' responses to global warming, design climate adaptation measures and select appropriate species for future planting activities. This thesis focuses on the Himalayas, as they are amongst the global hotspots of biodiversity (Mittermeier et al., 2004). The Himalayas present one of the longest and steepest elevational gradients in the world while at the same time they are being severely affected by global warming (Luitel et al., 2020; Sabin et al., 2020). This thesis analyses patterns of plant species distribution along the Himalayan elevational gradient in Nepal with the aims to understand 1) which environmental factors best predict the elevational distributions of species?; 2) how do plant functional traits determine species' elevational positions?; and 3) how will future climate warming affect species' elevational ranges and distribution areas?

1.2 Environmental factors that control the elevational distributions of plant species

In nature, environmental conditions filter species from the species pool leaving behind only the subset of species adapted to local conditions (community assembly rules: Keddy, 1992; Woodward & Diament, 1991). To predict how plant species will respond to climate change, it is, therefore, crucial to understand which environmental factors control species distributions along environmental gradients. In montane landscapes, with increasing elevation, multiple abiotic factors change in a predictable way affecting different aspects of plant functioning. The decrease in temperature may reduce metabolic rates and transpiration of plant species (Gates, 1968; Körner, 2016). The gradual decrease in atmospheric pressure and atmospheric partial pressure of CO_2 may affect gas exchange in plants and consequently reduce photosynthesis (Friend & Woodward, 1990; Körner & Diemer, 1987). However, such effects of lower temperature and atmospheric pressure may be partially mitigated by increases in clear-sky solar radiation and diffusion coefficients for water vapour and CO_2 with elevation (Gale, 1972a, 1972b; Smith & Geller, 1979; Terashima et al., 1995; Wang et al., 2017). The stronger winds that are common at mountaintops and ridges (Barry, 1992b) may increase the risks of wind-induced physical damage to the plant species (Onoda & Anten, 2011). Soils often become thinner, less developed and less fertile with increasing elevation (FAO, 2015), with potential negative implications for the regeneration and growth of species (Müller, Schickhoff, et al., 2016; Müller, Schwab, et al., 2016). Since temperature decreases linearly with elevation and it directly influences plant metabolic rates and physiological processes, and controls growing season length, temperature is an important limiting factor influencing species distributions in montane landscapes. Since topography becomes steeper and soil becomes shallower with increase in elevation, slope and soil conditions are likely to limit species distributions by limiting growth conditions in montane landscapes in addition to temperature. Multiple environmental factors thus play a crucial role in shaping plant species distribution along elevational gradients, however their relative importance is still contested (Bhattarai et al., 2004; Dubuis et al., 2013; Müller, Schickhoff, et al., 2016).

1.3 Do species' elevational ranges change with elevation?

Environmental conditions become harsher, more stressful and variable with increase in elevation (Pintor et al., 2015; Rasmann et al., 2014; Stevens, 1992). It is, therefore, likely that species living at high elevations would have wider physiological tolerances to environmental conditions and occupy broader elevational ranges. In the montane landscapes, shifts in species distribution range will be particularly problematic for plant species with narrow elevational ranges as they are likely to be forced to move upward rapidly, and for those living near mountaintops as smaller land surface area is available at higher elevations (Körner, 2007). To predict how montane plant species will respond to climate change, it is crucial to understand how they are spatially distributed in montane landscapes. The diurnal and seasonal variability of environmental factors increase with increasing elevation (Rasmann et al., 2014) and thus contribute to a harsher, more stressful and variable environment of high-elevation plants. The climatic variability hypothesis (more generally the environmental variability hypothesis) posits that species occurring in climatically variable habitats, such as those at high elevations, should develop wider environmental tolerances and, hence, occupy wider elevational ranges than species occurring in climatically stable habitats, such as those at low elevations (Pintor et al., 2015; Stevens, 1992). This phenomenon is also known as "Rapoport's elevational rule" (Stevens, 1992). The generality of Rapoport's elevational rule is still contested–some studies found strong support for it (Pintor et al., 2015; Rasmann et al., 2014; Schellenberger Costa et al., 2018; Subedi et al., 2020), while others have found little (Feng et al., 2016) or no support (Bhattarai & Vetaas, 2006; Lee et al., 2013; Vetaas & Grytnes, 2002). Possibly these studies found different patterns because they considered different lengths of the elevational gradient. In this thesis, I tested the applicability of the rule for plant species along the slopes of the Himalayas in Nepal.

1.4 Role of functional traits in shaping plant species distribution

Community assembly rules (Keddy, 1992; Woodward & Diament, 1991) postulate that species are filtered out of the metacommunity, based on their functional traits. Functional traits are defined as morphological, physiological or phenological attributes that affect plant growth, survival and reproduction and, hence, distribution (Violle et al., 2007). Researchers have studied individual traits related to nutrient use (Nielsen et al., 2019), cold tolerance (Yin et al., 2018), UV stress (Chen et al., 2013) and light (Sterck et al., 2006), but very few have analysed the association of comprehensive suite of traits to plant adaptations and compromises to multiple environmental constraints. Díaz et al. (2004) analysed the variation in 12 traits among four floras across three continents. They showed the existence of a fundamental axis of evolutionary specialization across ecosystems and biomes that runs from plant species with a conservative strategy characterised by small, thick and tough leaves with slow turnover to plant species with an acquisitive strategy characterised by large, thin and soft leaves with rapid turnover. In a follow-up study, Díaz et al. (2016) analysed the variation in six major traits critical to growth, survival and reproduction of vascular plant species across the globe. They showed two major axes of evolutionary specialization, namely the plant size spectrum (that runs from short species with small diaspores to tall species with large diaspores) and the leaf economics spectrum (that runs from species with cheaply constructed acquisitive leaves to species with conservative leaves). These two axes together accounted for 74% of the trait variation across the globe. In this thesis, we focus on traits of tree species and the plant size spectrum may therefore be less marked. We thus tested whether a conservative-acquisitive strategy spectrum identified for a limited set of traits for vascular plant species across the globe (Díaz et al., 2004, 2016) also holds for an extended set of traits for tree species along the elevational gradient.

1.5 Climate change induced species range shifts

In tropical montane landscapes, the presence of steep mountain ranges and a shallow latitudinal gradient in climatic conditions are likely to leave plant species with only one option to respond to global warming–to shift their distributions upward. Such shifts in species elevational distribution range will be particularly problematic for 1) plant species with narrow elevational ranges as they are likely to be forced to move upward rapidly and for 2) those living near mountaintops as less land surface area is available at higher elevations, leading to contractions in species distributions and a smaller and potentially less viable population size. The Himalayas are experiencing substantial warming particularly at higher elevations (~0.5 °C decade^{-1}, Gao et al., 2018; Luitel et al., 2020; Pepin et al., 2015). Species are currently shifting upslope to cooler elevations in response to rising temperatures at rates as high as 27 m decade^{-1} (Bhatta et al., 2018; Gaire et al., 2014;

Suwal et al., 2016; Telwala et al., 2013). Since upslope movements along steep slopes result in rapid changes in temperature, it is likely that small geographic displacements will be enough to keep pace with climate warming in the highlands. However, larger geographic displacements will be required in flatter areas and along more gentle slopes in valleys and lowland plains. Mamantov et al. (2021), in a meta-analysis from 16 montane regions worldwide including the Eastern Himalayas, showed that rates of species range shift indeed decreased with increase in elevation. In this PhD thesis, we tested whether the same relationship holds for the (Central) Himalayan elevational gradient, meaning that low-elevation species have to shift faster upslope than high-elevation species to track the environmental changes.

1.6 Can traits predict species range shifts?

Plant functional traits determine plant performance (Poorter & Bongers, 2006) and have potential to shape & predict species distributions (Violle et al., 2007) and are, therefore, important to understand and predict species' potential responses to climate change. The competitive ability of the plant could be interpreted from their leaf-economic traits (Estrada et al., 2016). High competitive ability in combination with effective dispersal may facilitate establishment and proliferation outside the species' current distribution range. Indeed the traits related to dispersal capacity, such as fruit type and dispersal mode have been shown to effectively predict observed species range shifts among subtropical montane plants in the Chinese Hengduan Mountains (Zu et al., 2021). Although plant traits can reflect the ability of species to disperse, establish, grow and colonize new sites (Estrada et al., 2016; Zu et al., 2021), little is known about how the variation in plant traits with elevation affect the capacity of species to shift their elevational ranges. Therefore, in this thesis, I analysed whether traits can be used as proxies to predict the magnitude of the shifts in species distribution range.

1.7 Research questions and hypotheses

In this thesis, I present the analyses of the distribution patterns of 277 plant species (Table S2.1) along an elevational gradient in the Himalayas in Nepal. Specifically, I addressed the following questions 1) Which environmental factors best predict species' elevational distributions and do highland species have larger elevational ranges than lowland species (*Chapter 2*)?, 2) How do functional traits shape species' elevational positions and lead to species partitioning of the elevational gradient (*Chapter 3*)? and 3) How will future global warming affect species' elevational ranges and distribution areas (*Chapter 4*, Figure 1.1)?

This thesis consists of five chapters, including this general introduction (*Chapter 1*).

In *Chapter 2*, I asked which environmental factors best predict species' elevational distributions and do highland species have larger elevational ranges than lowland species? I modelled the ecological niches of 277 plant species based on presence data from a network of 2,039 forest inventory plots systematically distributed across the country and botanical collections. I used MaxEnt (Phillips et al., 2006, 2004) to develop species distribution/ecological niche models by relating species presence data to 19 climatic, topographic and soil variables, prepared species distribution maps, and analysed which environmental factors best predict species' elevational distributions and whether highland species have larger elevational ranges. Because temperature 1) decreases predictably with elevation, 2) directly influences plant physiology and soil processes vital for plant survival, growth and reproduction, and 3) constrains the growth of plant species by controlling growing season length, I hypothesized that temperature would be the key environmental factor predicting the distribution of plant species along an elevational gradient. Because environmental conditions become harsher, more stressful and variable with increase in elevation, I hypothesized that species living at high elevations would have wider physiological tolerances to environmental conditions and occupy broader elevational ranges.

In *Chapter 3*, I asked how functional traits shape species' elevational positions and lead to species partitioning of the elevational gradient? I quantified for 31 tree species a set of 39 plant traits related to resource uptake, use and conservation. I specifically analysed how traits cluster into separate functions, how traits and clusters associate into distinct plant strategies, and which traits best predict species positions along the elevational gradient. Because environmental conditions become harsher with increasing elevation, I hypothesized that harsher environmental conditions at higher elevations select for species with more conservative trait values and vice versa. Traits associated with conservative-acquisitive strategy spectrum should therefore best predict species' positions along an elevational gradient.

In *Chapter 4*, I asked how future global warming will affect species' elevational ranges and distribution areas? For a subset of 137 tree species, near current (1985) and future (2050) species distribution maps were made by projecting the species distribution models developed in *Chapter 2* to the near current and the future environmental conditions. The elevational ranges in 1985 were compared with the predicted elevational ranges in 2050 to evaluate shifts in species' distribution range and changes in distribution area and whether they vary with their elevational niche and with their conduit diameter – an easy to measure trait that best explains tree species' positions in the Himalayas. Because upslope movements along steep slopes results in rapid decreases in temperature and surface area, we hypothesized that lowland species would shift geographically at faster rates than highland species and consequently would show the largest absolute reductions in distribution area. Because the Himalayas are predicted to become warmer and wetter, we hypothesized that species for which species distribution models are driven by responses to temperature and precipitation would show upslope shifts in their optimum elevation resulting in a reduction of their distribution area. Because wide conduits facilitate water transport and growth, and enhance competitive ability (Ch. 3), we hypothesized that species with wide conduits exhibit large predicted range shifts and changes in distribution area.

In *Chapter 5*, I combined the results of the aforementioned three chapters (Ch. 2-4) and discussed the importance of understanding the mechanisms that shape current and predicted future species' elevational distributions to inform conservation measures for the Himalayan forests, designing climate adaptation measures, and to select plant species that will require assisted migration for their survival. Further, I also discussed the role of science and its research priorities and the society in general for safeguarding the diversity and functioning of tropical montane landscapes.

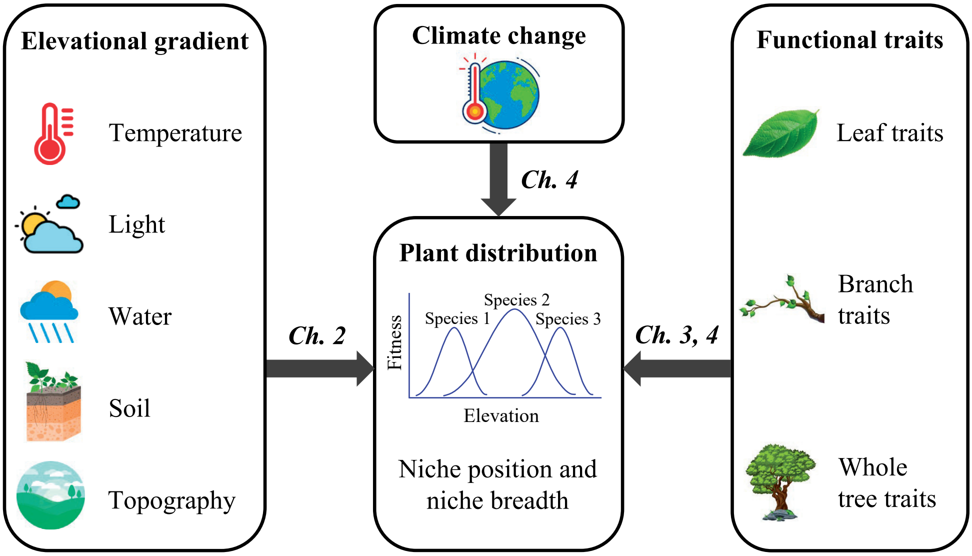


Figure 1.1. Conceptual diagram showing the linkages between the three chapters (Ch.). Ch. 2 focuses on the role of environmental factors in predicting present-day species elevational distributions; Ch.3 focuses on the role of plant traits in shaping present-day species elevational distributions; and Ch.4 focuses on the effects of climate change and plant traits on change in species' elevational distributions, i.e. species elevational range shifts.

1.8 Study area

In this thesis, I focused on Himalayan forests across elevational gradient within Nepal, representing one of the longest and steepest elevational gradients in the world. Within a horizontal span of mere 200 km, elevation varies from 60 m a.s.l. in the south to the highest 8.9 km a.s.l. high peak of the world in the north (HMGN/MFSC, 2002) resulting into a roughly south-facing elevational gradient. Along this gradient, temperature decreases approximately linearly and precipitation rapidly drops beyond 2,000 m a.s.l. (Figure 1.2). Potential evapotranspiration follows the temperature trend, wind speed shows an increasing trend, while topography becomes steeper and soils become shallower (Figure 1.2).

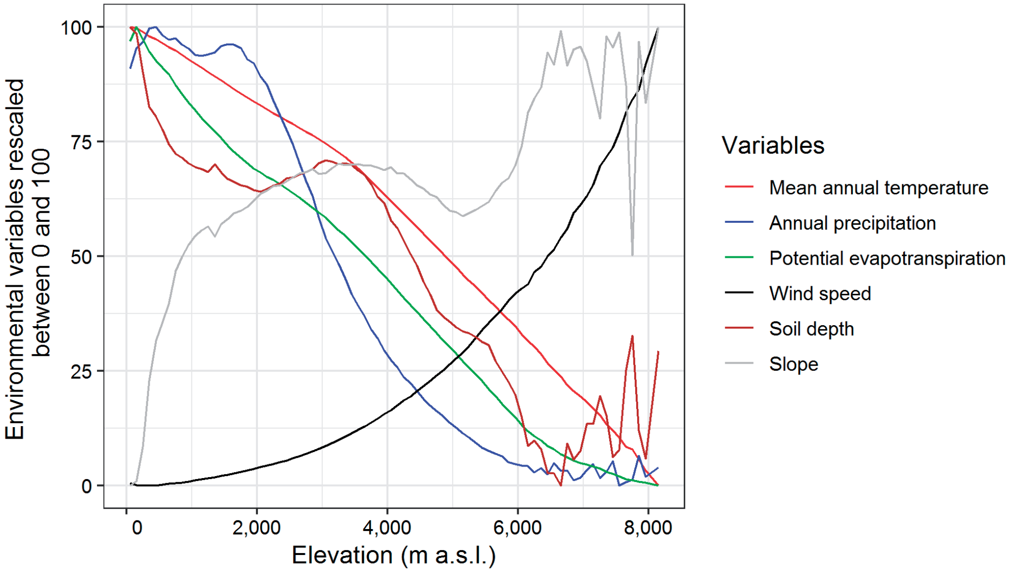


Figure 1.2. Changes in mean annual temperature, annual precipitation, potential evapotranspiration, wind speed, soil depth and slope along the Himalayan elevational gradient. Here mean values of environmental variables for 100 m elevational belts rescaled between 0-100 are plotted against elevation (for data sources, see Chapter 2).

Vegetation follows changes in temperature and precipitation patterns and changes from wet (1,738 mm yr^{-1}) and warm (24.1 °C) tropical deciduous *Shorea robusta* forests to intermediate temperate moist forests co-dominated by oaks and conifers to relatively drier (1,132 mm yr^{-1}) and colder (6.9 °C) sub-alpine forests co-dominated by birches, rhododendrons and junipers (Lillesø et al., 2005; Shrestha et al., 2015; Figure 1.3; Figure 1.4). In addition to these species that are considered typical for these different forest types, many other tree species co-occur and were also investigated in this thesis.

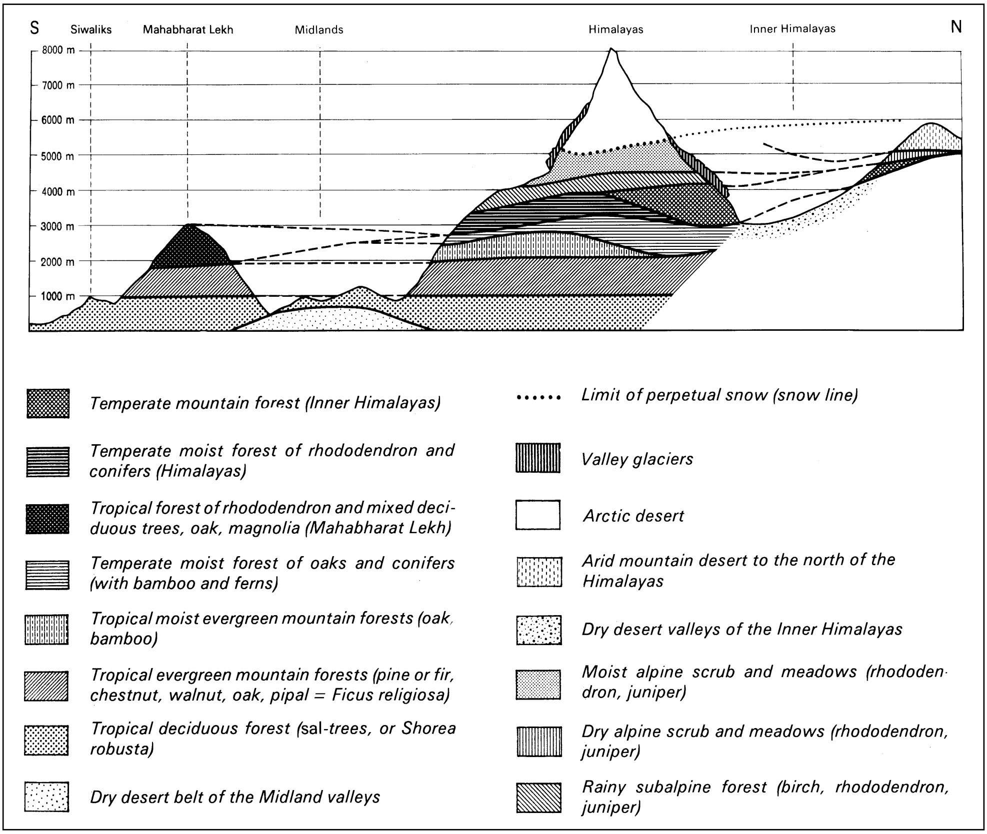


Figure 1.3. Cross-section of the vegetation of Nepal. Source: Hagen, 1998 in HMGN/MFSC, 2002.

(c) Treeline forest co-dominated by Rhododendrons, birch species and conifer species

(b) Intermediate forest co-dominated by oak species and conifer species

(a) Lowland *Shorea robusta* forest

Figure 1.4. Three major vegetation types of Nepal: (a) Lowland *Shorea robusta* forest, (b) Intermediate forest co-dominated by oak species and conifer species and (c) Treeline forest co-dominated by Rhododendrons, birch species and conifer species. (Photo credit: Bishnu Prasad Dhakal)

1.9 Study species

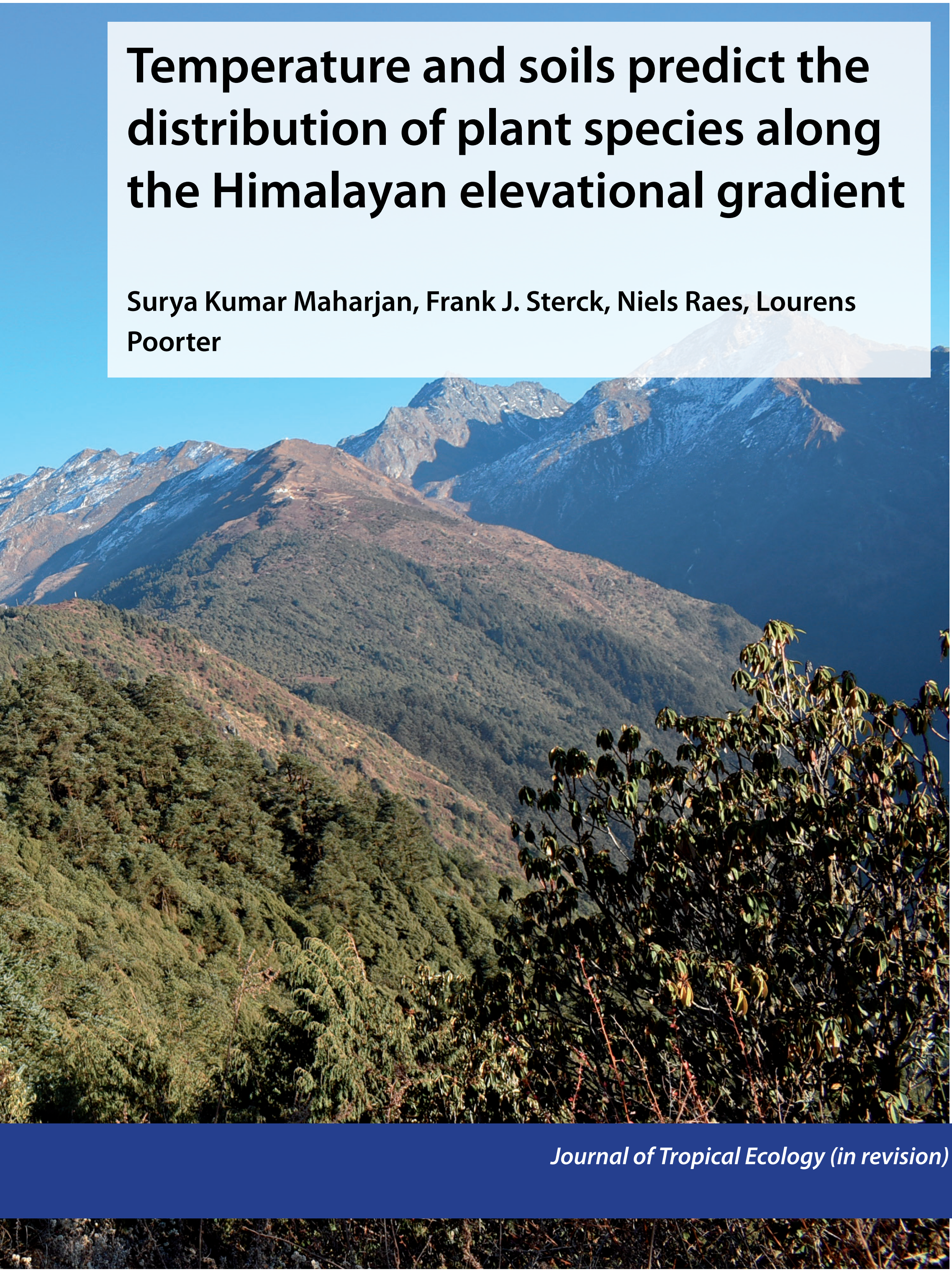
Based on forest inventories, I selected 277 plant species that occur along the entire elevation gradient from lowlands at 60 m a.s.l. to treeline at approximately 4,000 m a.s.l. Species were selected when they showed at least five spatially unique presence records at 30 arc seconds (~1km) raster resolution. This includes 143 tree, 76 shrub, 23 herb, 13 grass, 9 liana, 7 fern, 4 orchid, 1 palm and 1 sedge species. The species cover a wide range of 89 families and 198 genera (for the detailed list of study species see Table S2.1). Subsets of these species were analysed in Chapter 3 (31 tree species, Table S3.1) and 4 (137 tree species, Table S4.2). Images of few exemplary species are shown in Figure 1.5.

(a) *Shorea robusta* (b) *Pinus roxburghii* (c) Rhododendrons

Figure 1.5. Few exemplary species of Nepal: (a) *Shorea robusta*, (b) *Pinus roxburghii* and (c) Rhododendrons. (Photo credit: (a) Bishnu Prasad Dhakal and (b-c) Surya Kumar Maharjan)

CHAPTER

2



Temperature and soils predict the distribution of plant species along the Himalayan elevational gradient

Surya Kumar Maharjan, Frank J. Sterck, Niels Raes, Lourens Poorter

Journal of Tropical Ecology (in revision)

Abstract

Tropical montane systems are characterised by a high plant species diversity and complex environmental gradients. Climate warming may force species to track suitable climatic conditions and shift their distribution upward, which may be particularly problematic for species with narrow elevational ranges. To better understand the fate of montane plant species in the face of climate change, we evaluated a) which environmental factors best predict the distribution of 277 plant species along the Himalayan elevational gradient in Nepal, and b) whether species elevational ranges increase with increasing elevation. To this end, we developed ecological niche models using MaxEnt by combining species survey and presence data with 19 environmental predictors. Key environmental factors that best predicted the distribution of Himalayan plant species were mean annual temperature (for 54.5% of the species) followed by soil clay content (10.2%) and slope (9.4%). Although temperature is the best predictor, it is associated with many other covariates that may explain species distribution, such as irradiance and potential evapotranspiration. Species at both ends of the Himalayan elevational gradient had narrower elevational ranges than species in the middle. Our results suggest that with further global warming most Himalayan plant species have to migrate upward, which is especially critical for upland species with narrow distribution ranges.

Keywords: climate change, distribution range, environmental gradients, Himalayan plant species, MaxEnt, Nepal, species distribution model, temperature

2.1 Introduction

One of the central questions in ecology is what controls the distribution of species. This question has become more urgent because climate change is forcing species to track suitable climatic conditions and shift their distribution ranges either poleward or upward (Chen et al., 2011; IPCC, 2014). Particularly in montane landscapes in (sub-)tropical biomes, the presence of steep mountain ranges and shallow latitudinal gradient in climatic conditions are likely to leave plant species with only one option–shift their ranges upward. In these landscapes, such shift in species distribution ranges will be particularly problematic for plant species with narrow elevational ranges as they are likely to be forced to move upward rapidly to maintain viable population sizes, and for those living near mountaintops as smaller land surface area is available at higher elevations (Körner, 2007). To better understand the fate of montane plant species in the face of climate change, it is urgently needed to understand which environmental factors best predict their distribution and how they are spatially distributed in montane landscapes.

The elevational gradient (sometimes referred to as an "altitudinal gradient") is an ideal system to study the multiple factors that control species distribution, as it presents a complex, multiple-factor gradient that affects plant species distribution in multiple ways. Temperature, solar radiation, precipitation and soil properties are important determinants of plant species distribution, since they set the local site conditions and thus the abiotic niches (Hemp, 2006). Temperature decreases linearly with increasing elevation and it regulates plant metabolic rates that are vital for plant survival, growth and reproduction. Lower temperature at higher elevations may not only impair plant performance, but also lead to slower soil microbial activity and other soil processes, hence lower nutrient availability (Müller, Schickhoff, et al., 2016; Vincent et al., 2014). Under clear-sky, solar radiation increases with increasing elevation because of reduced atmospheric turbidity. But the amount of solar radiation received by organisms depends on clouds and fog, and both often increase with increasing elevation (Adhikary, 2012; Körner, 2007). Consequently, in the areas often covered with clouds, productivity of montane species may be strongly limited by irradiance (Fyllas et al., 2017). With increasing elevation, in the subtropics, precipitation usually increases up to cloud condensation elevation and decreases beyond (Körner, 2007). Montane soils are, in general, poorly developed, stony, shallow, relatively infertile and often acidic. With increasing elevation, soils become thinner, less developed and less fertile (FAO, 2015). Precipitation, evapotranspiration, topography and soil water holding capacity determine water availability, hence plant survival. Particularly in steep montane landscapes, thin, stony and infertile soils have a low water-holding capacity, which impedes seedling and sapling establishment (Müller, Schickhoff, et al., 2016; Müller, Schwab, et al., 2016). Additionally, diurnal and seasonal variability of environmental factors increase with increasing elevation (Rasmann et al., 2014) exposing high elevation plants to comparatively harsher, more stressful and variable environmental conditions. All the aforementioned environmental factors play crucial roles in shaping plant species distribution along elevational gradients, however their relative importance is still contested (Bhattarai et al., 2004; Dubuis et al., 2013; Müller, Schickhoff, et al., 2016).

Rapoport's elevational rule

The elevational ranges of various groups of organisms (trees, mammals, birds, reptiles, insects and amphibians) increase with increasing elevation, a phenomenon which has been coined "Rapoport's elevational rule" (Stevens, 1992). Stevens (1992) suggested that these wider ranges are the result of higher climatic variability that species experience at higher elevations. The climatic variability hypothesis (more generally the environmental variability hypothesis) posits that species occurring in climatically variable habitats, such as those at high elevations, would develop wider environmental tolerances and, hence, occupy wider elevational ranges than species occurring in climatically stable habitats, such as those at low elevations (Pintor et al., 2015; Stevens, 1992). The generality of Rapoport's elevational rule is still contested–some studies found strong support for it (Pintor et al., 2015; Rasmann et al., 2014; Schellenberger Costa et al., 2018; Subedi et al., 2020), while others have found little (Feng et al., 2016) or no support (Bhattarai & Vetaas, 2006; Lee et al., 2013; Vetaas & Grytnes, 2002).

In this study, we focused on the Himalayan elevation gradient in Nepal because: 1) it is one of the longest and steepest elevational gradients in the world, 2) it is a global hotspot of biodiversity (Mittermeier et al., 2004), 3) global warming is forcing numerous treeline species along this gradient to move upward at a rate as high as 26 m decade^{-1} (Chhetri et al., 2018; Gaire et al., 2014; Suwal et al., 2016) and 4) the distribution of species along an elevational gradient according to Rapoport's elevational rule can be tested along this gradient. Some studies have reported unimodal patterns in tree species' elevational ranges along this elevational gradient (Bhattarai & Vetaas, 2006; Vetaas & Grytnes, 2002), while others have reported a monotonic increase in elevational ranges among other groups of plant species (Feng et al., 2016; Subedi et al., 2020) supporting Rapoport's elevational rule. These studies used an elevation band (100 m bands) approach. Firstly, based on the data on species' elevational ranges in the published floral databases, they estimated species' elevational ranges as the differences between the maximum and minimum elevations of species rounded to the nearest 100 m and elevational midpoints as the averages of the elevational limits of species. Then they used average elevational ranges of all species that occur in each elevation band or species whose elevational midpoints occur in each elevation band to evaluate the relationship between species' elevational ranges and elevation. However, species' elevational midpoints and average elevational ranges based on presence records may not be representative of the species' elevational optima–points where species occurrence or abundance peak (Pintor et al., 2015) and elevational tolerance - the elevational range where species could actually occur. For example, the elevational midpoint of a species with its elevational range between 100 and 1,500 m a.s.l. is 800 m a.s.l. However, its elevational optimum may be higher or lower than 800 m a.s.l. depending on whether species abundance is left- or right-skewed. The species' elevational optima should be in the middle of species' niches rather than the middle of their elevational ranges, and the modelled ecological niches and their projected reciprocal spatial distributions may provide a better measure of species' elevational tolerance than the elevation of presence records alone. Therefore, in this study, we used MaxEnt (Phillips et al., 2006, 2004) to model ecological niches and project spatial distributions of 277 plant species that are most common among the 1,169 inventoried plant species, and that belong to 9 different life forms, and subsequently used these niches and distribution maps to calculate species' elevational optima and ranges (see Methods for details).

Here we addressed two research questions. First, which environmental factors best predict the distribution of plant species along an elevational gradient? We hypothesized that temperature would be the key environmental factor that best predicts the distribution of plant species along an elevational gradient because it 1) decreases predictably with elevation, 2) directly influences plant physiology and soil processes vital for plant survival, growth and reproduction and 3) constrains growth of plant species by controlling growing season length. Second, how do species' elevational ranges change with elevation along an elevational gradient? We hypothesized that plant species living at high elevations, where environmental conditions are harsher, more stressful and variable, would have wider physiological tolerances to environmental conditions and occupy broader elevational ranges compared to plant species living at low elevations, where environmental conditions are more benign and stable, according to Rapoport's elevational rule (Pintor et al., 2015; Stevens, 1992).

2.2 Materials and Methods

2.2.1 Study site

For our study, we selected the Himalayan elevational gradient in Nepal, one of the longest and steepest elevational gradients in the world. Within a horizontal span of mere 200 km, elevation varies from 60 m a.s.l. in the south to the highest peak of the world in the north (HMGN/MFSC, 2002) resulting into a roughly south-facing elevational gradient. Along the gradient, trees can grow at up to 4,000 m a.s.l. (treeline) while alpine meadows can be found at up to 5,000 m a.s.l. (TISC, 2002). Temperature decreases linearly along this gradient (Lillesø et al., 2005) and precipitation shows a mid-elevation maximum (Acharya et al., 2011; Kansakar et al., 2004). This gives rise to an extensive bioclimatic gradient ranging from wet, warm and stable tropical climate in the lowlands in south to cold, more stressful and variable alpine climate in the Himalayas in the north (HMGN/MFSC, 2002; Lillesø et al., 2005). As a result of this elevation-driven variation in environmental conditions and habitats, Nepal is a home to disproportionately higher percentage of the world's flora and fauna (5.1% of gymnosperms, 2.7% of angiosperms, 9.3% of birds, and 4.5% of mammals in 0.1% of global land area, HMGN/MFSC, 2002)–a global hotspot of biodiversity (Mittermeier et al., 2004).

2.2.2 MaxEnt

As modelled ecological niches and their projected spatial distributions may provide a better measure of species' elevational tolerance than the elevation of presence records alone, we used a modelling approach. MaxEnt version 3.3.3k (Phillips et al., 2006, 2004) was selected over other species distribution modelling (SDM) algorithms because: 1) it is a powerful presence-only SDM algorithm that can efficiently handle complex interactions between species presence records and environmental predictors (Elith et al., 2006, 2011), 2) it makes relatively accurate predictions with small number of presence records (Pearson et al., 2007; van Proosdij et al., 2016; Wisz et al., 2008), 3) it has been reported to outperform other SDM algorithms (Aguirre-Gutiérrez et al., 2013; Elith et al., 2006; Giovanelli et al., 2010; Hao et al., 2020; Merckx et al., 2011; Wisz et al., 2008), 4) it doesn't require species absence records which are difficult to confirm (MacKenzie, 2005; Raes & Aguirre-Gutiérrez, 2018) and 5) it allows using all species presence records available in floral databases and natural history collections. For their improved predictive performances, ensemble models are increasingly being used for species distribution modelling (Aguirre-Gutiérrez et al., 2013; Araújo & New, 2007; Hao et al., 2020). However, it is very difficult to estimate contributions of individual environmental variables to the final species distribution model from an ensemble model. As one of our main aims is to identify key environmental factors that best predict plant species distribution along the elevational gradient (factors contributing the most to species distribution models), MaxEnt alone was used instead of ensemble of different SDM algorithms. MaxEnt uses species presence records, environmental predictors and randomly drawn background samples to model species' ecological niches and project their spatial distributions.

2.2.3 Study species and their presence records

The national forest inventory (2010-2014) undertaken by Forest Research and Training Centre (then Department of Forest Research and Survey) Nepal served as the main source of species presence records. Two-phase stratified systematic cluster sampling was used for the inventory. In the first phase, Nepal was divided into 4 × 4 km grids. At each grid node, a sample cluster of 4-6 concentric circular plots (four (2 x 2) plots 300 m apart in north-south and east-west directions in lowlands with relatively homogenous forests and six (3 x 2) plots 150 m apart in north-south and 300 m apart in east-west directions in hills and mountains with heterogeneous forests) was positioned starting at the grid node and moving first towards north and then towards east. Each plot had four concentric circular sub-plots of radii 4, 8, 15 and 20 m that were used to identify the trees to species, and measure individual stem diameter at breast height (DBH), and tree height of trees of DBH ranges 5-9.9, 10-19.9, 20-29.9 and 30 cm and more, respectively. In addition to that, each plot had four 1 m^2 sub-plots each located 5 m away from the centre of the plot in four cardinal directions that were used to assess species-wise stem count of non-woody vascular plants. Next, each plot had four circular sub-plots of 2 m radii each located 10 m away from the centre of the plot in four cardinal directions that were used to assess species-wise stem count and mean height of seedlings, saplings and shrubs with DBH <5 cm. In the second phase, 450 sample clusters representing 2,544 sample plots located in the forests below 4,000 m a.s.l. and with a slope <45° were selected for field measurements (for details see DFRS 2015). Of these 2,544 sample plots, we used species presence data from 2,039 sample plots for which plant species were reliably identified to species level. Plant species names were standardized using multiple sources (Tropicos, Taxonomic Name Resolution Service, The Plant List and The International Plant Names Index) and, in case of discrepancies, verified by a taxonomist from Tribhuvan University, Nepal to synonymise all taxonomic names to their currently accepted taxonomic names. In case of conflict, the currently accepted taxonomic names in The Plant List were used. Finally, of the 1,169 inventoried plant species, 333 species (167 tree, 85 shrub, 31 herb, 14 fern, 14 grass, 14 liana, 5 orchid, 2 palm and 1 sedge species) were recorded in at least 10 unique sample plots and were selected for the study. The detailed list of the selected plant species is presented in Table S2.1. Orchid was used as a separate life form to be consistent with the national forest inventory, Nepal database-that was used as the main source of species presence records for this study.

To supplement the aforementioned surveyed presence records, additional presence records were compiled from the online floral databases (Global Biodiversity Information Facility: http://www.gbif.org, Integrated Digitized Biocollections: http://www.idigbio.org and iNaturalist: http://www.inaturalist.org) and supplementary fieldwork (undertaken in Oct-Dec 2017). Both currently accepted taxonomic names and their unambiguous synonyms retrieved from The Plant List – that was used as the starting point for the taxonomic backbone of the World Flora Online – were used to download presence records from the online floral databases. Citations for the records thus downloaded will be included as an online appendix in the final journal publication.

2.2.4 Cleaning species presence records

The species presence records were cleaned in two steps. In the first step, all duplicate records (using currently accepted taxonomic names and their synonyms to download records from the online floral databases returned duplicate records); records based on fossil specimens and plants not from wild; records with missing coordinates, zero coordinates, coordinates with latitude = longitude (impossible in case of Nepal), invalid coordinates and coordinates likely to be based on country centroids or country capitals (records within threshold of 0.0083 degrees ≈ 1 km of country centroids or country capitals); records with coordinates country mismatch; and records with coordinates uncertainty ≥1 km were removed using process described in the R-package SPECIESGEOCODER (Zizka & Antonelli, 2015). To avoid pseudo-replication all duplicates at 0.0083 degrees ≈ 1 km spatial resolution (also the raster resolution of environmental predictors, see below) were also removed.

In the second step, species' elevational ranges reported in published literature (Fraser-Jenkins & Kandel, 2019; Fraser-Jenkins et al., 2015; http://www.efloras.org/, 2019; Jackson, 1994; Paudyal & Haq, 2008; Rajbhandari & Rai, 2019; Shrestha et al., 2018) were used to identify and discard doubtful presence records i.e. presence records beyond the reported species' elevational ranges. Furthermore, to make sure the cleaned presence records are representative of the reported species' elevational ranges, species with presence records covering <50% of the reported elevational ranges were also discarded. This reduced the number of spatially unique presence records to 10,775 and the number of selected plant species to 281 with per species spatially unique presence records ranging from 3-324. Since cleaning of species presence records reduced the number of spatially unique presence records of four out of 281 species to less than five i.e. the absolute minimum number of presence records required for MaxEnt modelling (Pearson et al., 2007; van Proosdij et al., 2016), only 277 species (143 tree, 76 shrub, 23 herb, 13 grass, 9 liana, 7 fern, 4 orchid, 1 palm and 1 sedge species) were considered for further analysis.

2.2.5 Environmental predictors

To avoid edge effects as result of modelling truncated niches (Raes, 2012), we defined Nepal plus 200 km buffer surrounding the Nepalese border as our area of interest. We included this buffer to include a wide range of environmental conditions, so that it is easier to model the drivers of species distribution. To relate species presence records to environmental predictors, 53 climatic, topographic and edaphic variables were compiled. Freely available global datasets were downloaded, cropped to the area of interest and aggregated to 30 arc-seconds (~1 km) spatial resolution, as and when necessary. Climatic variables (monthly temperature, precipitation, solar radiation, wind speed and water vapour pressure and 19 bioclimatic variables) were downloaded from WorldClim (http://worldclim.org/version2, Fick & Hijmans, 2017). WorldClim 2 was selected because it has improved estimates for areas with low station density and areas with sharp gradients such as rain-shadows (Fick & Hijmans, 2017). Mean annual solar radiation, wind speed and water vapour pressure were computed using WorldClim 2 monthly data. Aridity (Thornthwaite's aridity index), climatic moisture index, growing degree days (base temperature = 10 ˚C) and potential evapotranspiration (annual PET, PET extremes and PET seasonality) were computed using WorldClim 2 monthly data using ENVIREM R-package (Title & Bemmels, 2018).

Cloud cover variables (mean annual cloud frequency and cloud cover seasonality) were downloaded from EarthEnv (http://www.earthenv.org/cloud, Wilson & Jetz, 2016). Maximum climatic water deficit (MCWD) was computed using WorldClim v2.0 monthly data based on Malhi et al., 2009.

Soil variables were downloaded from ISRIC-SoilGrids (ftp://ftp.soilgrids.org/data/aggregated/1km/, Hengl et al., 2017). SoilGrids provides predictions at seven standard depths (0, 5, 15, 30, 60, 100 and 200 cm) for standard soil variables like organic carbon, bulk density, Cation Exchange Capacity (CEC), pH, soil texture fractions, coarse fragments, available water capacity and water content. As topsoil conditions determine whether a seedling can establish or not, the first four SoilGrids layers were used to compute the weighted average over a depth interval of 0–30 cm, i.e. topsoil, using trapezoidal rule for numerical integration (Hengl et al., 2017).

Topographic variables like elevation, aspect and slope were computed using digital elevation model (DEM) downloaded from CGIAR-CSI (https://cgiarcsi.community/data/srtm-90m-digital-elevation-database-v4-1/). Finally, distance to water sources was computed using river network data downloaded from HydroSHEDS (http://www.hydrosheds.org/) and global lakes and wetlands data downloaded from WWF (https://www.worldwildlife.org/pages/global-lakes-and-wetlands-database). The detailed list of thus compiled 53 environmental variables is presented in Table S2.2.

2.2.6 Selection of environmental predictors for MaxEnt modelling

As multicollinearity among environmental variables can distort model estimation and prediction, we used a Spearman's rank correlation coefficient of 0.7 as threshold to identify highly correlated environmental variables (Dormann et al., 2013). Correlations among environmental variables are presented as a cluster dendrogram and as a bivariate correlation matrix in Figure 2.1 and Table S2.3, respectively. Then, to identify the variables that best describe the ecological variations along the studied elevational gradient, we used a principal component analysis (PCA). Loadings of environmental variables along the first two principal components are presented in Figure S2.1. As we were interested in modelling elevational distributions of species based on their observed presence records, we used 52 environmental variables (elevation excluded) of 1,437 spatially unique presence locations (of 281 species left after cleaning) for correlation analysis and PCA. Also, the results were similar when doing correlation analysis and PCA on the whole area of interest (data not shown). Highly correlated environmental variables are not necessarily ecologically redundant, but they often have the same spatial patterns and cannot always be distinguished. Therefore, from each cluster of highly correlated variables, we selected one variable that was thought to be the ecologically most relevant factor that determines the elevational distribution of species and/or that had highest loading along one of the

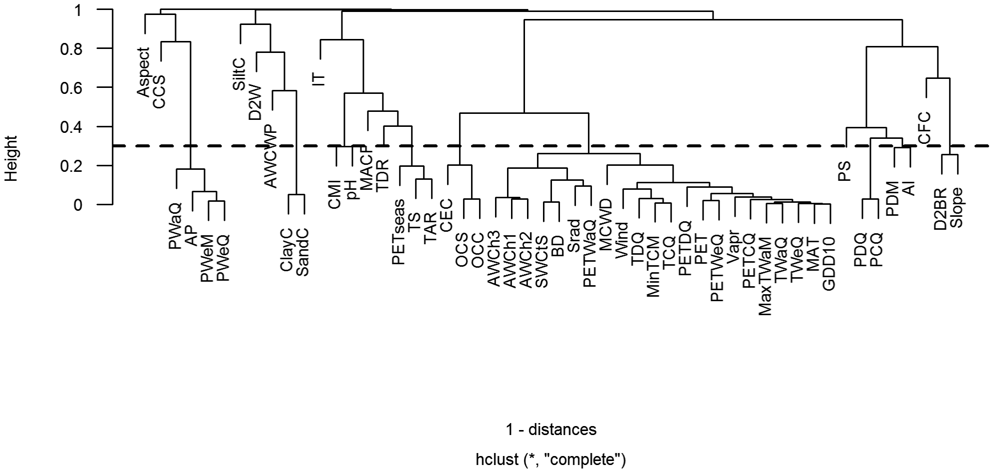


Figure 2.1. Cluster dendrogram showing correlation among environmental variables. Fifty-two environmental variables (elevation excluded) of 1,437 spatially unique presence locations were used for the correlation analysis. In this case a height of 0.3, indicated by dotted line, is taken as a threshold. Height is defined as 1–Spearman's rank correlation coefficient. All the variables with height ≤ 0.3 (or Spearman's rank correlation coefficient > 0.7) are considered highly correlated. Details of environmental variable abbreviations used in the plot are presented in Table S2.2.

first three principal components. This resulted into a selection of 19 least correlated environmental variables (10 climatic, 6 edaphic and 3 topographic, Table 2.1). To represent the cluster of correlated temperature (e.g. temperature extremes) and non-temperature variables (such as irradiance and PET), we selected mean annual temperature (MAT). Although temperature extremes (e.g. maximum temperature of warmest month, minimum temperature of coldest month) may co-shape species distribution boundaries, we believe that MAT is more important in shaping species performance and distribution. Across the 1,437 spatially unique presence locations, MAT is closely correlated with maximum temperature of warmest month (Spearman's rank $r = 0.99$, $p < 0.001$) and with minimum temperature of coldest month (Spearman's rank $r = 0.98$, $p < 0.001$). Hence, to avoid multicollinearity problems we used only MAT, as it captures both the variation in summer and winter temperature and the average growing conditions during the year.

2.2.7 MaxEnt modelling

Samples with data (SWD) format of MaxEnt version 3.3.3k (Phillips, 2010) in R-package DISMO (Hijmans et al., 2017) was used to construct species distribution models for 277 plant species. As we were interested in modelling elevational distributions of species based on their observed presence records, we used 1,437 spatially unique presence locations as background sample. To comply with the ecological theory that species responses to environmental gradients are often unimodal (Austin, 2007), MaxEnt was restricted to use only linear and quadratic features (Boucher-Lalonde et al., 2012; Merow et al., 2013), where

Table 2.1. List of 19 least correlated environmental variables selected for this study. Variable categories, sub-categories, names and their corresponding units and abbreviations are shown.

Category	Sub-category	Name and unit	Abbreviation
Climatic	Temperature	Isothermality (Mean temperature diurnal range/Temperature annual range) * 100	IT
		Mean annual temperature (°C)	MAT
		Mean temperature diurnal range (Mean of monthly (maximum temperature–minimum temperature), °C)	TDR
		Temperature annual range (Maximum temperature of warmest month–Minimum temperature of coldest month, °C)	TAR
	Precipitation	Annual precipitation (mm)	AP
		Precipitation of driest quarter (mm)	PDQ
		Precipitation seasonality (coefficient of variation)	PS
	Other climatic	Cloud cover seasonality (standard deviation * 100)	CCS
		Mean annual cloud frequency (% * 100)	MACF
		Thornthwaite's aridity index	AI
Edaphic	Chemical	Soil organic carbon content (gm/kg)	OCC
		Soil pH * 10 in water	pH
	Physical	Available soil water capacity until wilting point (%)	AWCWP
		Soil clay content (%)	ClayC
		Soil coarse fragments content (%)	CFC
		Soil silt content (%)	SiltC
Topographic		Aspect (deg)	Aspect
		Distance to water (arc sec)	D2W
		Slope (deg)	Slope

linear features represent one side of a unimodal response due to partial representation of the entire gradient.

To test the significance of the models, we compared the AUC (area under the receiver operating characteristic curve) values of the models to the AUC values of the bias corrected null models i.e. models based on the random presence records (Raes & Ter Steege, 2007). For this, for each species, 100 bias corrected null models were constructed with the presence records randomly drawn from 1,437 spatially unique presence records. The number of randomly drawn presence records was kept equal to the number of true presence records of the target species. The models with AUC values >95th percentile AUC value of the null models were considered to perform significantly better than expected by chance. Only the significant models were retained for further analysis.

2.2.8 Data analysis

To evaluate which environmental factors best predict the distribution of plant species along an elevational gradient, we analysed the frequency with which environmental variables were found to be the most important (cf. Bradie & Leung, 2016). For this, for each species with a significant species distribution model, we identified the environmental variable that contributed the most to the model (i.e. the most important environmental variable) based on the relative percentage contributions of the variables to the model.

To test whether species elevational ranges increase with increasing elevation along an elevational gradient, a simple linear regression was carried out with species' elevational ranges and elevational optima. For this, firstly, all significant species distribution models were projected onto the geographical space using MaxEnt's 'density.Project' function to derive probability of occurrence maps for the entire study area. Secondly, these maps were reclassified using '10 percentile training presence logistic threshold' (one of the most conservative and absence independent thresholds in MaxEnt) to produce discrete presence-absence maps i.e. species distribution maps (Liu et al., 2011). Finally, these species distribution maps were used to compute species' elevational distribution parameters i.e. the elevational minimum, maximum, optimum and range. To have a conservative estimate of a species' elevational distribution parameters, the 5th and 95th percentile elevation values were used as estimates of the elevational "minimum" and "maximum", respectively. The difference between elevational maximum and minimum was used as an estimate of the elevational "range". The mid-value of the elevation class with the highest proportion of pixels predicted to be occupied was used as an estimate of the elevational "optimum". For this, the distribution map of each species was classed into 100 m elevational bins and for each elevational bin the proportion of pixels predicted to be occupied was calculated. This procedure effectively corrects for the smaller available surface area at higher elevational bins. All calculations and analyses were done with R-3.4.3 (R Core Team, 2017).

2.2.9 Limitations of methods

A few methodological limitations might have influenced our results. First, we used global environmental datasets with a spatial resolution of 1 × 1 km as sources of our environmental predictors. It is likely that these datasets did not fully capture all the local details in the Himalayas because: i) the environmental conditions may vary over short distances in the Himalayas and ii) the observed data that are bases of these global interpolations are sparse in the Himalayas (Deblauwe et al., 2016). However, in absence of reliable national/regional datasets these were the best datasets available for the study area.

Second, although it is established that species distributions are jointly regulated by abiotic environments and biotic interactions (e.g. Godsoe et al., 2017; MacArthur, 1972; Peterson et al., 2011; Soberón & Peterson, 2005; Wisz et al., 2013), we did not account for biotic interactions as predictor variables in our study because biotic interactions are inherently complex, and especially so when we consider several species at a time. Moreover, although changes in land use may affect species distributions, we only focused here on natural forest vegetation and did not include land use change in the analysis. For example, in Nepal, nearly two thirds of the total forest area is affected by grazing by free roaming cattle (DFRS, 2015). Because standardized country-wide data on the occurrence and intensity of grazing is not available, we only focused on how climatic, edaphic and topographic environmental variables affect species distribution ranges.

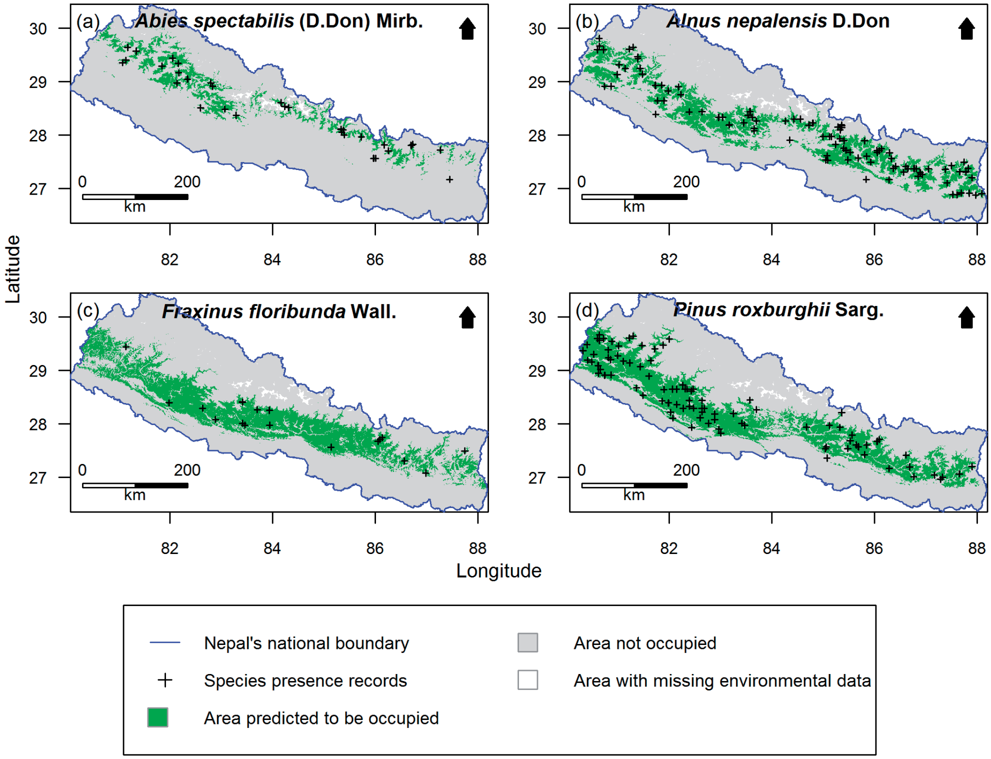


Figure 2.2. Examples of species distribution maps for four plant species as predicted by MaxEnt: a) *Abies spectabilis*, b) *Alnus nepalensis*, c) *Fraxinus floribunda* and d) *Pinus roxburghii*. Maps are clipped to Nepal. The blue line indicates national boundary of Nepal. The Government of Nepal published on 20th May 2020 a new political map including Kalapani, Lipulekh and Limpiyadhura inside the Nepal borders. As our research started in 2016, in our research, we used the previous version of map without these territories. Species presence records outside the green distribution areas represent the 10% of the presence records with the lowest MaxEnt probability of occurrence values used to threshold the distribution maps. Areas with missing environmental data were excluded from MaxEnt modelling.

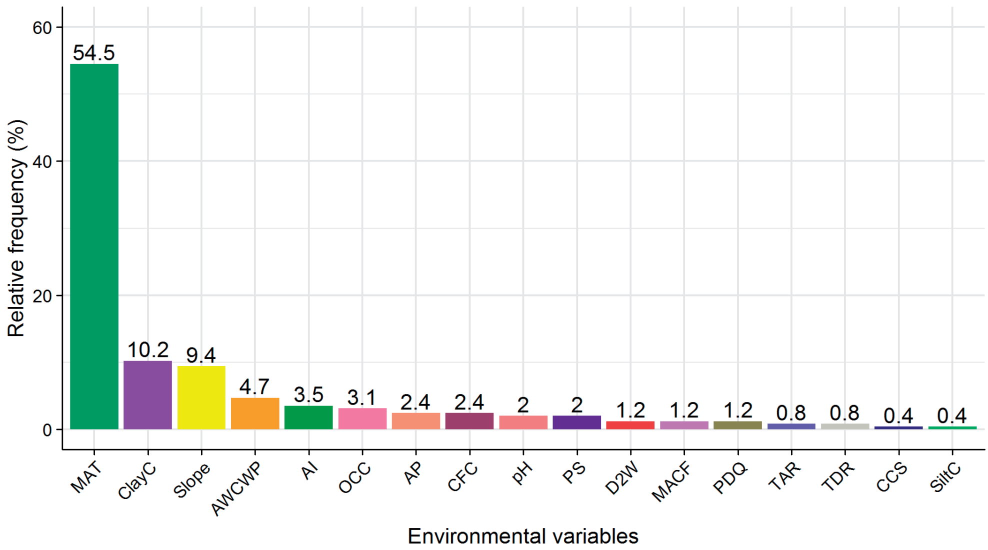


Figure 2.3. Relative frequencies of environmental variables that had the highest contribution to the significant distribution models of 255 Himalayan plant species. The three most important variables were mean annual temperature (MAT), soil clay content (ClayC) and slope. For abbreviations of the other environmental variables, see Table 2.1.

2.3 Results

Out of 277 species, 255 species (92%) had distribution models performing significantly better than expected by chance. Only the significant models were retained for further analysis. Examples of the predicted species distribution maps are shown in Figure 2.2.

2.3.1 Environmental factors predicting the distribution of plant species along the elevational gradient

All 255 species had a relationship with one or more of the environmental predictors. Mean annual temperature (MAT) followed by soil clay content (ClayC) and slope were the most important environmental variables predicting the distribution of plant species along the elevational gradient. MAT contributed the most to the distributions of 139 out of 255 species (54.5%), followed by ClayC (10.2%) and slope (9.4%) (Figure 2.3). Examples of species' response to MAT, ClayC and slope are shown in Figure 2.4. Spatial GIS maps of these three environmental variables are presented in Figure S2.2.

2.3.2 Relationship between elevational ranges and elevation along the elevational gradient

The species elevational ranges initially increased with the elevational optima of the species, but this increase peaked between 2,000 and 3,000 m a.s.l. and then decreased beyond 3,000

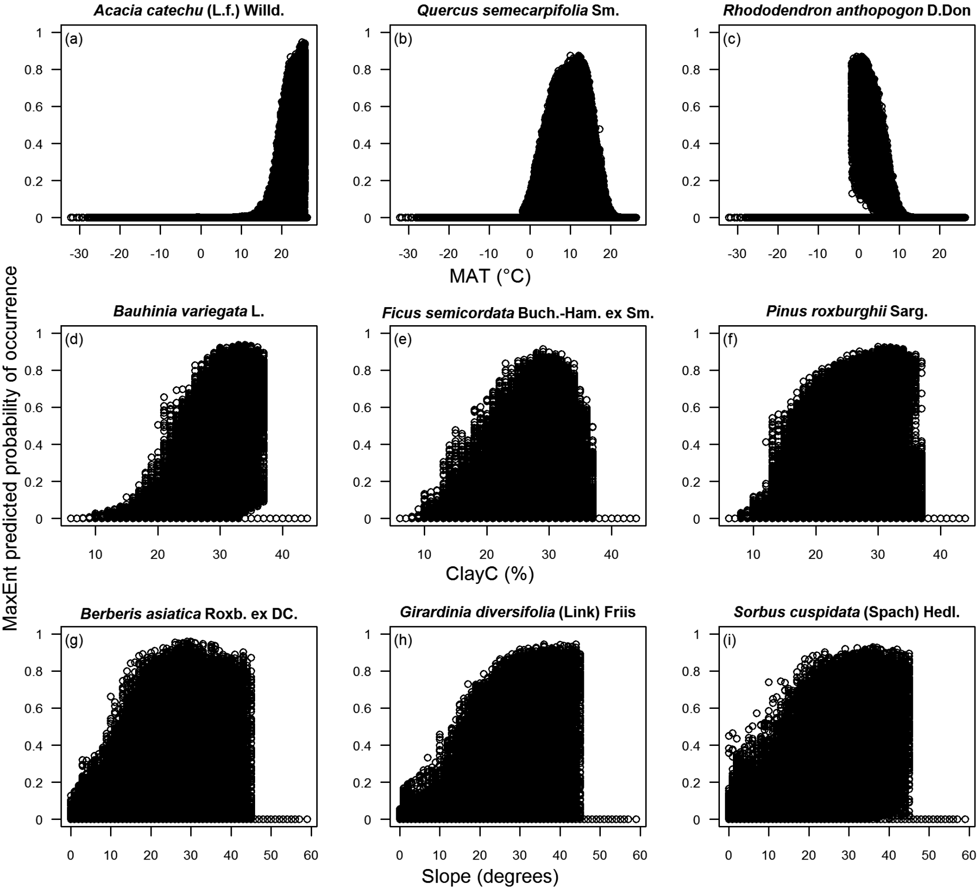


Figure 2.4. Examples of probabilities of species occurrence as predicted by MaxEnt in relation to a) mean annual temperature (MAT, top panels), b) soil clay content (ClayC, middle panels) and c) slope (bottom panels). Each point represents one of the 906,794 1 x 1 km grids of the study area.

m a.s.l. (Figure 2.5, adj.$R^2 = 0.47$, $p < 0.001$). Also, the results were similar when regression analysis was carried out with species elevational ranges and elevational midpoints (the averages of the lowest and highest elevations of species; data not shown). The majority of species had their elevational optima at or towards the lower end of the elevational gradient. There were comparatively more tree species at low elevations and more shrub species at high elevations. Liana species occurred mainly in the lowlands. As some of the life forms e.g. fern, orchid and sedge had too few species for the comparison, we pooled them into a non-woody class together with herbs and grasses for this analysis. Some species showed wide distribution ranges irrespective of their elevational optima, e.g. *Stephania japonica* var. *discolor* (Blume) Forman and *Cotoneaster ellipticus* (Lindl.) Loudon (Figure 2.5).

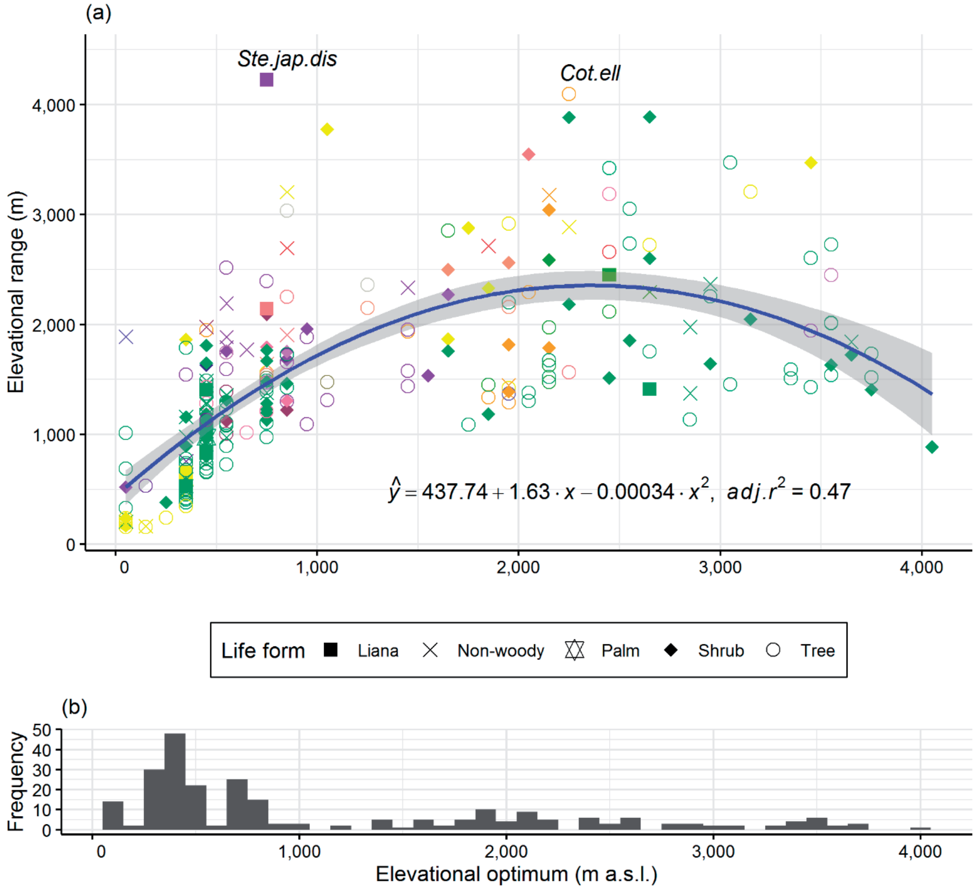


Figure 2.5. Relationship between elevational range and elevational optimum for 255 Himalayan plant species (represented by coloured shapes). Shapes correspond to life forms of the studied species. Ferns, grasses, herbs, orchids and sedges were grouped into a single non-woody class. Colours of shapes correspond to colours of environmental variables contributing the most to the models in Figure 2.3. Regression line and coefficient of determination (adj.R^2) are shown. Shade around the regression line indicates the 95% confidence interval. Both the intercept and slopes are significant at $p < 0.001$. Adj.R^2 went up to 0.49 without outliers i.e. without species labelled with their name abbreviations. Species name abbreviations used in the plot refer to first three letters of their genus, species and variety. The species list is shown in Table S2.1. The histogram in the bottom panel shows frequencies of species elevational optima along the gradient.

2.4 Discussion

We evaluated which environmental factors predict the distribution of plant species along an elevational gradient and whether species' elevational ranges increase with increasing elevation. We found that mean annual temperature followed by soil clay content and slope are the key environmental factors predicting the distribution of plant species along an elevational gradient. Species' elevational ranges showed a unimodal relationship with elevation.

It should be acknowledged that the importance of environmental factors may change with varying spatial scales of analysis (Blundo et al., 2012). For example, we used environmental datasets with a spatial resolution of 1 x 1 km, which may conceal more subtle responses to local topography and elevational gradients. However, since our studied elevational gradient is very large (60 m a.s.l. in the south to 8,848 m a.s.l. in the north), we think this is less of a problem. It should also be acknowledged that we describe statistical relationships between species distribution and environmental variables, and that correlation does not necessarily mean mechanistic causation, although there are clear physiological and ecological reasons why these environmental variables may be important. Below we discuss the mechanisms likely to underlie the aforementioned elevational patterns that we found and the likely effects of future global warming on plant species distributions along an elevational gradient.

2.4.1 Environmental factors predicting the distribution of plant species along the elevational gradient

Climatic factors

Temperature–We hypothesized that temperature would be the key environmental factor predicting the distribution of plant species along the elevational gradient because it directly influences plant metabolic rates and physiological processes and controls growing season length. Mean annual temperature indeed contributed the most to the distributions of the majority (54.5%) of the Himalayan plant species (Figure 2.3), suggesting that mean annual temperature is the core factor shaping the distribution of species in the Himalayas (Angelo & Daehler, 2015; Chhetri et al., 2018; Guisan et al., 1998). However, mean annual temperature correlated closely with a suite of other temperature and non-temperature environmental variables (Figure 2.1). The majority of these variables are quite similar to mean annual temperature like mean temperatures of different quarters (e.g. coldest, warmest, driest and wettest quarters) and temperature extremes (e.g. minimum temperature of coldest month and maximum temperature of warmest month) while others are derived or directly related to temperature like growing degree-days and potential evapotranspiration. However, other variables that correlated with mean annual temperature, like solar radiation, water vapour pressure, wind speed, maximum climatological water deficit and edaphic variables like available soil water content and bulk density are not directly linked to temperature. These variables could affect species distributions through very different ecological mechanisms than mean annual temperature. In this sense, our current approach of selecting one variable from each cluster of highly correlated variables for species distribution modelling did not allow to tease apart a single ecological mechanism regulating plant niches along the elevational gradient. Nevertheless, it has been useful in highlighting the relative importance of temperature and its associated temperature and non-temperature covariates in shaping plant niches along the gradient (cf. Whittaker 1967).

Precipitation–Precipitation affects species distributions along African mountains and lowlands (Amissah et al., 2014; Maharjan et al., 2011; Schmitt et al., 2013) and in Neotropical lowlands (Toledo et al., 2012), but in Nepal aridity and annual precipitation were only fifth and seventh in importance for determining species distributions (Figure 2.3). Precipitation in Nepal is driven by summer monsoon and winter westerlies. Summer monsoon enters Nepal from the east and migrates west, as east-west ranging Himalayas deflect the monsoon winds westwards and prevent northward penetration. Additionally, in winter, westerlies supply precipitation to the northwest mountains. Because of the topographic barrier posed by east-west ranging Himalayas, precipitation in Nepal is more region-specific rather than showing a strong trend with elevation (Kansakar et al., 2004; Lillesø et al., 2005). This region-specific nature of precipitation in Nepal may have weakened the roles of precipitation and aridity in defining plant species distributions along the elevational gradient.

Irradiance–Many tropical forests are light-limited. In Peru, irradiance was, surprisingly, one of the key environmental factors regulating forest productivity along an Andean elevational gradient (Fyllas et al., 2017). This suggests that irradiance could also affect plant species distributions along the elevational gradient in Nepal. A strong positive correlation between solar radiation and mean annual temperature ($r = 0.84$, $p < 0.001$, Table S2.3) suggests that Himalayan plant species distribution could also be predicted by growth potential and carbon gain (cf. Maharjan et al. 2011; Sterck et al. 2014). Yet, this is not very likely, as cloud cover (i.e. mean annual cloud frequency and cloud cover seasonality), which is another good proxy for irradiance, hardly affected the distribution of plant species (Figure 2.3).

Edaphic factors

Soil clay content–Soil clay content was the second most important environmental factor predicting the distribution of 10.2% of the species (Figure 2.3). A high soil clay content improves water availability for plants as soils with many small clay particles have a larger surface area that increases the soil water holding capacity (r with available soil water capacity until wilting point = 0.42, $p < 0.001$, Table S2.3), which positively affects water uptake, plant water status, evaporative cooling, and carbon gain. Counterintuitively, soil clay content was negatively correlated with soil nutrient availability (r with soil cation exchange capacity = -0.44, $p < 0.001$; r with soil organic carbon content = -0.69, $p < 0.001$, Table S2.3). Perhaps, in case of relatively young mountains such as the Himalayas, higher temperature and precipitation in the lowlands are accompanied by increased weathering and leaching, resulting in nutrient-poor clayey soils, whereas in the highlands exposed bedrock and recent weathering may result in nutrient-rich soils. This suggests that plants growing at low elevations may therefore be limited by low nutrient availability whereas plants growing at high elevations may be limited by water scarcity. In general, our results support previous findings that inclusion of edaphic variables considerably improves the prediction of species distribution along elevational gradients (Cianfrani et al., 2019; Dubuis et al., 2013; Walthert & Meier, 2017).

Topographic factors

Slope–Slope was the third most important environmental factor predicting the distribution of 9.4% of the species (Figure 2.3). Areas with steep slopes are typical for relatively young mountains such as the Himalayas. They provide extreme conditions for plants, as they are less stable, suffer more from water run-off (Mu et al., 2015) and erosion (Cha & Kim, 2011). Steep slopes are also more shallow (r between slope and depth to bedrock = -0.74, $p < 0.001$, Table S2.3), which reduces the opportunity for rooting and water and nutrient uptake. Topographic variation in slopes may range from crests to slopes and valleys, which results in a marked edaphic and hydrological gradient that might be partitioned by different plant species (Huggett, 2004; Schietti et al., 2014).

2.4.2 Elevational distribution ranges are widest for plant species from intermediate elevation

In line with Rapoport’s elevational rule, we hypothesized that plant species from high elevations (where environmental conditions are harsher, more stressful and variable) would have wider physiological tolerances to environmental conditions and therefore occupy broader elevational ranges than plant species from low elevations, that experience more benign and stable environmental conditions (Pintor et al., 2015; Stevens, 1992). In contrast, we found that species distribution ranges were widest for species that had their optimum between 2,000 and 3,000 m a.s.l. elevation (Figure 2.5). Earlier Himalayan studies (Bhattarai & Vetaas, 2006; Vetaas & Grytnes, 2002) suggested that in the lowlands and highlands, a high species richness (overall species richness in the lowlands and endemic species richness in the highlands) may lead to stronger interspecific competition and narrower species ranges. Schellenberger Costa et al. (2018) has confirmed this stronger interspecific competition hypothesis for the lower slopes of Mt. Kilimanjaro. Compliant with the suggestion, the majority of the studied species had their elevational optimum at or towards the lowlands (Figure 2.5). Alternatively, broad elevational ranges at the middle of the gradient could be the result of a mid-domain effect (Colwell & Hurtt, 1994), which suggests that species with wide elevational ranges have their elevational optima closer to the centre of the domain (cf. Bhattarai & Vetaas 2006; Colwell & Lees 2000).

2.4.3 Potential effects of climate change on future distribution of plant species

Our results suggest that temperature and its temperature (e.g. temperature extremes) and non-temperature covariates (such as irradiance and PET) followed by soil clay content and slope are the key environmental factors predicting the distribution of plant species along the Himalayan elevational gradient, and that species at both ends of the Himalayan elevational gradient have narrower elevational ranges than species in the middle. With further global warming these species will be forced to 1) acclimate or adapt to the changed conditions, 2) track suitable climatic ranges through dispersal and move upward, or 3) go extinct. Thus, as long as competition of plants from the lowlands does not affect the distribution of mid-elevation species, their distributions might be less affected by climate warming as they occupy broad elevational ranges. In contrast, given the identified species ranges are due to abiotic conditions and the lowland species are likely already living at their thermal maximums, the distribution of warm-adapted and cold-adapted species at both ends of the gradient might be affected more by climate warming because they occupy narrower elevational ranges. All plant species have, to a certain extent, the ability to acclimate physiologically to increased warming (Slot & Winter, 2017), but the question is whether these species will not be outcompeted by warm-adapted species that move upwards. Furthermore, it is likely that lowland species are already living at their thermal maximums. Thus, tracking suitable climatic ranges could probably be the best long-term survival strategy. Given a maximum predicted warming of 0.35 °C decade^{-1} in South Asia (IPCC, 2013) and a thermal lapse rate of 0.5 °C per 100 m (Barry, 1992a), the species should move 70 m decade^{-1}. This is only feasible when elevational corridors are available, or through assisted regeneration. However, assisted regeneration at such a scale would be challenging. Consequently, the Himalayan plant species may face an uncertain future, in the face of climate change.

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Supplementary information

Table S2.1. Complete list of 333 plant species selected for this study. Species names and their respective families and life forms are presented for all species while number of spatially unique presence records are presented only for 281 plant species left after cleaning. Orchid was used as a separate life form to be consistent with the national forest inventory, Nepal database – that was used as the main source of species presence records for this study.

Species name	Family	Life form	Presence records
Abies densa Griff.	Pinaceae	Tree	9
Abies pindrow (Royle ex D.Don) Royle	Pinaceae	Tree	25
Abies spectabilis (D.Don) Mirb.	Pinaceae	Tree	40
Acacia catechu (L.f.) Willd.	Fabaceae	Tree	66
Acampe praemorsa (Roxb.) Blatt. & McCann	Orchidaceae	Orchid	5
Acer acuminatum Wall. ex D.Don	Aceraceae	Tree	
Acer campbellii Hook.f. & Thomson ex Hiern	Aceraceae	Tree	11
Acer oblongum Wall. ex DC.	Aceraceae	Tree	23
Achyranthes aspera L.	Amaranthaceae	Herb	
Aegle marmelos (L.) Corrêa	Rutaceae	Tree	38
Aesculus indica (Wall. ex Cambess.) Hook.	Hippocastanaceae	Tree	9
Ageratina adenophora (Spreng.) R.M.King & H.Rob.	Asteraceae	Herb	
Ageratum conyzoides (L.) L.	Asteraceae	Herb	11
Albizia chinensis (Osbeck) Merr.	Fabaceae	Tree	21
Albizia lebbeck (L.) Benth.	Fabaceae	Tree	9
Albizia odoratissima (L.f.) Benth.	Fabaceae	Tree	6
Albizia procera (Roxb.) Benth.	Fabaceae	Tree	45
Allium wallichii Kunth	Alliaceae	Herb	11
Alnus nepalensis D.Don	Betulaceae	Tree	133
Alstonia scholaris (L.) R.Br.	Apocynaceae	Tree	
Amomum subulatum Roxb.	Zingiberaceae	Herb	10
Ampelocissus divaricata (Wall. ex M.A.Lawson) Planch.	Vitaceae	Shrub	14
Anogeissus latifolia (Roxb. ex DC.) Wall. ex Guillem. & Perr.	Combretaceae	Tree	44
Antidesma acidum Retz.	Euphorbiaceae	Shrub	37
Aporosa octandra (Buch.-Ham. ex D.Don) Vickery	Euphorbiaceae	Tree	12
Ardisia solanacea Roxb.	Myrsinaceae	Shrub	29
Argemone mexicana L.	Papaveraceae	Herb	19
Artemisia indica Willd.	Asteraceae	Herb	30
Artocarpus lacucha Buch.-Ham.	Moraceae	Tree	16
Arundinella nepalensis Trin.	Poaceae	Grass	26
Asparagus penicillatus H.Hara	Asparagaceae	Herb	
Asparagus racemosus Willd.	Asparagaceae	Herb	131

Species name	Family	Life form	Presence records
Bambusa tulda Roxb.	Poaceae	Grass	20
Bauhinia malabarica Roxb.	Fabaceae	Tree	36
Bauhinia purpurea L.	Fabaceae	Tree	43
Bauhinia vahlii Wight & Arn.	Fabaceae	Liana	178
Bauhinia variegata L.	Fabaceae	Tree	40
Berberis angulosa Wall. ex Hook.f. & Thomson	Berberidaceae	Shrub	12
Berberis aristata DC.	Berberidaceae	Shrub	139
Berberis asiatica Roxb. ex DC.	Berberidaceae	Shrub	55
Berberis erythroclada Ahrendt	Berberidaceae	Shrub	5
Bergenia ciliata (Haw.) Sternb.	Saxifragaceae	Herb	9
Betula alnoides Buch.-Ham. ex D.Don	Betulaceae	Tree	24
Betula utilis D.Don	Betulaceae	Tree	43
Boehmeria rugulosa Wedd.	Urticaceae	Tree	23
Bombax ceiba L.	Bombacaceae	Tree	56
Bridelia retusa (L.) A.Juss.	Euphorbiaceae	Tree	61
Brucea javanica (L.) Merr.	Simaroubaceae	Tree	32
Buchanania cochinchinensis (Lour.) M.R.Almeida	Anacardiaceae	Tree	121
Buddleja asiatica Lour.	Loganiaceae	Shrub	
Bulbophyllum careyanum (Hook.) Spreng.	Orchidaceae	Orchid	10
Caesalpinia bonduc (L.) Roxb.	Fabaceae	Shrub	9
Caesalpinia decapetala (Roth) Alston	Fabaceae	Shrub	25
Callicarpa macrophylla Vahl	Verbenaceae	Shrub	30
Capillipedium assimile (Steud.) A.Camus	Poaceae	Grass	29
Careya arborea Roxb.	Lecythidaceae	Tree	36
Carissa carandas L.	Apocynaceae	Shrub	6
Casearia graveolens Dalzell	Flacourtiaceae	Tree	71
Casearia tomentosa Roxb.	Flacourtiaceae	Tree	28
Cassia fistula L.	Fabaceae	Tree	73
Castanopsis hystrix Hook.f. & Thomson ex A.DC.	Fagaceae	Tree	
Castanopsis indica (Roxb. ex Lindl.) A.DC.	Fagaceae	Tree	66
Castanopsis tribuloides (Sm.) A.DC.	Fagaceae	Tree	39
Catunaregam spinosa (Thunb.) Tirveng.	Rubiaceae	Tree	107
Cedrus deodara (Roxb. ex D.Don) G.Don	Pinaceae	Tree	
Celtis australis L.	Ulmaceae	Tree	
Centella asiatica (L.) Urb.	Apiaceae	Herb	16
Ceropegia pubescens Wall.	Asclepiadaceae	Herb	
Cheilanthes bicolor (Roxb.) Fraser-Jenk.	Adiantaceae	Fern	15
Cheilanthes dalhousiae Hook.	Adiantaceae	Fern	

Species name	Family	Life form	Presence records
Cinnamomum tamala (Buch.-Ham.) T.Nees & Eberm.	Lauraceae	Tree	22
Cissampelos pareira L.	Menispermaceae	Shrub	61
Cissus repens Lam.	Vitaceae	Herb	37
Citrus maxima (Burm.) Merr.	Rutaceae	Tree	15
Clematis heynei M.A.Rau	Ranunculaceae	Liana	
Clerodendrum indicum (L.) Kuntze	Verbenaceae	Shrub	10
Clerodendrum infortunatum L.	Verbenaceae	Shrub	85
Coccinia grandis (L.) Voigt	Cucurbitaceae	Liana	3
Cochlospermum religiosum (L.) Alston	Bixaceae	Tree	
Colebrookea oppositifolia Sm.	Lamiaceae	Shrub	111
Colysis elliptica (Thunb.) Ching	Polypodiaceae	Fern	
Corchorus capsularis L.	Tiliaceae	Herb	10
Coriaria nepalensis Wall.	Coriariaceae	Shrub	16
Cornus oblonga Wall.	Cornaceae	Tree	
Cotoneaster ellipticus (Lindl.) Loudon	Rosaceae	Tree	10
Cryptomeria japonica (Thunb. ex L.f.) D.Don	Taxodiaceae	Tree	3
Curculigo orchioides Gaertn.	Hypoxidaceae	Herb	19
Cynodon dactylon (L.) Pers.	Poaceae	Grass	12
Cyperus rotundus L.	Cyperaceae	Sedge	14
Dalbergia latifolia Roxb.	Fabaceae	Tree	33
Dalbergia sissoo DC.	Fabaceae	Tree	29
Daphne bholua Buch.-Ham. ex D.Don	Thymelaeaceae	Shrub	67
Daphne bholua var. *glacialis* (W.W.Sm. & Cave) B.L.Burtt	Thymelaeaceae	Shrub	20
Daphne papyracea Wall. ex G.Don	Thymelaeaceae	Shrub	19
Daphniphyllum himalense (Benth.) Müll.Arg.	Daphniphyllaceae	Tree	7
Debregeasia saeneb (Forssk.) Hepper & J.R.I.Wood	Urticaceae	Shrub	6
Dendrobium plicatile Lindl.	Orchidaceae	Orchid	30
Dendrobium transparens Wall. ex Lindl.	Orchidaceae	Orchid	7
Dendrophthoe falcata (L.f.) Ettingsh.	Loranthaceae	Shrub	8
Desmodium elegans DC.	Fabaceae	Shrub	10
Desmodium gangeticum (L.) DC.	Fabaceae	Shrub	10
Desmodium multiflorum DC.	Fabaceae	Shrub	3
Desmodium oojeinense (Roxb.) H.Ohashi	Fabaceae	Tree	83
Desmostachya bipinnata (L.) Stapf	Poaceae	Grass	23
Dicranopteris linearis (Burm.f.) Underw.	Gleicheniaceae	Fern	
Digitaria ciliaris (Retz.) Koeler	Poaceae	Grass	10
Dillenia pentagyna Roxb.	Dilleniaceae	Tree	
Dioscorea bulbifera L.	Dioscoreaceae	Herb	188

Species name	Family	Life form	Presence records
Dioscorea deltoidea Wall. ex Griseb.	Dioscoreaceae	Herb	56
Dioscorea pentaphylla L.	Dioscoreaceae	Herb	72
Dioscorea prazeri Prain & Burkill	Dioscoreaceae	Herb	7
Diospyros exsculpta Buch.-Ham.	Ebenaceae	Tree	
Diospyros malabarica (Desr.) Kostel.	Ebenaceae	Tree	39
Diplazium esculentum (Retz.) Sw.	Athyriaceae	Fern	20
Diploknema butyracea (Roxb.) H.J.Lam	Sapotaceae	Tree	54
Dodecadenia grandiflora Nees	Lauraceae	Tree	18
Drepanostachyum falcatum (Nees) Keng f.	Poaceae	Grass	5
Drepanostachyum intermedium (Munro) Keng f.	Poaceae	Grass	17
Drynaria propinqua (Wall. ex Mett.) Bedd.	Polypodiaceae	Fern	
Dryopteris cochleata (Buch.-Ham. ex D.Don) C.Chr.	Dryopteridaceae	Fern	18
Duabanga grandiflora (DC.) Walp.	Sonneratiaceae	Tree	13
Duhaldea cappa (Buch.-Ham. ex D.Don) Pruski & Anderb.	Asteraceae	Shrub	102
Dysoxylum excelsum Blume	Meliaceae	Tree	6
Dysoxylum gotadhora (Buch.-Ham.) Mabb.	Meliaceae	Tree	
Ehretia acuminata R.Br.	Cordiaceae	Tree	
Ehretia laevis Roxb.	Cordiaceae	Tree	14
Elaeagnus parvifolia Wall. ex Royle	Elaeagnaceae	Shrub	8
Elephantopus scaber L.	Asteraceae	Herb	23
Engelhardia spicata Lesch. ex Blume	Juglandaceae	Tree	68
Erythrina stricta Roxb.	Fabaceae	Tree	6
Eulaliopsis binata (Retz.) C.E.Hubb.	Poaceae	Grass	41
Eurya acuminata DC.	Theaceae	Tree	81
Falconeria insignis Royle	Euphorbiaceae	Tree	96
Feronia limonia (L.) Swingle	Rutaceae	Tree	
Ficus auriculata Lour.	Moraceae	Tree	36
Ficus benghalensis L.	Moraceae	Tree	15
Ficus glaberrima Blume	Moraceae	Tree	11
Ficus hispida L.f.	Moraceae	Tree	28
Ficus lacor Buch.-Ham.	Moraceae	Tree	21
Ficus neriifolia Sm.	Moraceae	Tree	55
Ficus racemosa L.	Moraceae	Tree	15
Ficus religiosa L.	Moraceae	Tree	29
Ficus semicordata Buch.-Ham. ex Sm.	Moraceae	Tree	89
Flacourtia indica (Burm.f.) Merr.	Flacourtiaceae	Tree	15
Flemingia macrophylla (Willd.) Merr.	Fabaceae	Shrub	14
Flemingia strobilifera (L.) W.T.Aiton	Fabaceae	Shrub	20

Species name	Family	Life form	Presence records
Fragaria nubicola (Lindl. ex Hook.f.) Lacaita	Rosaceae	Herb	28
Fraxinus floribunda Wall.	Oleaceae	Tree	18
Garuga pinnata Roxb.	Burseraceae	Tree	39
Gaultheria fragrantissima Wall.	Ericaceae	Shrub	17
Girardinia diversifolia (Link) Friis	Urticaceae	Herb	16
Gleichenia longissima Blume	Gleicheniaceae	Fern	8
Gmelina arborea Roxb.	Verbenaceae	Tree	9
Grevillea robusta A.Cunn. ex R.Br.	Proteaceae	Tree	19
Grewia asiatica L.	Tiliaceae	Tree	48
Grewia optiva J.R.Drumm. ex Burret	Tiliaceae	Tree	17
Haldina cordifolia (Roxb.) Ridsdale	Rubiaceae	Tree	85
Hedera nepalensis K.Koch	Araliaceae	Liana	20
Hemarthria compressa (L.f.) R.Br.	Poaceae	Grass	
Heynea trijuga Roxb. ex Sims	Meliaceae	Tree	
Holarrhena pubescens Wall. ex G.Don	Apocynaceae	Shrub	21
Holoptelea integrifolia (Roxb.) Planch.	Ulmaceae	Tree	
Huperzia pulcherrima (Wall. ex Hook. & Grev.) T.Sen & U.Sen	Lycopodiaceae	Fern	9
Hydrangea robusta Hook.f. & Thomson	Hydrangeaceae	Shrub	8
Hymenodictyon orixense (Roxb.) Mabb.	Rubiaceae	Tree	18
Hypericum cordifolium Choisy	Hypericaceae	Shrub	7
Hypericum uralum Buch.-Ham. ex D.Don	Hypericaceae	Shrub	19
Ichnocarpus frutescens (L.) W.T.Aiton	Apocynaceae	Liana	8
Ilex dipyrena Wall.	Aquifoliaceae	Tree	16
Imperata cylindrica (L.) Raeusch.	Poaceae	Grass	65
Indigofera atropurpurea Hornem.	Fabaceae	Shrub	11
Indigofera cassioides DC.	Fabaceae	Shrub	46
Jasminum arborescens Roxb.	Oleaceae	Shrub	
Jasminum multiflorum (Burm.f.) Andrews	Oleaceae	Shrub	
Juglans regia L.	Juglandaceae	Tree	23
Justicia adhatoda L.	Acanthaceae	Shrub	15
Kydia calycina Roxb.	Malvaceae	Tree	9
Lagerstroemia parviflora Roxb.	Lythraceae	Tree	222
Lannea coromandelica (Houtt.) Merr.	Anacardiaceae	Tree	102
Lantana camara L.	Verbenaceae	Shrub	6
Larix griffithii Hook.f.	Pinaceae	Tree	10
Leea macrophylla Roxb. ex Hornem.	Vitaceae	Shrub	
Lepisorus loriformis (Wall. ex Mett.) Ching	Polypodiaceae	Fern	
Leucaena leucocephala (Lam.) de Wit	Fabaceae	Tree	11

Species name	Family	Life form	Presence records
Leucosceptrum canum Sm.	Lamiaceae	Tree	12
Ligustrum confusum Decne.	Oleaceae	Tree	5
Lindera pulcherrima (Nees) Hook.f.	Lauraceae	Tree	24
Lithocarpus elegans (Blume) Hatus. ex Soepadmo	Fagaceae	Tree	3
Litsea doshia (D.Don) Kosterm.	Lauraceae	Tree	27
Litsea lancifolia (Roxb. ex Nees) Fern.-Vill.	Lauraceae	Shrub	
Litsea monopetala (Roxb.) Pers.	Lauraceae	Tree	104
Luisia tristis (G.Forst.) Hook.f.	Orchidaceae	Orchid	
Lygodium flexuosum (L.) Sw.	Lygodiaceae	Fern	37
Lygodium japonicum (Thunb.) Sw.	Lygodiaceae	Fern	35
Lyonia ovalifolia (Wall.) Drude	Ericaceae	Tree	126
Lyonia villosa (Wall. ex C.B.Clarke) Hand.-Mazz.	Ericaceae	Tree	7
Macaranga denticulata (Blume) Müll.Arg.	Euphorbiaceae	Tree	19
Macaranga indica Wight	Euphorbiaceae	Tree	6
Machilus duthiei King	Lauraceae	Tree	47
Madhuca longifolia (J.Koenig ex L.) J.F.Macbr.	Sapotaceae	Tree	
Maesa chisia Buch.-Ham. ex D.Don	Myrsinaceae	Shrub	53
Maesa macrophylla Wall.	Myrsinaceae	Shrub	13
Magnolia champaca (L.) Baill. ex Pierre	Magnoliaceae	Tree	
Mahonia napaulensis DC.	Berberidaceae	Shrub	5
Mallotus philippensis (Lam.) Müll.Arg.	Euphorbiaceae	Tree	219
Mangifera indica L.	Anacardiaceae	Tree	13
Marsdenia lucida Edgew. ex Madden	Apocynaceae	Liana	
Marsdenia tinctoria R.Br.	Apocynaceae	Liana	
Meizotropis buteiformis Voigt	Fabaceae	Shrub	10
Melastoma malabathricum L.	Melastomataceae	Shrub	70
Melia azedarach L.	Meliaceae	Tree	28
Mesua ferrea L.	Clusiaceae	Tree	7
Mikania micrantha Kunth	Asteraceae	Herb	16
Miliusa velutina (A.DC.) Hook.f. & Thomson	Annonaceae	Tree	60
Millettia extensa (Benth.) Baker	Fabaceae	Liana	50
Mitragyna parvifolia (Roxb.) Korth.	Rubiaceae	Tree	9
Molineria capitulata (Lour.) Herb.	Hypoxidaceae	Herb	
Murraya koenigii (L.) Spreng.	Rutaceae	Shrub	85
Murraya paniculata (L.) Jack	Rutaceae	Shrub	6
Mussaenda frondosa L.	Rubiaceae	Shrub	
Myrica esculenta Buch.-Ham. ex D.Don	Myricaceae	Tree	75
Myrsine semiserrata Wall.	Myrsinaceae	Shrub	11

Species name	Family	Life form	Presence records
Neolamarckia cadamba (Roxb.) Bosser	Rubiaceae	Tree	7
Neolitsea umbrosa (Nees) Gamble	Lauraceae	Tree	8
Nephrolepis auriculata Trimen	Nephrolepidaceae	Fern	
Nyctanthes arbor-tristis L.	Oleaceae	Tree	22
Ocotea lancifolia (Schott) Mez	Lauraceae	Tree	9
Oroxylum indicum (L.) Kurz	Bignoniaceae	Tree	7
Osbeckia nepalensis Hook.f.	Melastomataceae	Shrub	11
Osbeckia stellata Buch.-Ham. ex Ker Gawl.	Melastomataceae	Shrub	9
Osyris lanceolata Hochst. & Steud.	Santalaceae	Shrub	14
Paris polyphylla Sm.	Melanthiaceae	Herb	31
Parthenocissus semicordata (Wall.) Planch.	Vitaceae	Liana	10
Pavetta indica L.	Rubiaceae	Shrub	10
Persea odoratissima (Nees) Kosterm.	Lauraceae	Tree	30
Phoenix loureiroi Kunth	Arecaceae	Palm	113
Phoenix sylvestris (L.) Roxb.	Arecaceae	Palm	
Phyllanthus emblica L.	Phyllanthaceae	Tree	143
Phyllanthus parvifolius Buch.-Ham. ex D.Don	Phyllanthaceae	Shrub	16
Picea smithiana (Wall.) Boiss.	Pinaceae	Tree	13
Pinus roxburghii Sarg.	Pinaceae	Tree	117
Pinus wallichiana A.B.Jacks.	Pinaceae	Tree	59
Piper longum L.	Piperaceae	Shrub	18
Pogostemon benghalensis (Burm.f.) Kuntze	Lamiaceae	Shrub	27
Potentilla lineata Trevir.	Rosaceae	Herb	12
Premna interrupta Wall. ex Schauer	Lamiaceae	Shrub	
Prunus cerasoides Buch.-Ham. ex D.Don	Rosaceae	Tree	34
Prunus napaulensis (Ser.) Steud.	Rosaceae	Tree	17
Prunus persica (L.) Batsch	Rosaceae	Tree	11
Psidium guajava L.	Myrtaceae	Tree	8
Pterospermum acerifolium (L.) Willd.	Malvaceae	Tree	
Pueraria peduncularis (Benth.) Benth.	Fabaceae	Herb	
Pyracantha crenulata (Roxb. ex D.Don) M.Roem.	Rosaceae	Shrub	32
Pyrrosia costata Tagawa & K.Iwats.	Polypodiaceae	Fern	
Pyrus pashia Buch.-Ham. ex D.Don	Rosaceae	Tree	69
Quercus floribunda Lindl. ex A.Camus	Fagaceae	Tree	11
Quercus glauca Thunb.	Fagaceae	Tree	36
Quercus lamellosa Sm.	Fagaceae	Tree	20
Quercus lanata Sm.	Fagaceae	Tree	78
Quercus oblongata D.Don	Fagaceae	Tree	21

Species name	Family	Life form	Presence records
Quercus oxyodon Miq.	Fagaceae	Tree	15
Quercus semecarpifolia Sm.	Fagaceae	Tree	121
Reinwardtia indica Dumort.	Linaceae	Shrub	22
Rhododendron anthopogon D.Don	Ericaceae	Shrub	15
Rhododendron arboreum Sm.	Ericaceae	Tree	171
Rhododendron arboreum var. *cinnamomeum* (Wall. ex G.Don) Lindl.	Ericaceae	Tree	12
Rhododendron barbatum Wall. ex G.Don	Ericaceae	Tree	25
Rhododendron campanulatum D.Don	Ericaceae	Shrub	16
Rhus parviflora Roxb.	Anacardiaceae	Shrub	6
Rosa sericea Lindl.	Rosaceae	Shrub	25
Rubia manjith Roxb. ex Fleming	Rubiaceae	Herb	25
Rubus ellipticus Sm.	Rosaceae	Shrub	130
Rubus paniculatus Sm.	Rosaceae	Shrub	30
Rubus pedunculosus D.Don	Rosaceae	Shrub	13
Saccharum spontaneum L.	Poaceae	Grass	18
Salix babylonica L.	Salicaceae	Tree	
Sambucus javanica Blume	Adoxaceae	Shrub	
Sarcococca pruniformis Lindl.	Buxaceae	Shrub	63
Saurauia napaulensis DC.	Actinidiaceae	Tree	17
Schima wallichii (DC.) Korth.	Theaceae	Tree	138
Schleichera oleosa (Lour.) Merr.	Sapindaceae	Tree	15
Scindapsus officinalis (Roxb.) Schott	Araceae	Herb	
Semecarpus anacardium L.f.	Anacardiaceae	Tree	127
Shorea robusta Gaertn.	Dipterocarpaceae	Tree	324
Smilax aspera L.	Smilacaceae	Shrub	84
Smilax ferox Wall. ex Kunth	Smilacaceae	Shrub	6
Smilax ovalifolia Roxb.	Smilacaceae	Shrub	77
Smilax perfoliata Lour.	Smilacaceae	Shrub	5
Smilax zeylanica L.	Smilacaceae	Shrub	16
Sorbus cuspidata (Spach) Hedl.	Rosaceae	Tree	12
Sorbus foliolosa (Wall.) Spach	Rosaceae	Tree	20
Spatholobus parviflorus (DC.) Kuntze	Fabaceae	Shrub	89
Spondias pinnata (L.f.) Kurz	Anacardiaceae	Tree	
Stephania japonica (Thunb.) Miers	Menispermaceae	Liana	
Stephania japonica var. *discolor* (Blume) Forman	Menispermaceae	Liana	18
Sterculia villosa Roxb.	Malvaceae	Tree	9
Stereospermum tetragonum DC.	Bignoniaceae	Tree	26
Streblus asper Lour.	Moraceae	Tree	

Species name	Family	Life form	Presence records
Symplocos lucida (Thunb.) Siebold & Zucc.	Symplocaceae	Tree	9
Symplocos pyrifolia Wall. ex G.Don	Symplocaceae	Tree	7
Symplocos racemosa Roxb.	Symplocaceae	Tree	5
Symplocos ramosissima Wall. ex G.Don	Symplocaceae	Tree	29
Syzygium cumini (L.) Skeels	Myrtaceae	Tree	256
Syzygium jambos (L.) Alston	Myrtaceae	Tree	6
Syzygium nervosum A.Cunn. ex DC.	Myrtaceae	Tree	89
Tamilnadia uliginosa (Retz.) Tirveng. & Sastre	Rubiaceae	Tree	
Taxus wallichiana Zucc.	Taxaceae	Tree	24
Terminalia alata Roth	Combretaceae	Tree	261
Terminalia bellirica (Gaertn.) Roxb.	Combretaceae	Tree	44
Terminalia chebula Retz.	Combretaceae	Tree	90
Tetrastigma dubium (M.A.Lawson) Planch.	Vitaceae	Shrub	16
Tetrastigma serrulatum (Roxb.) Planch.	Vitaceae	Liana	56
Thamnocalamus spathiflorus (Trin.) Munro	Poaceae	Grass	26
Thespesia lampas (Cav.) Dalzell	Malvaceae	Shrub	15
Thysanolaena latifolia (Roxb. ex Hornem.) Honda	Poaceae	Grass	44
Tinospora sinensis (Lour.) Merr.	Menispermaceae	Liana	17
Toddalia asiatica (L.) Lam.	Rutaceae	Liana	21
Toona ciliata M.Roem.	Meliaceae	Tree	36
Toxicodendron wallichii (Hook.f.) Kuntze	Anacardiaceae	Tree	42
Trachelospermum lucidum (D.Don) K.Schum.	Apocynaceae	Shrub	40
Trewia nudiflora L.	Euphorbiaceae	Tree	
Tsuga dumosa (D.Don) Eichler	Pinaceae	Tree	52
Typha angustifolia L.	Typhaceae	Herb	
Urtica dioica L.	Urticaceae	Herb	20
Viburnum cotinifolium D.Don	Adoxaceae	Shrub	9
Viburnum erubescens Wall.	Adoxaceae	Shrub	23
Viburnum mullaha Buch.-Ham. ex D.Don	Adoxaceae	Shrub	8
Wendlandia heynei (Schult.) Santapau & Merchant	Rubiaceae	Shrub	71
Wendlandia puberula DC.	Rubiaceae	Tree	7
Woodfordia fruticosa (L.) Kurz	Lythraceae	Shrub	178
Zanthoxylum armatum DC.	Rutaceae	Shrub	19
Ziziphus jujuba Mill.	Rhamnaceae	Tree	22
Ziziphus rugosa Lam.	Rhamnaceae	Tree	8

Table S2.2. Detailed list of 53 environmental variables compiled for this study. Variable categories, sub-categories, names and their respective units, abbreviations and sources or remarks on computation methods are presented.

Category	Sub-category	Name and unit	Abbreviation	Source/remarks
Climatic	Temperature	Isothermality (Mean temperature diurnal range/ Temperature annual range) * 100	IT	WorldClim 2 data (www.worldclim.org/ version2)
		Maximum temperature of warmest month (°C)	MaxTWaM	
		Mean annual temperature (°C)	MAT	
		Mean temperature diurnal range (Mean of monthly (maximum temperature–minimum temperature), °C)	TDR	
		Mean temperature of coldest quarter (°C)	TCQ	
		Mean temperature of driest quarter (°C)	TDQ	
		Mean temperature of warmest quarter (°C)	TWaQ	
		Mean temperature of wettest quarter (°C)	TWeQ	
		Minimum temperature of coldest month (°C)	MinTCM	
		Temperature annual range (Maximum temperature of warmest month–Minimum temperature of coldest month, °C)	TAR	
		Temperature seasonality (standard deviation * 100)	TS	
	Precipitation	Annual precipitation (mm)	AP	
		Precipitation of coldest quarter (mm)	PCQ	
		Precipitation of driest month (mm)	PDM	
		Precipitation of driest quarter (mm)	PDQ	
		Precipitation of warmest quarter (mm)	PWaQ	
		Precipitation of wettest month (mm)	PWeM	
		Precipitation of wettest quarter (mm)	PWeQ	
		Precipitation seasonality (coefficient of variation)	PS	
	Other climatic	Annual potential evapotranspiration (mm)	PET	Computed using WorldClim 2 monthly data
		Climatic moisture index (Annual precipitation/ Annual potential evapotranspiration–1 when Annual precipitation < Annual potential evapotranspiration and 1–Annual potential evapotranspiration/Annual precipitation when Annual precipitation ≥ Annual potential evapotranspiration)	CMI	
		Cloud cover seasonality (standard deviation * 100)	CCS	Global 1-km cloud cover data (www. earthenv.org/cloud)
		Growing degree days (sum of all monthly temperatures > 10 °C, multiplied by total number of days)	GDD10	Computed using WorldClim 2 monthly data
		Maximum climatological water deficit (the most -ve value of climatological water deficit (CWD) attained over a year, where CWD of a month = CWD of previous month + Precipitation of the month–Evapotranspiration of the month)	MCWD	
		Mean annual cloud frequency (% * 100)	MACF	Global 1-km cloud cover data (www. earthenv.org/cloud)
		Potential evapotranspiration of coldest quarter (mm)	PETCQ	Computed using WorldClim 2 monthly data
		Potential evapotranspiration of driest quarter (mm)	PETDQ	
		Potential evapotranspiration of warmest quarter (mm)	PETWaQ	
		Potential evapotranspiration of wettest quarter (mm)	PETWeQ	
		Potential evapotranspiration seasonality (standard deviation * 100)	PETseas	
		Solar radiation (Mean of monthly means, kJ/sq m/day)	Srad	
		Thornthwaite's aridity index	AI	
		Water vapour pressure (Mean of monthly means, kPa)	Vapr	
		Wind speed (Mean of monthly means, m/s)	Wind	

Category	Sub-category	Name and unit	Abbreviation	Source/remarks
Edaphic	Chemical	Soil cation exchange capacity (cmol/kg)	CEC	Computed using ISRIC-SoilGrids (ftp://ftp.soilgrids.org/data/aggregated/1km/)
		Soil organic carbon content (gm/kg)	OCC	
		Soil organic carbon stock (tonnes/ha)	OCS	
		Soil pH * 10 in water	pH	
	Physical	Available soil water capacity until wilting point (%)	AWCWP	
		Available soil water capacity with FC = pF 2.0 (%)	AWCh1	
		Available soil water capacity with FC = pF 2.3 (%)	AWCh2	
		Available soil water capacity with FC = pF 2.5 (%)	AWCh3	
		Bulk density (kg/cu m)	BD	
		Depth to bedrock (R horizon) up to 200 cm	D2BR	
		Saturated water content teta-S (%)	SWCtS	
		Soil clay content (%)	ClayC	
		Soil coarse fragments content (%)	CFC	
		Soil sand content (%)	SandC	
		Soil silt content (%)	SiltC	
Topographic		Elevation (m)	Elev	Computed using SRTM 90m digital elevation database v4.1 (www.cgiarcsi.community/data/srtm-90m-digital-elevation-database-v4-1)
		Aspect (deg)	Aspect	
		Distance to water (arc sec)	D2W	Computed using river network data (http://www.hydrosheds.org/) and global lakes and wetlands data (www.worldwildlife.org/pages/global-lakes-and-wetlands-database)
		Slope (deg)	Slope	Computed using SRTM 90m digital elevation database v4.1 (www.cgiarcsi.community/data/srtm-90m-digital-elevation-database-v4-1)

Table S2.3. Bivariate correlation matrix showing correlation among environmental variables. Fifty-two environmental variables (elevation excluded) of 1,437 spatially unique presence locations were used for the correlation analysis. Spearman's rank correlation coefficient (*r*) and their corresponding *p*-values are shown. For the details of environmental variable abbreviations used in the table see Table S2.2. The sequence of environmental variable abbreviations in the table follows that of environmental variables in Table S2.2.

Environmental variable abbreviation	Variable, correlation coefficient and corresponding *p*-value					
	MAT		ClayC		Slope	
	r	*p*	*r*	*p*	*r*	*p*
IT	-0.19	<0.001	-0.17	<0.001	0.15	<0.001
MaxTWaM	0.99	<0.001	0.60	<0.001	-0.66	<0.001
MAT	1.00	NA	0.61	<0.001	-0.67	<0.001
TDR	0.33	<0.001	0.10	<0.001	-0.27	<0.001
TCQ	0.99	<0.001	0.60	<0.001	-0.66	<0.001
TDQ	0.98	<0.001	0.60	<0.001	-0.66	<0.001
TWaQ	0.99	<0.001	0.61	<0.001	-0.66	<0.001
TWeQ	1.00	<0.001	0.61	<0.001	-0.66	<0.001
MinTCM	0.98	<0.001	0.60	<0.001	-0.65	<0.001
TAR	0.41	<0.001	0.17	<0.001	-0.36	<0.001
TS	0.28	<0.001	0.16	<0.001	-0.26	<0.001
AP	0.40	<0.001	0.27	<0.001	-0.26	<0.001
PCQ	-0.44	<0.001	-0.22	<0.001	0.35	<0.001
PDM	-0.51	<0.001	-0.28	<0.001	0.40	<0.001
PDQ	-0.40	<0.001	-0.17	<0.001	0.35	<0.001
PWaQ	0.25	<0.001	0.21	<0.001	-0.12	<0.001
PWeM	0.56	<0.001	0.38	<0.001	-0.41	<0.001
PWeQ	0.50	<0.001	0.33	<0.001	-0.35	<0.001
PS	0.69	<0.001	0.46	<0.001	-0.52	<0.001
PET	0.96	<0.001	0.59	<0.001	-0.63	<0.001
CMI	-0.17	<0.001	-0.05	0.08	0.17	<0.001
CCS	-0.13	<0.001	-0.01	0.70	0.02	0.42
GDD10	1.00	<0.001	0.61	<0.001	-0.67	<0.001
MCWD	-0.87	<0.001	-0.52	<0.001	0.63	<0.001
MACF	-0.59	<0.001	-0.34	<0.001	0.42	<0.001
PETCQ	0.98	<0.001	0.60	<0.001	-0.65	<0.001
PETDQ	0.93	<0.001	0.55	<0.001	-0.65	<0.001
PETWaQ	0.89	<0.001	0.55	<0.001	-0.58	<0.001
PETWeQ	0.96	<0.001	0.56	<0.001	-0.64	<0.001
PETseas	0.57	<0.001	0.38	<0.001	-0.35	<0.001
Srad	0.84	<0.001	0.54	<0.001	-0.62	<0.001
AI	0.70	<0.001	0.39	<0.001	-0.58	<0.001

Environmental variable abbreviation	Variable, correlation coefficient and corresponding *p*-value					
	MAT		ClayC		Slope	
	r	*p*	*r*	*p*	*r*	*p*
Vapr	0.97	<0.001	0.60	<0.001	-0.65	<0.001
Wind	-0.93	<0.001	-0.52	<0.001	0.62	<0.001
CEC	-0.64	<0.001	-0.44	<0.001	0.54	<0.001
OCC	-0.78	<0.001	-0.69	<0.001	0.60	<0.001
OCS	-0.69	<0.001	-0.70	<0.001	0.51	<0.001
pH	0.32	<0.001	-0.01	0.61	-0.34	<0.001
AWCWP	-0.13	<0.001	0.42	<0.001	0.19	<0.001
AWCh1	-0.87	<0.001	-0.73	<0.001	0.61	<0.001
AWCh2	-0.87	<0.001	-0.73	<0.001	0.61	<0.001
AWCh3	-0.87	<0.001	-0.72	<0.001	0.61	<0.001
BD	0.86	<0.001	0.58	<0.001	-0.63	<0.001
D2BR	0.42	<0.001	0.10	<0.001	-0.74	<0.001
SWCtS	-0.84	<0.001	-0.49	<0.001	0.62	<0.001
ClayC	0.61	<0.001	1.00	NA	-0.39	<0.001
CFC	-0.35	<0.001	-0.12	<0.001	0.40	<0.001
SandC	-0.52	<0.001	-0.95	<0.001	0.33	<0.001
SiltC	-0.20	<0.001	0.09	0.001	0.15	<0.001
Aspect	0.00	0.86	0.01	0.62	-0.02	0.57
D2W	-0.10	<0.001	0.22	<0.001	-0.05	0.06
Slope	-0.67	<0.001	-0.39	<0.001	1.00	NA

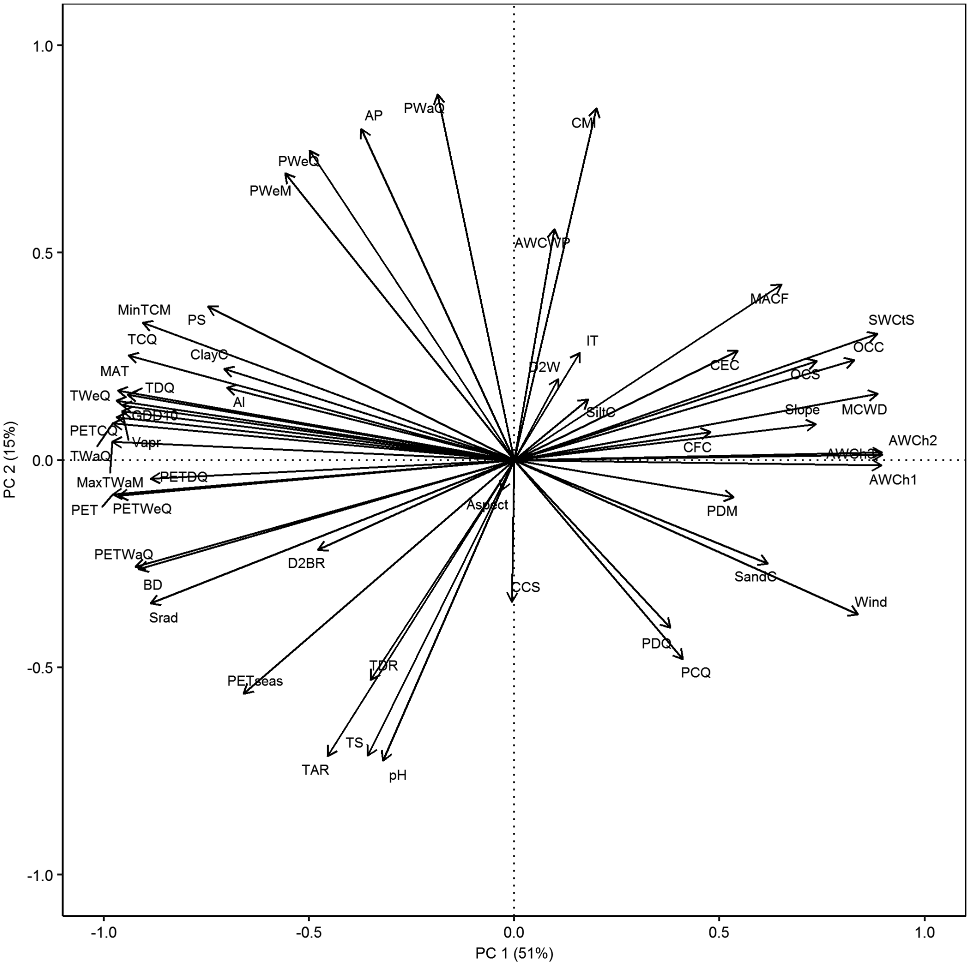


Figure S2.1. Loadings of environmental variables plotted on the first two principal components derived from 52 environmental variables of 1,437 spatially unique presence locations. Higher loadings indicate higher importance of a variable in describing the ecological gradient of the study area. Details of environmental variables and abbreviations used in the plot are presented in Table S2.2.

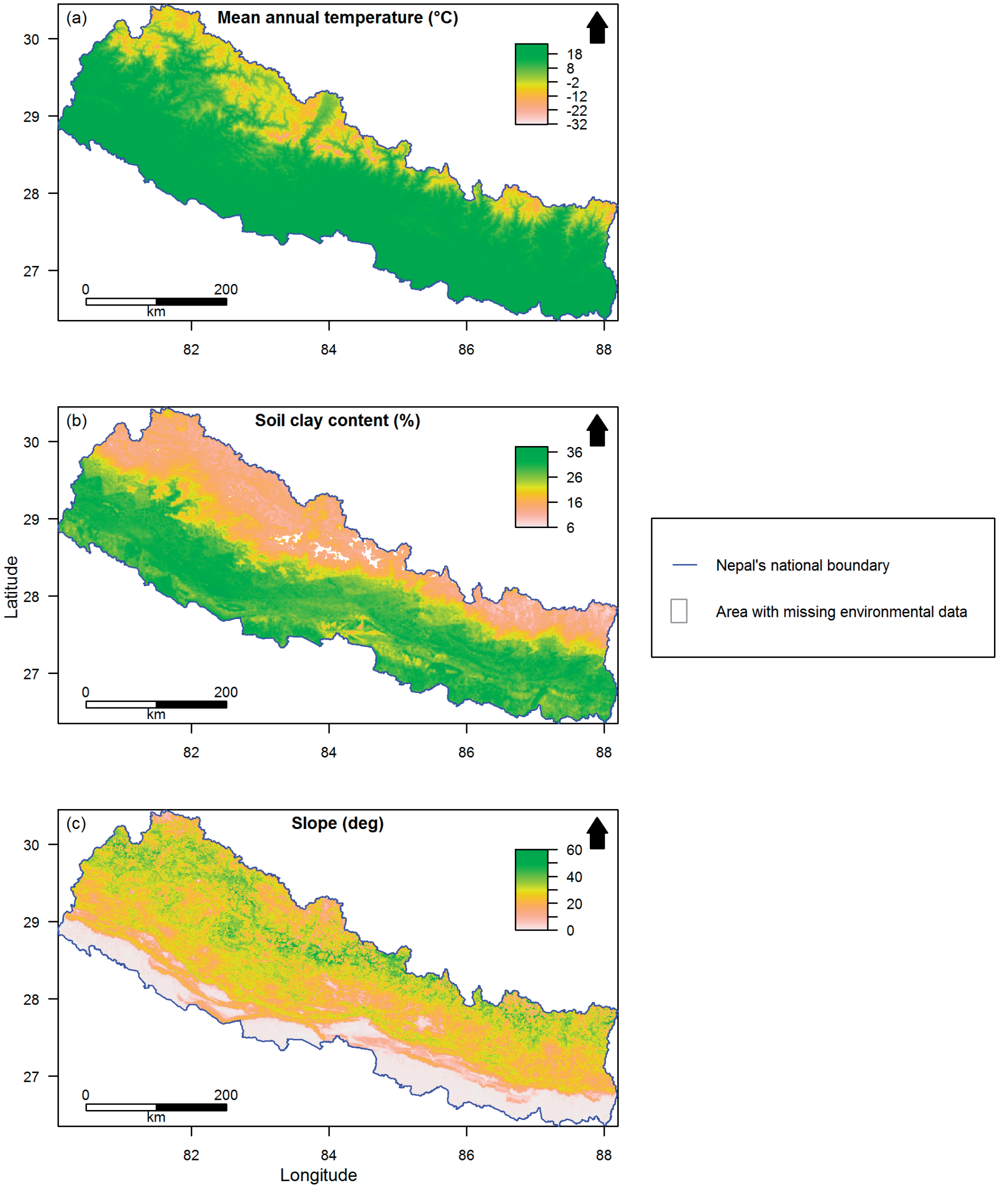
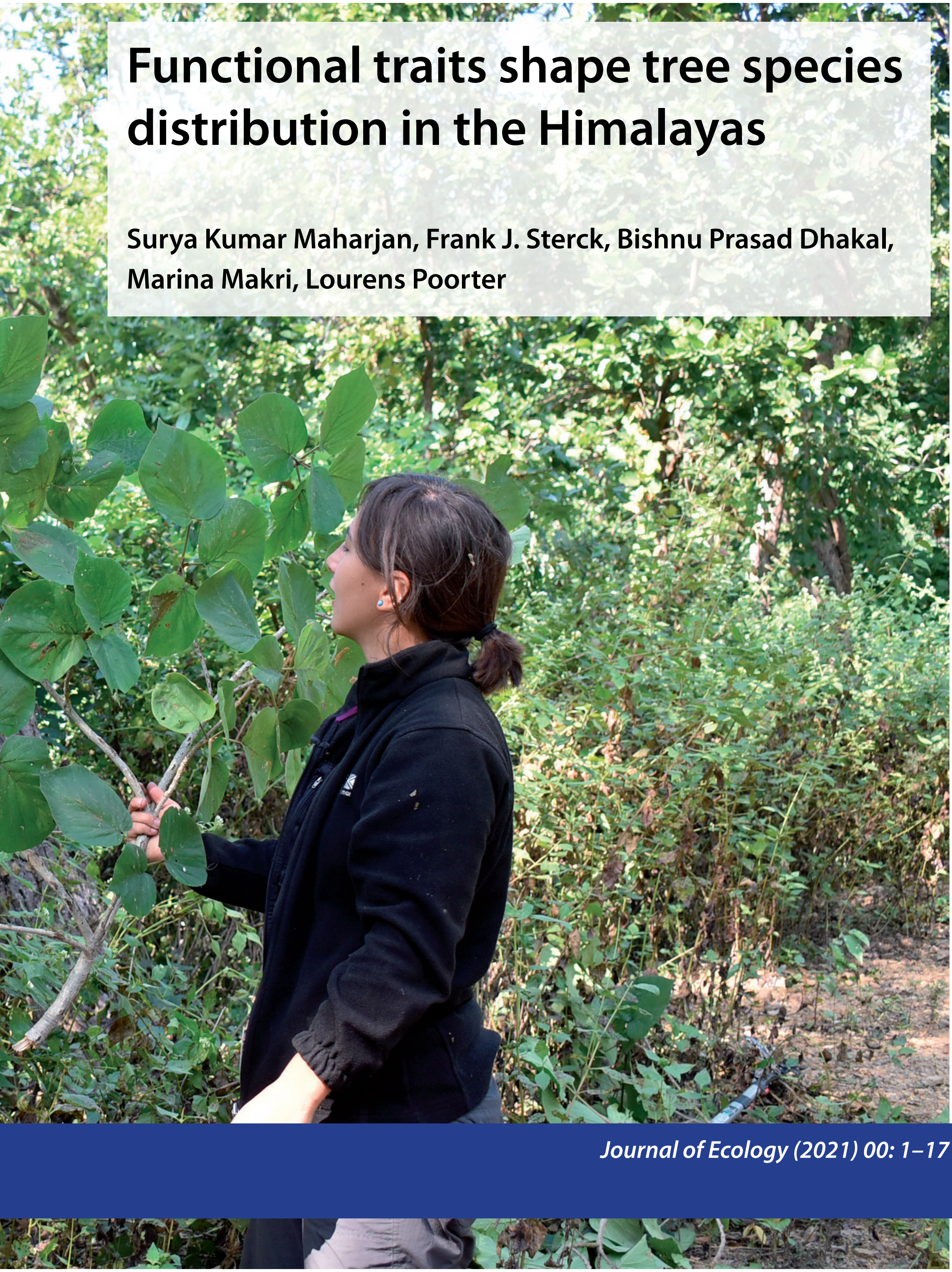


Figure S2.2. Spatial GIS maps of three key environmental variables namely, a) mean annual temperature, b) soil clay content and c) slope. Maps are clipped to Nepal. The blue line indicates national boundary of Nepal. The Government of Nepal published on 20th May 2020 a new political map including Kalapani, Lipulekh and Limpiyadhura inside the Nepal borders. As our research started in 2016, in our research, we used the previous version of the map without these territories. The darker colors indicate higher values of the environmental variables.

CHAPTER 3



Functional traits shape tree species distribution in the Himalayas

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Abstract

Plant functional traits determine plant performance and have therefore the potential to shape and predict species distributions along environmental gradients. This study analyses how traits affect tree species distribution along an elevational gradient in the Himalayas, Nepal. We addressed three questions: (a) what plant strategies can be distinguished among tree species? (b) how are plant traits and strategies associated with elevation? and (c) what plant traits are the best predictors of species positions along elevational gradient?

We quantified for 31 tree species a set of 39 plant traits related to resource uptake, use and conservation. We analysed how traits cluster into separate functions using a cluster analysis, and how traits and clusters associate into distinct plant strategies using a principal component analysis.

The cluster analysis showed five clusters of traits, reflecting (a) efficiency in vertical expansion, (b) efficiency in horizontal expansion, (c) efficiency in metabolism, (d) physical defence and (e) tree functional groups (conifers vs. broadleaf species). The first PCA axis reflects trade-offs in traits and clusters linked to elevation: highland species had trait values that increase safety against freezing induced cavitation, high solar radiation and strong wind, and that increase resource conservation. In contrast, lowland species had trait values that increase efficiency of resource acquisition, metabolism and expansion. Additionally, a bivariate analysis showed that the first PCA axis is more strongly related to elevation than the individual traits, indicating that the combination of traits is more important than the individual traits. An all subsets regression analysis showed that a small set of traits best explain species distribution: highland species had smaller size (low basal area), safer hydraulics (low conduit diameter) and lower leaf and branch display efficiency (low leaf area per xylem area, specific branch length) that increase persistence under harsh conditions. Remarkably, leaf traits were poor predictors of species' elevational positions.

Synthesis: Multiple trade-offs in plant size, hydraulics and light competitiveness shape species distribution along the elevational gradient. Along this extreme environmental gradient, stem and branch traits that integrate multiple plant organs and functions are better predictors of species' elevational distributions than leaf traits.

Keywords: conservative-acquisitive paradigm, elevational gradient, interspecific trait variation, landscape ecology, Nepal, plant strategy, trade-off, tropics

3.1 Introduction

One of the most fundamental quests in ecology is to understand the mechanisms that shape species distributions along environmental gradients. Such knowledge is also fundamental to predict species' potential responses to environmental changes. As warming climate forces species to track their climatic niche and shift their distribution ranges poleward and/or upward (Chen et al., 2011; Cramer et al., 2014), the need to predict species' potential responses to environmental changes has never been more urgent. Warming occurs at relatively higher rates at higher elevations, which is referred to as elevation-dependent warming (EDW: Palazzi et al., 2019; Wang et al., 2014). In tropical montane landscapes, EDW could force species to shift their distribution ranges rapidly upward (Chen et al., 2011), with little remaining area left to go. Understanding the mechanisms that shape species distribution along elevational gradient is urgent for species-rich tropical montane landscapes to predict species' responses to global warming, conserve biodiversity, design climate adaptation measures and select appropriate species for future planting activities.

Plant functional traits are defined as morphological, physiological or phenological attributes that affect plant growth, survival and reproduction and, hence, distribution (Violle et al., 2007). Traits vary considerably within and among plant species. In nature, environmental filtering selects a subset of species from the species pool (community assembly rules: Keddy, 1992; Woodward & Diament, 1991) resulting into associations between traits and environmental conditions at local (Cavender-Bares et al., 2004; Marteinsdóttir & Eriksson, 2014) and regional scales (Boet et al., 2020; Díaz et al., 1998). Additionally, the partitioning of resource niches across species results into patterns of covariation or trade-off among traits that represent different plant strategies that allow for differential success in different environmental conditions (Reich et al., 2003; Sterck et al., 2014). Díaz et al. (2004) analysed the variation in 12 traits among four floras across three continents and revealed the existence of a fundamental axis of evolutionary specialization across ecosystems and biomes that runs from plant species with high resource conservation strategy (i.e. a conservative strategy) to high resource acquisition strategy (i.e. an acquisitive strategy; see also Reich et al., 1992). At one end of the axis are species with conservative strategy characterised by small, thick and tough leaves with slow turnover, whereas on the other end of the axis are species with acquisitive strategy characterised by large, thin and soft leaves with rapid turnover. In a follow-up study, Díaz et al. (2016) analysed the variation in six major traits critical to growth, survival and reproduction of vascular plant species across the globe. They revealed two major axes of evolutionary specialization, namely the plant size spectrum (that runs from short species with small diaspores to tall species with large diaspores) and the leaf economics spectrum (that runs from species with cheaply constructed acquisitive leaves to species with conservative leaves). These two axes together accounted for 74% of the trait variation across the globe. Despite increasing knowledge on how these plant strategies and their underlying functional traits structure plant communities along environmental gradients (e.g. Díaz et al., 1998, 2004; Pollock et al., 2012; Reich et al., 2003), studies testing these concepts in species-rich tropical montane landscapes are limited.

In montane landscapes, with increasing elevation, multiple abiotic factors change in a predictable way affecting different aspects of plant functioning. The decrease in temperature may reduce metabolic rates and transpiration of plant species (Gates, 1968; Körner, 2016). The gradual decrease in atmospheric pressure and atmospheric partial pressure of CO_2 may affect gas exchange in plants and consequently influence photosynthesis (Friend & Woodward, 1990; Körner & Diemer, 1987). However, such effects of temperature and pressure reduction may be partially mitigated by increases in clear-sky solar radiation and the diffusion coefficients for water vapour and CO_2 with elevation (Gale, 1972a, 1972b; Smith & Geller, 1979; Terashima et al., 1995; Wang et al., 2017). The stronger winds that are common at mountaintops and ridges (Barry, 1992b) may increase the risks of wind-induced physical damage to the plant species (Onoda & Anten, 2011). Soil conditions also change with elevation and soils often become thinner, less developed and less fertile with increasing elevation (FAO, 2015), with potential negative implications for the regeneration and growth of species (Müller, Schickhoff, et al., 2016; Müller, Schwab, et al., 2016).

Overall, plants that grow at lower elevations experience benign (i.e. favourable) environmental conditions for plant growth and survival whereas plants that grow at higher elevations experience harsh environmental conditions. Consequently, plants that grow at lower elevations feature taller stems (Mao et al., 2018) to compete for light (Coomes & Allen, 2007), larger and thinner leaves to capture more light (Liu et al., 2020), higher leaf nutrient concentrations to increase photosynthetic capacity (Drollinger et al., 2017) and conductive stems and branches to increase water transport and gas exchange (Sterck et al., 2014; Yang et al., 2020). These trait values are characteristic of an acquisitive strategy that increases resource capture and growth. In contrast, plants that grow at higher elevations have shorter stems (Mao et al., 2018) to ensure safety against strong winds (Onoda & Anten, 2011), smaller and thicker leaves to protect photosynthetic system against high UV-B radiations (Turunen & Latola, 2005), higher leaf dry matter content and lower specific leaf area (SLA, Körner et al., 1989) to enhance leaf durability, leaf defence and/or leaf lifespan, and cavitation resistant stems and branches to ensure water transport and gas exchange at freezing temperature (Olson et al., 2018; Yang et al., 2020). These trait values are characteristic of a conservative strategy that increases resource conservation and survival. Although studies have found that there are differences in plant growth and traits at low and high elevations, there have not been sufficient conclusive tests for relationships between plant traits and strategies and elevation, the forms and strengths of such relationships are poorly understood.

In this study, we tested for such elevational patterns in traits for 31 trees species occurring from a warm and wet lowlands with tropical climate to a colder and drier highlands with sub-alpine climate in the Nepalese Himalayas (HMGN/MFSC, 2002; Lillesø et al., 2005, see Section 3.2 for details on the studied elevational gradient). We measured a comprehensive set of 39 leaf, branch and whole-plant traits that are important for resource acquisition, use and conservation and play a key role in defence, metabolism or adaptation to harsh environmental conditions. Specifically, we addressed the following three research questions and corresponding hypotheses.

First, what plant strategies can be distinguished among tree species? In this study, we focused on tree species that reduces the meaning of looking for size effects (although over the entire elevational gradient it might be important with shrubs above the treeline). We thus tested whether a conservative-acquisitive strategy spectrum identified for a limited set of traits for vascular plant species across the globe (Díaz et al., 2004, 2016) also holds for an extended set of 39 traits for tree species along Himalayan elevational gradient in Nepal.

Second, how are plant traits and strategies associated with elevation? Because environmental conditions become harsher with increasing elevation, we predicted, in line with earlier observations, that the harsher conditions at higher elevations select for species with more conservative trait values, for example, a small stature, small and thick leaves with low nutrient contents, and stems and branches that are more resistant to freezing but less efficient in water transport. Vice versa, the more favourable conditions at lower elevations select for species with more acquisitive trait values. This has been tested for a few traits (see above) but now we expand this to an assessment of a comprehensive set of 39 traits.

Third, what plant traits are the best predictors of species' positions along elevational gradient? We hypothesized that plant traits associated with resource conservation vs. rapid resource acquisition can best predict species' positions along an elevational gradient.

3.2 Materials and Methods

3.2.1 Study area and species

The research was carried out along a species-rich steep elevational gradient along the southern slopes of the Himalayas in central Nepal (Figure S3.1). Within a horizontal span of ca. 110 km, elevation varies from ca. 90 m a.s.l. at Nijgadh in Bara district in the south to ca. 3,850 m a.s.l. (treeline) at Lauribinayak in Rasuwa district in the north. Along this gradient, temperature decreases linearly, and precipitation peaks around 1,000 m a.s.l. and then decreases rapidly (Figure S3.2). Potential evapotranspiration follows the temperature trend, wind speed shows increasing trend, while topography becomes steeper and soil becomes shallower (Figure S3.2). Vegetation follows changes in temperature and precipitation patterns and changes from wet (1,738 mm yr^{-1}) and warm (24.1 °C) tropical forests to intermediate temperate forests to drier (1,132 mm yr^{-1}) and colder (6.9 °C) subalpine forests (Lillesø et al., 2005; Shrestha et al., 2015).

To understand how traits shape the distribution of plant species along the elevational gradient, we selected 31 common tree species that partitioned the elevational gradient (Figure 3.1; Table S3.1). We focused on the most abundant tree species in the study area because they contribute most to the forest biomass and ecosystem functioning and because they are easier to find and sample a sufficient number of individuals at each elevation. Species included 10 deciduous broadleaf species still with leaves at the time of fieldwork, 16 evergreen broadleaf species and five (evergreen) conifers from 18 different families (Table S3.1), thus guaranteeing a wide phylogenetic coverage. As some of the mid- and

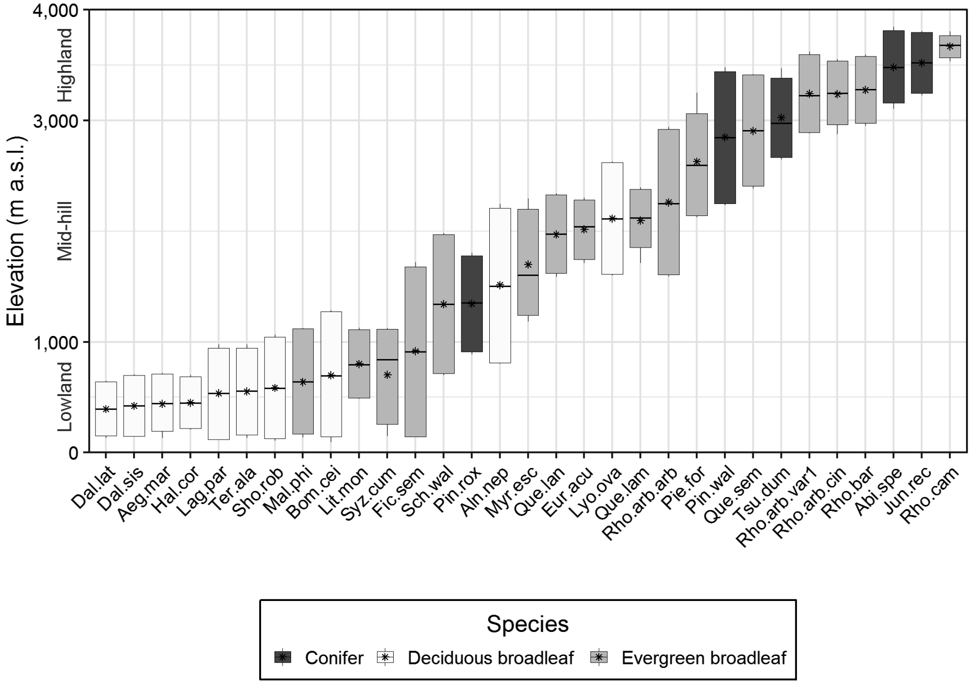


Figure 3.1. Positions of 31 Himalayan tree species along the elevational gradient (lowland: <1,000 m a.s.l.; mid-hill: 1,000 – 3,000 m a.s.l.; and highland: >3,000 m a.s.l.) based on the field data. Boxplots indicate species' elevational positions and elevation ranges (box – inter-quartile range, a horizontal line within the box - median elevation and whiskers extending from the box – minimum and maximum elevations). Asterisks within boxplots indicate mean elevations of species. Species included 10 deciduous broadleaf species (white boxplots), 16 evergreen broadleaf species (grey boxplots) and five conifers (black boxplots). Species name abbreviations are based on the first three letters of their genus, species and variety names, wherever applicable. For the complete list of study species see Table S3.1.

high-elevation deciduous species were already losing their leaves at the time of fieldwork, we could not include them in this study.

3.2.2 Sampling design

To adequately describe species' trait values and account for altitudinal trait variation, we sampled for each species six trees; three trees from the lower limits of their elevational distribution ranges and three trees from the upper limits. To assure that the traits are fully expressed, we sampled healthy-looking trees with sun-exposed crowns (crown illumination index ≥2.5, Clark and Clark, 1992). To reduce ontogenetic variation, we sampled adult trees with a stem diameter at breast height (DBH) between 10 and 30 cm. Due to lack of appropriate trees, we selected two trees for *Quercus lamellosa* (9.8 cm) and *Q. semecarpifolia* (32 cm) outside that size range. Trees were sampled mainly from the natural forests in areas with a slope of <45 degrees. For six species (*Aegle marmelos*, *Dalbergia sissoo*, *Ficus semicordata*, *Litsea monopetala*, *Mallotus philippensis* and *Syzygium cumini*) insufficient trees were available inside the forest, and therefore naturally regenerated trees were selected from nearby farmlands. Coordinates and elevation of all sampled trees were recorded using GPSmap 60CSx (Garmin Ltd.) to mark their positions along the elevational gradient.

3.2.3 Trait measurements

We selected 39 traits (Table 3.1) that are important for resource acquisition, use and conservation and play a key role in defence, metabolism or adaptation to harsh environmental conditions (e.g. freezing, drought and low nutrient availability). Traits were measured following standardized protocols (Pérez-Harguindeguy et al., 2013; Scholz et al., 2013; Zhang et al., 2016). We measured 8 whole-plant traits, 21 branch traits and 10 leaf traits. Fieldwork was conducted between October and December 2017.

Whole-tree traits: Tree height and crown height were measured using Vertex IV (Haglof, Inc.). DBH was measured using diameter tape. Crown width was measured using a measuring tape. The deciduousness of species were determined based on personal experience and literature (http://www.efloras.org/, 2019; Jackson, 1994).

Branch traits: A healthy-looking exposed branch (with crown illumination index ≥2.5) of ≥75 cm length was clipped from each sample tree using a tree pruner. To assure similar hydraulic path lengths, branches were sampled between 5 and 8 m height, if possible. But some trees in subalpine regions (e.g. some trees of *Abies spectabilis*, *Juniperus recurva* and *Rhododendron* species) and in open habitats such as forest edges or forests along trails or ridges (e.g. some trees of *F. semicordata* and *Lyonia ovalifolia*) were lower in height (dwarf trees). To obtain a standardized size, branches longer than 75 cm were clipped to 75 cm. The bottom 5 cm of each sample branch was clipped, and diameters with bark and without bark were measured using a calliper and stored in 50% ethanol for later conduit, xylem and pith area measurement in the laboratory. For the remaining 70 cm long sample branch, the number of ramifications was counted and crown diameter was measured using a measuring tape. All leaves were detached, and leaves and branch were weighed separately for their fresh weights. Approximately 200 g of leaves were stored in an air-tight plastic bag for later nutrient analysis. Next, the middle 10 cm of each sample branch was clipped, and diameters with and without bark were measured using a calliper. Wood and bark were weighed separately for their fresh weights and stored in an envelope for later oven-dry weight measurement in the laboratory.

In the laboratory, the stored bottom 5 cm sections of sample branches were sliced using a sliding microtome (RMT-45, Radical Scientific Equipments Pvt. Ltd.), the section slices were mounted on glass slides, and photographed using a camera (EOS 1200D or 60D, Canon Inc.) mounted on a microscope (TC-XSP-13A, TICARE). Section slicing and mounting of slices on glass slides were carried out at the Anatomy Laboratory of National Herbarium and Plant Laboratories, Godawari, Nepal. Then to quantify conduit, xylem and pith dimensions, photographs were analysed semi-automatically in ImageJ 1.52e (Schneider et al., 2012) using VesselJ plugin (I. García-González, unpubl. data) following standardized protocol described in Scholz et al. (2013). Finally, to quantify wood and bark oven-dry weights, the stored wood and bark from the middle 10 cm sections of sample branches were oven-dried at 80 °C for 48 hr at the Soil and Plant Analysis Laboratory of Local Initiatives for Biodiversity, Research and Development (LI-BIRD), Pokhara, Nepal.

Leaf traits: Eight fully-developed healthy-looking leaves were sampled from each sample branch. For *A. spectabilis* and *Tsuga dumosa* with tiny scale-like leaves, 24 leaves were sampled. Laminae and petioles were separated where applicable (some species had sessile leaves) and weighed separately. Laminae and petioles were photographed using D3400 (Nikon Inc.). The one-sided leaf and petiole area were estimated by analysing these photographs semi-automatically in ImageJ v1.52e (Schneider et al., 2012). Leaf thickness was measured using a micrometre. Leaf chlorophyll content was measured using SPAD-502 (Konica Minolta Inc.). As values provided by SPAD-502 are unitless, later in the laboratory, they were calibrated using an equation leaf chlorophyll content (µg cm^{-2}) = (117.1 x SPAD)/(148.84–SPAD) (Coste et al., 2010). Sample laminae and petioles were then stored in airtight plastic bags. Later in the laboratory, they were oven-dried for 48 hr at 80 °C and weighed separately for their oven-dry weights. Leaf N, P and K concentration were estimated using Kjeldahl (block digestion) method (AOAC 981.10) at the Soil and Plant Analysis Laboratory of LI-BIRD, Pokhara, Nepal.

3.2.4 Data analysis

To evaluate what plant strategies can be distinguished among tree species, we carried out cluster analysis and ordination analysis. First, to identify clusters of correlated traits that could reflect major trait covariations or trade-offs, we clustered species' traits based on absolute pairwise Pearson's correlation coefficients using a hierarchical clustering algorithm. Since parametric and nonparametric correlation analyses produce similar results, we preferred to use parametric analysis because it is a more powerful test and it is therefore easier to detect significance. We used the R-package HMISC function 'rcorr' for calculating pairwise Pearson's correlation coefficients among species traits and the R-package STATS function 'hclust' for clustering species traits. In 'hclust' function, maximum or complete linkage clustering method was used. It computes all pairwise dissimilarities between the elements in cluster 1 and the elements in cluster 2, and considers the largest value (i.e. maximum value) of these dissimilarities as the distance between the two clusters. It tends to produce compact clusters. Then, to further represent trait covariations or trade-offs based on their principal components, we carried out categorical principal component analysis (CatPCA, Linting & van der Kooij, 2012), which can accommodate both categorical and continuous traits. For continuous traits, trait means by species were calculated by averaging the trait values over the sampled six trees per species, and were standardized by centring by mean and scaling by standard deviation before CatPCA. We used the R-package GIFI function 'princals' for CatPCA. Preliminary analysis (Figure S3.3) indicated that only first two principal components have eigenvalues greater than the mean eigenvalues from random datasets, and therefore only the first two principal components are presented and discussed.

To evaluate how plant traits and strategies are associated with elevation, we carried out bivariate correlation analysis. We used the R-package HMISC function 'rcorr' to calculate Pearson's correlation coefficients between the first two CatPCA axes – representing two major plant strategies – and the associated traits, and species' mean elevations. We also calculated Spearman's rank correlation coefficients to account for potential nonlinear patterns with elevation. These correlations reflect ecological relations (i.e. how do traits determine present-day distributions). In addition, we also calculated phylogenetically independent correlations (PICs), which reflect evolutionary relationships (i.e. whether these traits reflect adaptations to altitude). For this, first we built phylogenetic tree of the study species using the R-package V.PHYLOMAKER function 'phylo.maker'. Using this phylogenetic tree, we calculated phylogenetically independent contrasts using the R-package APE function 'pic'. Based on these phylogenetically independent contrasts, we calculated PICs using the R-package PICANTE function 'cor.table'. As more representative estimates of the species' mean elevations, we used mean elevations of the tree species calculated based on elevation data from wide network of permanent plots established by Forest Research and Training Centre (then Department of Forest Research and Survey), Nepal (DFRS, 2015; Table S3.1) instead of mean elevations calculated based on elevation data of six trees that we actually measured in the field for this and the following analysis. For description of the plot network see Chapter 2.

To evaluate what plant traits are the best predictors of tree species' position along elevational gradient, we regressed the species' average elevational positions against species' trait means using all subsets regression analysis. Furthermore, the relative contributions of traits as predictors of tree species' position along the elevational gradient, the relative importance of the traits to the best explanatory models, were calculated. We used the R-package MuMIn function 'dredge' for all subsets regression analysis. As multicollinearity among functional traits can distort regression analysis, two traits per trait cluster (see Figure 3.2) with a strong correlation with elevation (see Table 3.2) were shortlisted. Then from the list of thus shortlisted traits, we selected traits with variance inflation factor (VIF) <10 for all subsets regression analysis.

3.3 Results

3.3.1 Trait variation

Plant trait values varied widely across Himalayan tree species, as illustrated by the 5th and 95th percentiles values of traits (Table 3.1). Tree species ranged in median height from 5 to 17 m; in basal area from 87 to 661 cm^2; and in conduit density from 19 to 2,564 conduits mm^{-2}. Likewise, tree species ranged in SLA from 41 to 143 cm^2 g^{-1} and in leaf thickness from 0.2 to 0.8 mm. Tree species showed a substantial variation in their traits, mainly because they occupied different elevational ranges along Himalayan elevation gradient and partially because both conifers and broadleaf species were included (see Table 3.2).

3.3.2 Plant strategies among Himalayan trees species

To identify clusters of correlated traits that could reflect major trait covariations or trade-offs hierarchical clustering was used. This analysis identified five trait clusters (Figure 3.2), which were associated with different functionalities and were given corresponding names. The green cluster contains traits associated with **vertical expansion** – since the traits reflect vertical stem and crown expansion (tree height, crown base height, crown length and slenderness), efficient light interception (high SLA, LAR, leaf density and low leaf thickness) and efficient water transport (wide conduit diameter and deciduous leaf habit – a strategy to avoid cavitation). The blue cluster comprises traits associated with **horizontal expansion** – since the traits reflect horizontal stem and crown expansion (basal area, crown width and proportions of xylem and bark). The dark grey cluster includes traits associated with **metabolic efficiency** – high leaf nutrient concentrations (high leaf N, P and K concentrations) and high light interception efficiency at the branch level (high LAXA and LMF). The orange cluster consists of traits associated with **physical defence** – traits that refer to tissue toughness (density and dry matter content of branch, wood, bark and leaves) that enhance tissue resistance to physical damage (by wind, precipitation, pathogens and herbivores) and tissue lifespan. The purple cluster represents the split between **conifer**

Table 3.1. Overview of the studied plant functional traits: trait name; abbreviation; unit; function; and median, 5th and 95th percentile, and coefficient of variation (CV) of the trait values (based on $n = 31$ species x 6 trees). Traits are grouped by organizational level. Although it is acknowledged that traits can fulfil multiple functions (such as hydraulic efficiency [HE], hydraulic safety [HS], light interception [LI], mechanical support [MS], metabolic efficiency [ME], physical defence [PD] and seasonal stress avoidance [SSA]), here their main function is indicated.

Trait name	Abbreviation	Unit	Function	Median	Percentile		CV
					5th	95th	
Whole-tree trait							
Height	H	m	LI	9.2	4.5	17.1	0.4
Basal area	BA	cm^2	MS	263.0	87.4	660.5	0.6
Crown width	CrownW	m	LI	4.7	2.9	8.0	0.3
Crown base height	CrownH	m	LI	2.1	0.3	5.9	0.7
Crown length	CrownL	m	LI	6.4	2.8	13.1	0.5
Height diameter ratio (Slenderness)	Slender	m cm^{-1}	LI	0.5	0.3	1.1	0.4
Deciduous	Deciduous	NA	SSA				
Coniferous	Conifer	NA	-				
Branch trait							
Branching architecture	Branchy	count	LI	9.0	3.0	22.5	0.6
Branch density	BranchDen	g cm^{-3}	PD	0.5	0.3	0.7	0.2
Wood density	WoodDen	g cm^{-3}	PD	0.5	0.3	0.8	0.9
Bark density	BarkDen	g cm^{-3}	PD	0.5	0.3	0.7	0.3
Branch dry matter content	BranchDMC	NA	PD	0.5	0.3	0.6	0.2
Wood dry matter content	WoodDMC	NA	PD	0.5	0.3	0.6	0.2
Bark dry matter content	BarkDMC	NA	PD	0.4	0.3	0.6	0.2
Bark thickness	BarkThick	mm	MS	0.9	0.4	2.9	0.7
Specific branch length	SBL	cm g^{-1}	LI	4.2	1.4	11.3	0.6
Branch cross-sectional area	BranchCA	mm^2	MS	132.2	43.9	392.7	0.7
Leaf area per branch length	LABL	cm^2 cm^{-1}	LI	54.9	21.5	144.7	0.7
Leaf number per branch length	LNBL	count cm^{-1}	LI	1.7	0.3	43.6	3.3
Leaf area per xylem area	LAXA	cm^2 mm^{-2}	LI	55.5	17.0	125.6	0.6
Leaf mass fraction	LMF	g g^{-1}	LI	0.5	0.3	0.7	0.3
Leaf area ratio	LAR	cm^2 g^{-1}	LI	42.0	17.4	84.2	0.5
Bark proportion	BarkProp	NA	PD	0.4	0.2	0.6	0.3
Pith proportion	PithProp	NA	MS	0.03	0.003	0.1	1.1
Xylem proportion	XylemProp	NA	HE	0.6	0.3	0.8	0.2
Conduit diameter	ConduitDia	mm	HE	0.04	0.01	0.1	0.6
Conduit density	ConduitDen	count mm^{-2}	HS	112.6	18.7	2563.8	1.4
Conduit lumen fraction	CLF	NA	HE	0.2	0.1	0.4	0.5
Leaf trait							
Leaf area	LA	cm^2	LI	31.5	1.2	140.6	1.2
Specific leaf area	SLA	cm^2 g^{-1}	LI	82.2	40.8	143.0	0.4
Leaf thickness	LeafThick	mm	MS	0.3	0.2	0.8	0.5
Leaf dry matter content	LeafDMC	g g^{-1}	PD	0.4	0.3	0.6	0.2
Leaf density	LeafDen	g cm^{-3}	PD	0.3	0.2	0.5	0.2
Leaf chlorophyll content	Chlorophyll	µg cm^{-2}	LI	51.1	18.9	77.9	0.3
Leaf N concentration	N	%	ME	1.7	1.0	2.7	0.3
Leaf P concentration	P	%	ME	0.1	0.1	0.3	0.7
Leaf K concentration	K	%	ME	0.7	0.4	1.2	0.4
Leaf hairs	LeafHair	NA	PD				

and broadleaf tree species, with conifers characterised by a higher hydraulic safety (high conduit density and conduit lumen fraction), the formation of small needles rather than broad leaves (low leaf area, high leaf number per branch length, low leaf chlorophyll concentration and leaves without hairs but waxy cuticle) and thick ramified branches with thick bark (and consequently low specific branch length).

To further represent trait covariations and trade-offs based on their principal components, the CatPCA was used. The above-mentioned clusters were also visualized in the CatPCA (Figure 3.3). The first CatPCA axis explained 28% of the trait variation and was mainly associated with traits belonging to vertical expansion and metabolic efficiency, and partially with traits belonging to horizontal expansion and the difference between conifers and broadleaf trees (Figure 3.3). The axis showed at the left species with multiple indicators of small stature (low height, crown base height, crown length, slenderness, basal area and crown width), low light interception efficiency but high durability and safety (low leaf area, SLA, LAR and high leaf thickness), low metabolic efficiency (low leaf NPK concentrations, LAXA and LMF), low hydraulic efficiency (small conduit diameter) and high hydraulic safety (high conduit density) and species with the opposite suite of traits at the right. The axis thus represents a safety vs. efficiency spectrum and runs from species with trait values that increase safety against harsh environmental conditions and that increase resource conservation at the left to species with traits values that increase vertical and horizontal expansion through increased resource acquisition and metabolic efficiency at the right.

The second CatPCA axis explained 20% of the trait variation and was mainly associated with traits belonging to physical defence, the difference between conifers and broadleaf trees, and partially with traits belonging to horizontal expansion (Figure 3.3). The axis showed species with soft tissues (low branch, wood, bark, and, to a lesser extent, leaf density and dry matter content) and thick branches with thick bark (and thus high bark proportion and low xylem proportion) and densely packed leaves (high LNBL and LABL) at the bottom and species with the opposite suite of traits at the top. The axis thus represents a tissue toughness spectrum that runs from species with soft tissues that increase resource acquisition and growth at the bottom to species with tough tissues that increase carbon and nutrient residence times in plants (resource conservation) through enhancement of physical defence and tissue lifespan at the top. Rhododendrons with conservative traits of both CatPCA axes occupied the upper left quadrant whereas conifers with conservative traits of the first CatPCA axis and acquisitive traits of the second CatPCA axis occupied lower left quadrant. Overall, this analysis showed that 48% of the trait variation among the Himalayan tree species was jointly explained by two orthogonal strategy axes that both reflected parts of the conservative-acquisitive paradigm.

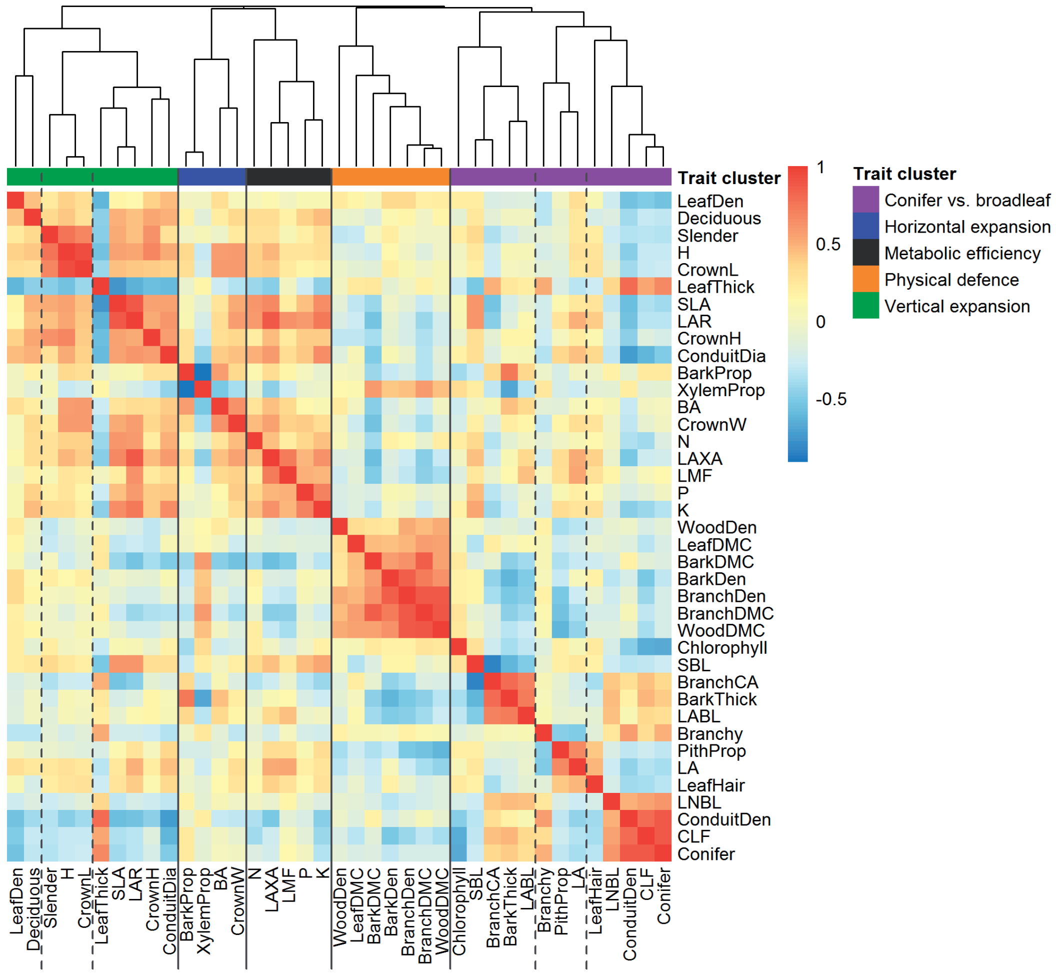
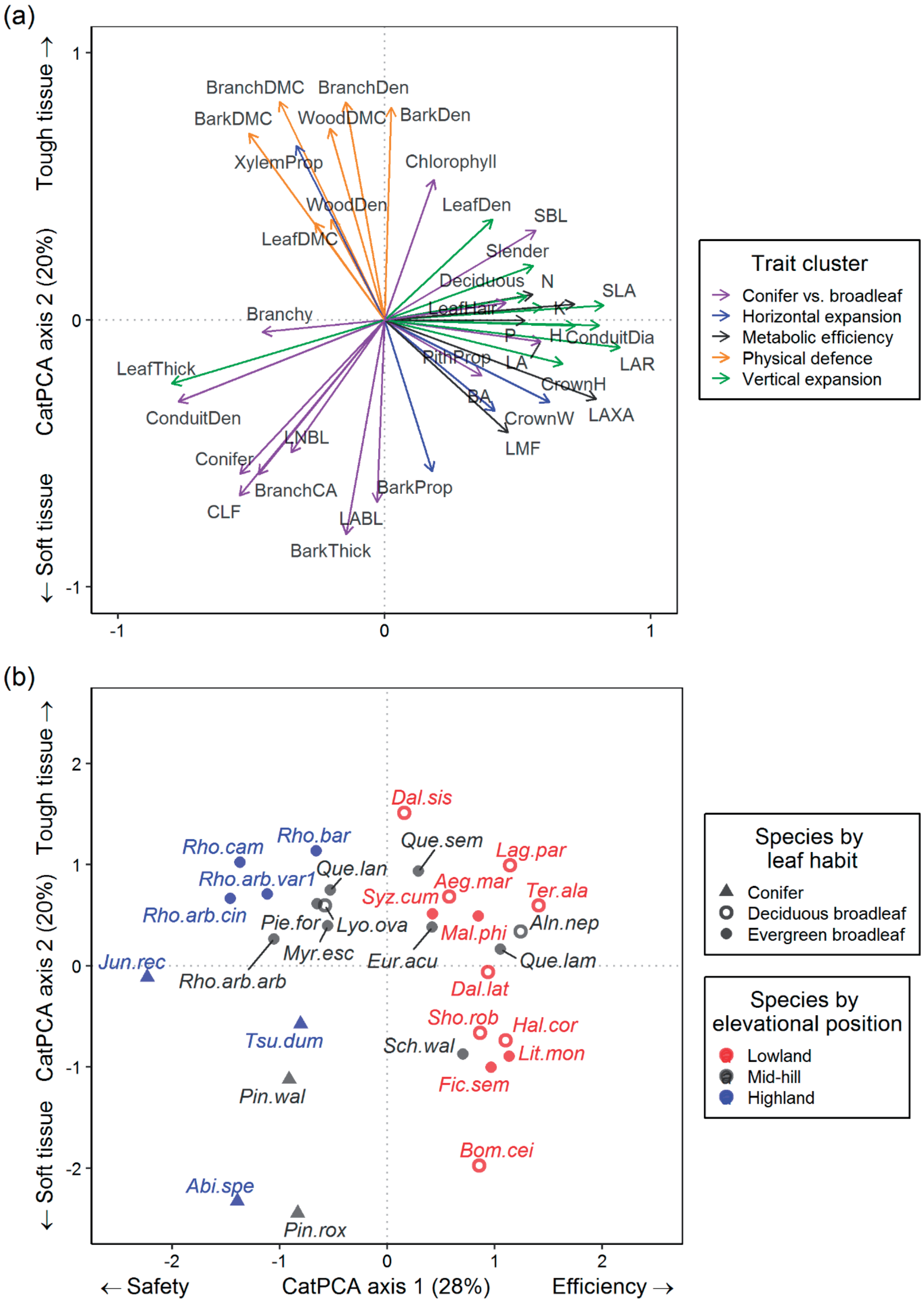


Figure 3.2. Covariance of plant functional traits (*n* = 31 species) analysed by cluster analysis (hierarchical clustering) combined with a heatmap of covariation among the 39 traits. Trait correlations are indicated using colours, warm shades indicate positive correlation and cool shades indicate negative correlation. The distance tree of traits derived from hierarchical clustering is illustrated on the top. Five resulting clusters are: 1. vertical expansion cluster comprising leaf density, deciduousness, slenderness, height, crown length, leaf thickness, SLA, LAR, crown base height and conduit diameter; 2. horizontal expansion cluster comprising bark proportion, xylem proportion, basal area and crown width; 3. metabolic efficiency cluster comprising leaf N concentration, leaf area per xylem area, leaf mass fraction, leaf P concentration and leaf K concentration; 4. physical defence cluster comprising wood density, leaf dry matter content (DMC), bark DMC, bark density, branch density, branch DMC and wood DMC; and 5. conifer vs. broadleaf cluster comprising leaf chlorophyll content, specific branch length, branch cross sectional area, bark thickness, leaf area per branch length, branchiness, pith proportion, leaf area, leaf hair, leaf number per branch length, conduit density, conduit lumen fraction and coniferousness.


(a)
Tough tissue →
CatPCA axis 2 (20%)
← Soft tissue
1
0
-1
-1
0
1
BranchDMC
BranchDen
BarkDMC
WoodDMC
BarkDen
XylemProp
Chlorophyll
WoodDen
LeafDen
SBL
LeafDMC
Slender
Deciduous
N
SLA
LeafHair
K
Branchy
P
H
ConduitDia
LeafThick
PithProp
LA
LAR
CrownH
ConduitDen
BA
CrownW
LAXA
LNBL
LMF
Conifer
BranchCA
BarkProp
CLF
LABL
BarkThick
Trait cluster
Conifer vs. broadleaf
Horizontal expansion
Metabolic efficiency
Physical defence
Vertical expansion
(b)
Tough tissue →
CatPCA axis 2 (20%)
← Soft tissue
2
1
0
-1
-2
-2
-1
0
1
2
← Safety
CatPCA axis 1 (28%)
Efficiency →
Dal.sis
Rho.bar
Que.sem
Lag.par
Rho.cam
Que.lan
Aeg.mar
Rho.arb.var1
Syz.cum
Ter.ala
Rho.arb.cin
Pie.for
Lyo.ova
Mal.phi
Aln.nep
Myr.esc
Eur.acu
Que.lam
Jun.rec
Rho.arb.arb
Dal.lat
Sho.rob
Hal.cor
Tsu.dum
Sch.wal
Lit.mon
Fic.sem
Pin.wal
Bom.cei
Abi.spe
Pin.rox
Species by leaf habit
Conifer
Deciduous broadleaf
Evergreen broadleaf
Species by elevational position
Lowland
Mid-hill
Highland

< Figure 3.3. Covariance of plant functional traits (*n* = 31 species) analysed by categorical principal component analysis (CatPCA). (a) Trait loadings along the first two CatPCA axes. Arrows are coloured according to trait clusters identified by the cluster analysis (Figure 3.2). For trait abbreviations, see Table 3.1. (b) Species scores along the first two CatPCA axes. Species are represented by different symbols and colours according to their leaf habits and elevational positions. Species name abbreviations are based on the first three letters of their genus, species and variety names, wherever applicable. For the complete list of study species see Table S3.1. CatPCA axis 1 explains 28% of trait variation and CatPCA axis 2 20%.

3.3.3 Trait-elevation relationships

To evaluate how plant traits and strategies are associated with elevation a bivariate correlation analysis was used. Similar results were obtained from parametric (Pearson) and nonparametric (Spearman) correlation analyses (Table 3.2). Because parametric analysis is a more powerful test and it is therefore easier to detect significance, we used the results from parametric analysis for further discussion. Pearson correlations were significant for 22 of 39 traits/strategy axes (56%) and phylogenetic correlations for 23 traits/strategy axes (59%), indicating that many ecological and evolutionary relationships with elevation are found. Yet, for only 10 cases, both present-day and evolutionary correlations are significant, indicating that they tell partly complementary stories. As our research question focuses on ecological relations (i.e. how do traits determine present-day distributions), we focused our discussion mainly on the regular cross-species correlations. The first CatPCA axis that reflects a trade-off between safety and efficiency was strongly negatively correlated with elevation (Pearson's $r = -0.81$, $p < 0.001$, Table 3.2, Figure 3.4), which is also confirmed by the phylogenetic correlation ($r = -0.39$, $p < 0.05$). This multivariate strategy axis was more strongly related to elevation than the individual traits (Table 3.2, Figure 3.4). This, in turn, indicates that stress-tolerant species (such as Rhododendrons and conifers) are found at high elevations whereas efficient species are found at low elevations (Figure 3.3). The second CatPCA axis that reflects trade-off between soft and tough tissues was not significantly correlated with elevation (Pearson's $r = 0.11$, Table 3.2, Figure 3.4).

3.3.4 Traits that best predict tree species positions along Himalayan elevational gradient

To identify plant traits that best predict the position of species along the Himalayan elevational gradient an all subsets regression analysis was used. The analysis of two shortlisted parsimonious models showed that basal area, conduit diameter, LAXA and SBL had an importance value of 1 and were selected by all models. Crown width was selected by only one model and was therefore less important and not significant (Table 3.3). All selected traits except for crown width were negatively associated with the elevational position of species, indicating that lower basal area, conduit diameter, LAXA and SBL characterise high elevation species (Table 3.3). The analysis showed that the whole-tree traits (basal area) and the branch traits (conduit diameter, LAXA and SBL) are more

Table 3.2. Bivariate relationships between species scores along the first two CatPCA axes and traits and elevation for 31 Himalayan tree species. Correlation coefficients in bold are significant at p <0.05, those in bold and italic are significant at p <0.01, and those in bold and underlined are significant at p <0.001. Variance inflation factor (VIF) as an indicator of severity of multicollinearity among the selected traits (two traits per cluster) with highest correlation to elevation are also shown. For trait abbreviations, see Table 3.1. Traits are grouped by clusters. Phylogenetically independent correlation (PIC) coefficients for 29 Himalayan tree species (without two *Rhododendron arboreum* varieties) are also shown.

Strategy axis and trait	Correlation with elevation		PIC	VIF
	Pearson's *r*	Spearman's *r*		
CatPCA axis 1	**-0.81**	**-0.74**	**-0.39**	
CatPCA axis 2	0.11	0.13	**0.80**	
Vertical expansion				
Height	***-0.49***	***-0.51***	**-0.81**	
Crown base height	**-0.59**	**-0.57**	-0.28	
Crown length	-0.34	***-0.50***	**-0.79**	
Height diameter ratio (Slenderness)	-0.19	-0.17	**-0.61**	
Deciduous	**-0.63**	**-0.67**	-0.17	
Leaf area ratio	**-0.75**	**-0.74**	-0.30	8.50
Conduit diameter	**-0.79**	**-0.73**	-0.34	4.42
Specific leaf area	**-0.68**	**-0.67**	0.36	
Leaf thickness	**0.64**	**0.79**	***-0.52***	
Leaf density	**-0.44**	-0.35	0.06	
Conifer vs. broadleaf				
Coniferous	**0.37**	**0.36**	0.05	
Branching architecture	0.34	0.22	-0.003	
Bark thickness	-0.05	0.01	**-0.77**	
Specific branch length	***-0.49***	***-0.51***	**0.63**	1.83
Branch cross-sectional area	0.25	0.32	**-0.81**	
Leaf area per branch length	-0.16	-0.15	**-0.80**	
Leaf number per branch length	0.26	0.17	-0.01	
Pith proportion	-0.19	-0.02	0.24	
Conduit density	**0.66**	**0.66**	***0.57***	3.31
Conduit lumen fraction	**0.38**	**0.42**	-0.23	
Leaf area	**-0.39**	-0.29	0.06	
Leaf chlorophyll content	0	0.08	**0.67**	
Leaf hairs	-0.15	-0.11	0.28	
Metabolic efficiency				
Leaf area per xylem area	**-0.76**	**-0.72**	***-0.50***	5.25
Leaf mass fraction	**-0.46**	**-0.42**	**-0.70**	
Leaf N concentration	**-0.42**	***-0.47***	**0.82**	
Leaf P concentration	***-0.46***	***-0.46***	0.37	
Leaf K concentration	**-0.59**	**-0.60**	**-0.71**	3.36
Physical defence				
Branch density	0.07	-0.03	**0.42**	
Wood density	0.03	0.02	-0.22	
Bark density	0.10	0.01	**0.73**	
Branch dry matter content	0.35	0.25	**0.59**	4.82
Wood dry matter content	0.08	-0.01	**0.75**	
Bark dry matter content	***0.55***	***0.51***	*-0.40*	6.88
Leaf dry matter content	0.03	0.12	***-0.54***	
Horizontal expansion				
Basal area	***-0.56***	**-0.58**	**-0.87**	2.32
Crown width	***-0.49***	***-0.56***	0.01	2.37
Bark proportion	-0.34	-0.34	**-0.86**	
Xylem proportion	**0.42**	**0.39**	**0.87**	

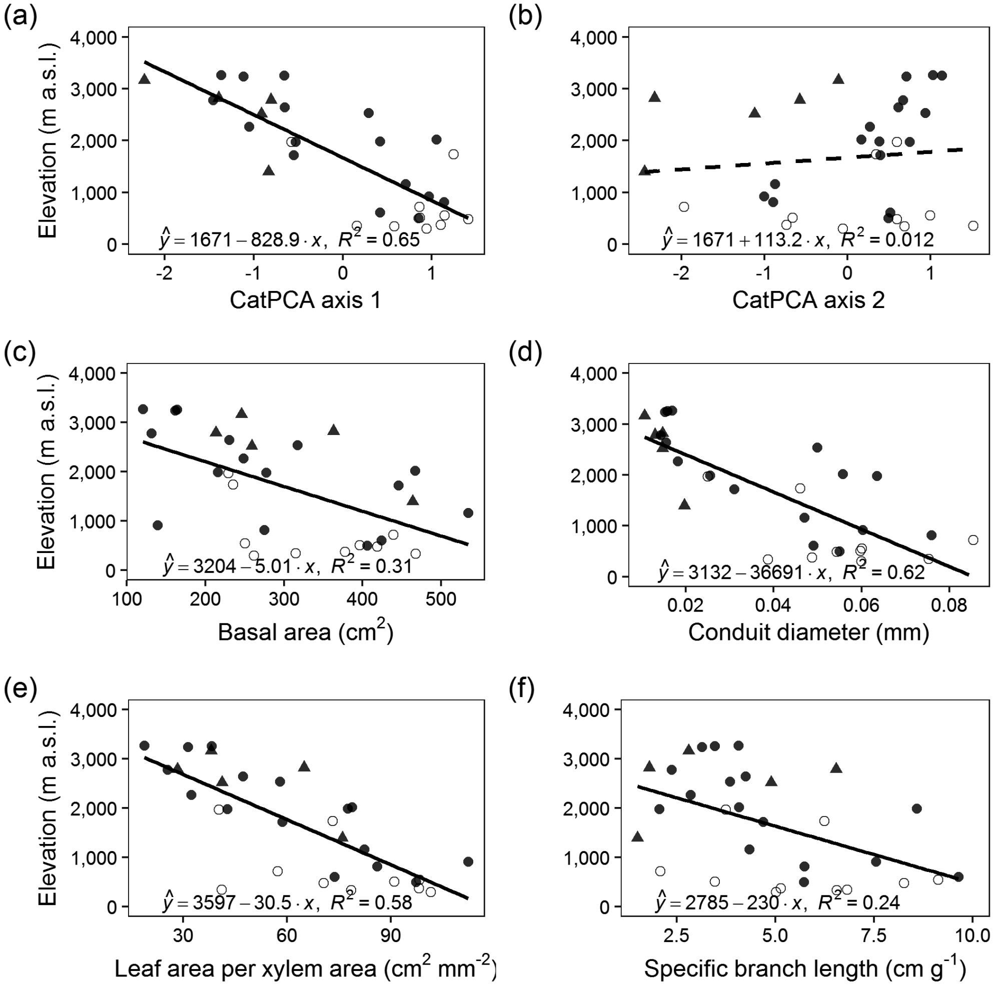


Figure 3.4. Scatterplots showing bivariate relationships between species scores along first two CatPCA axes: (a) CatPCA axis 1 and (b) CatPCA axis 2 and the selected traits: (c) basal area, (d) conduit diameter, (e) leaf area per xylem area and (f) specific branch length and elevation for 31 Himalayan tree species. Symbols indicate different functional tree groups (conifer species: filled triangles; broadleaved deciduous species: open circles; and broadleaved evergreen species: filled circles). Regression lines and coefficients of determination (R^2) are shown. Solid regression lines are significant at $p < 0.05$.

important for predicting the position of species along Himalayan elevational gradient than the leaf traits (K and LAR). The PIC also confirmed that these traits were significantly related to elevation (Table 3.2), indicating that these traits reflect evolutionary adaptations. Only for specific branch length, the direction of the correlation changed from a negative correlation with elevation for the cross-species correlation to a positive correlation with elevation for the PIC.

Table 3.3. The selected models (models with ΔAICc <2) predicting the effects of traits on species' position along the elevational gradient. All models are significant at p <0.001. Regression coefficients in bold are significant at p <0.05, those in bold and italic are significant at p <0.01, and those in bold and underlined are significant at p <0.001. Number of model parameters (*df*), Log-likelihood (logLik) values, AIC with small sample bias adjustment (AICc), AICc difference from the best model (ΔAICc), model weight (Weight) and adjusted coefficients of determination (adj.R^2) for the selected models and average regression coefficients (Avg) and importance value for individual predictors (Imp) are shown. For trait abbreviations, see Table 3.1.

Variables	Model 1	Model 2	Average	Importance value
Intercept	3.76E-17	8.10E-17	5.93E-17	
Basal area	**-0.25**	**-0.32**	**-0.28**	1.00
Bark dry matter content				
Branch dry matter content				
Conduit density				
Conduit diameter	**-0.45**	**-0.46**	**-0.45**	1.00
Crown width		0.13	0.13	0.27
Leaf K concentration				
Leaf area ratio				
Leaf area per xylem area	**-0.29**	**-0.32**	**-0.30**	1.00
Specific branch length	**-0.23**	**-0.23**	**-0.23**	1.00
df	6	7		
logLik	-16.63	-15.93		
AICc	48.77	50.73		
ΔAICc	0.00	1.96		
weight	0.12	0.05		
adj.R^2	0.80	0.80		

3.4 Discussion

We evaluated what plant strategies can be distinguished among Himalayan tree species, how plant traits and strategies are associated with elevation, and what plant traits best predict the tree species' positions with elevation. We found two orthogonal strategy axes among Himalayan tree species, the first axis showing a trade-off between multiple safeties and efficiencies and the second axis showing a trade-off between soft and tough tissues. The first strategy axis was tightly linked to elevation, showing that species with a trait values that increase safety against harsh environmental conditions and that increase resource conservation are found at high elevations. Four traits best predicted the tree species' positions with elevation, indicating that species from high elevations tend to be small, have narrow conduits, a relatively low leaf area per xylem area and specific branch length. Below, we discuss the underlying mechanisms.

3.4.1 Key plant strategies among Himalayan trees species

We hypothesized that trait variation among Himalayan tree species could be described by a single strategy axis, running from an acquisitive to a conservative strategy. Instead, we found two orthogonal strategy axes (Figure 3.3) that both reflected parts of the conservative-acquisitive paradigm, and that jointly explained nearly 50% of trait variation among Himalayan tree species. The first axis was mainly associated with traits belonging to vertical expansion and metabolic efficiency clusters, and reflected a trade-off between multiple safeties and efficiencies. At the left are the species with small stature, small and thick leaves with low nutrient concentrations, and many narrow (cavitation resistant) conduits, which would allow them to persist under harsh environmental conditions, such as cold, dry, exposed windy environments and nutrient-poor soils. At the right are the species with large stature, large and thin leaves with high nutrient concentrations and wide conduits, which would allow them to compete efficiently for light under benign conditions, such as warm, wet environments and nutrient-rich soils. The second axis was mainly associated with traits belonging to physical defence and the difference between conifers and broadleaf trees clusters, and reflected a trade-off between soft and tough tissues. At the bottom are the conifers with soft tissues and thick branches with thick bark. The thick branches would compensate for soft wood tissue to produce stable branches and the thick bark would protect soft wood tissue against insects by serving as a physical outer defence layer (Franceschi et al., 2005). At the top are the Rhododendrons with tough tissues, which would allow them to persist under harsh conditions, such as cold temperatures. Since tough tissues are assumed to enhance tissue longevity and nutrient residence time in plants (Hodgson et al., 2011; Onoda et al., 2011), theoretically, the second strategy that represents tissue toughness should align with the first strategy axis that represents variation in leaf nutrient concentrations. The uncoupling of the two strategy axes could just be the result of a phylogenetic split between conifers and Rhododendrons, as discussed further below. Díaz et al. (2016) analysed world-wide variation in six major plant traits and revealed the existence of two independent spectra: plant size and leaf economics. Probably because we looked only at trees (large size vascular plants), these spectra aligned closely together in our case. It also suggests that when zooming in a single life form, different strategy spectra can emerge (such as the second axis on tissue toughness).

3.4.2 Trait-elevation relationships

We hypothesized that harsh environmental conditions at higher elevations select for species with conservative trait values and that the relatively benign environmental conditions at lower elevations select for species with acquisitive trait values. Indeed, the first strategy axis that reflects a trade-off between multiple safeties and efficiencies was negatively associated with elevation. This multivariate strategy axis was more strongly related to elevation than the individual traits, indicating that it is the combination of traits that is important, rather than the individual traits, which is in line with the common notion that harsh environmental conditions and lower resource availability at high elevations promote stress-tolerant species.

Traits related to safety and persistence. The tolerant species at the left of the axis have a competitive advantage in relatively harsh highland environments, where productivity is low, the stands are relatively open, and where there is less competition for light. This is also reflected in the correlation between individual traits and species elevation (Table 3.2). Small size (e.g. tree height and basal area) is often observed at highlands (Table 3.2, cf. Körner, 2016; Mao et al., 2018) and results from growth limitations due to lower temperatures and/or a shorter growing season. Moreover, the small plant sizes reduce the wind-induced drag forces and minimise risks of physical damage with stronger wind in highlands (Onoda & Anten, 2011). Small and/or thick leaves (low SLA, Table 3.2) can protect photosynthetic system against high UV-B radiation (Turunen & Latola, 2005), which often increases with clear-sky conditions at higher elevations (Körner, 2007). Low leaf nutrient concentrations and an evergreen leaf habit increase nutrient residence times in highland species (Table 3.2), and may allow them to persist on nutrient-poor soils (Drollinger et al., 2017). Additionally, evergreen leaves can be freezing resistant through frost hardening at the end of summer (Neuner et al., 2020). Narrow tracheids (in case of the conifers) or narrow vessels (in case of the angiosperms) at high elevation (Table 3.2) may allow highland species to recover from freezing-induced cavitation and to better persist under cold conditions (Hacke & Sperry, 2001). Trees at highlands had less leaves on their branches (lower LAR, Table 3.2), thus contributing to more open forest canopy and reducing the level of competition for light at highlands (Coomes & Allen, 2007). This suggests that in overall, under the harsh highland conditions, investment in efficiency traits would not pay off, simply because growth is constrained by poor growing conditions rather than by the growth potential of the plants. Similar conclusion has been drawn by Macek et al. (2012) for alpine plants in Ladakh, NW Himalaya.

Traits related to efficiency. In contrast, the efficient species at the right of the first axis have a competitive advantage in relatively benign lowland environments, where productivity is high, the stands are relatively dense, and where there is high competition for light. Large size (e.g. tree height and basal area) and an efficient height growth (e.g. stem slenderness) enable lowland species to compete effectively for light (Coomes & Allen, 2007). An efficient leaf display (high SLA and LAR) increases their ability to capture light. A high metabolic efficiency (high leaf N, P and K) increases the capacity for photosynthesis, energy transport and growth (Wang et al., 2018). Wide conduits facilitate efficient water uptake to meet high photosynthetic capacity and high transpiration rates in lowland tropics (Sterck et al., 2014). The wider conduits may, however, make those trees more vulnerable to drought (or frost) induced cavitation (Olson et al., 2018; Pittermann & Sperry, 2006). Interestingly, a deciduous leaf habit was associated with the efficiency strategy, probably because Himalayan tree species experience a dry winter and may avoid freezing- and drought-induced xylem cavitation by dropping leaves. Overall, the first strategy axis thus shows how tree species coordinate their traits across organization levels (from leaves and wood to branch and whole tree) along an elevation gradient, consistent with our hypothesis that higher elevations limit plant performances while benign environmental conditions at lower elevations provide opportunities for plants to realise their growth potential.

Successful clades at high elevations; Gymnosperms vs. Rhododendrons. The second strategy axis, which reflects a trade-off between soft and tough tissues, was independent from elevation. At high-elevations (Figure 3.3), two large clades, the Gymnosperms and the Rhododendrons, represented this trade-off. The Gymnosperms are characterised by soft wood. Unlike Angiosperms, the Gymnosperms lack fibres (which tend to be relatively heavy) resulting in soft wood tissue (Bowes & Mauseth, 2008; Zhang et al., 2020). These soft tissues lack physical strength, and the Gymnosperms may compensate for their soft wood tissue by producing relatively thick and therefore stable branches. Soft wood is also more prone to pests and pathogen attack. Conifers may protect their soft wood against insects by making a relatively thick bark that serves as a physical outer defence layer (Franceschi et al., 2005). Rhododendrons, on the other hand, are characterised by the opposite suite of traits; they produce tough wood, bark and leaf tissues with a high density and dry matter content. Rhododendrons originate from the cool temperate zone (Shrestha et al., 2018), and have currently their main distribution in the mountains, with a centre of diversity in the Himalayas where 80% of all Rhododendrons occur (Ming & Fang, 1990). Tough tissues and thick leaves may protect Rhododendrons from membrane damage by freezing.

Mid and low elevations; a multitude of strategies and niches. Unlike at high elevations, the pattern is not obvious at mid and low elevations. Remarkably, many species at mid and low elevations are light demanders (e.g. *D. sisso*, *Bombax ceiba*) suggesting that many of the mid- and low-elevation forests are disturbed and are under high anthropogenic pressure (Chaudhary et al., 2016), thus creating opportunities for light-demanding species. Many of them are deciduous (Figure 3.3) and curiously, many species have a high wood density (>800 kg m^{-3}, e.g. *Dalbergia latifolia*, *Lagerstroemia parviflora*, *Quercus* species, *Shorea robusta and Terminalia alata*), which is not in line with the general idea of light demanders that need to grow rapidly to compete for light (Chen et al., 2017). In Nepal, the frost line occurs as low as 1,000 m a.s.l. elevation (Lillesø et al., 2005), wildfires are common in the region (Bhujel et al., 2017), and soils do differ strongly along the elevational transect not only in terms of soil depth but also other physical and chemical properties (FAO, 2015). Perhaps for this reason the species also differed a lot in their frost tolerance (e.g. *Quercus* species are frost resistant whereas *A. marmelos* and *D. latifolia* are frost sensitive), shade tolerance (e.g. *Q. lamellosa* and *Schima wallichii* are shade tolerant) and fire resistance (e.g. *T. alata* is fairly fire tolerant whereas *F. semicordata* is easily killed by fire), and occupied contrasting soils (e.g. *D. sisso and B. ceiba* prefer alluvial soils while *D. latifolia* prefers deep loam soils). These mid- and low-elevation species thus do not align in a straightforward way with the species strategy spectra presented in the literature (e.g. conservative vs. acquisitive or shade tolerant vs. light demander). Our results therefore suggest that, because climatic constraints are relaxed, mid and low elevations could provide a multitude of niches occupied by different species, with a variety of traits. Analysis zooming in at small spatial scales should reveal if and how these traits are linked to these different niches at lower elevations.

3.4.3 Traits that best predict tree species positions along Himalayan elevational gradient

Of the 39 traits analysed, only a small subset of four traits were significant and included in the best models to predict the elevational distribution of Himalayan tree species (Table 3.3; Figure 3.4). These traits indicate a key role of tree size (basal area), hydraulic efficiency (conduit diameter), the efficiency of leaf display (LAXA) and expansion at the branch level (SBL). Tree species with smaller size (i.e. smaller stem basal area) occupy higher elevations (Figure 3.4c), in line with the stronger growth limitations, whereas species with bigger size and taller stem occupy lower elevations, to compete efficiently for light (Coomes & Allen, 2007; Mao et al., 2018). A reduced conduit diameter with increasing elevation (Figure 3.4d) allows plant species to avoid freezing-induced cavitation (Pittermann & Sperry, 2006), whereas a concomitant increase in conduit density would allow continued plant functioning while some conduits cavitate (García-Cervigón et al., 2020). In combination, this would ensure increased hydraulic safety at higher elevations, whereas an increased hydraulic efficiency (wide conduit diameter) facilitates water transport and growth at low elevations (Sterck et al., 2014).

Leaf display efficiency (LAXA) had a negative effect on the elevational position of tree species (Figure 3.4e), indicating that highland species are less efficient in leaf display. This seems to contrast with the need for more leaf area to compensate for poorer photosynthetic conditions at higher elevations (e.g. lower temperature, higher UV-B radiation, lower atmospheric CO_2 partial pressure; Anfodillo et al., 2016). However, the metabolic costs of living tissues may also be lower in the highlands (Laiolo & Obeso, 2017), thus compensating for a lower efficiency in CO_2 uptake. Instead, the larger efficiency in leaf display and branch expansion (specific branch length) at lower elevations (Figure 3.4f) suggest that increased light competition at lower elevations largely structures tree species positions along the elevation gradient.

Interestingly, leaf traits (K and LAR) had little effect on species elevational positions, which suggests that for perennial plants along this harsh environmental gradient, traits at higher integration levels (i.e. plant-level and branch-level traits) are more important for plant performance than traits at lower integration level (i.e. leaf traits).

In conclusion, multiple trade-offs in plant size, hydraulics and light competitiveness shape species distribution along the elevational gradient. Himalayan tree species show a major strategy spectrum running from conservative species to acquisitive species. This strategic transition and underlying traits (tree size, conduit diameter and leaf display) and/or clusters (vertical expansion and metabolic efficiency) are tightly linked to elevation, showing that species with trait values that increase safety against harsh environmental conditions and that increase resource conservation are found at high elevations.

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Supporting information

Table S3.1. Complete list of tree species selected for this study. Species names and their respective families, leaf habits (deciduous [D] or evergreen [E]), leaf hairiness (without hair [N] or with hair [Y]), leaf types (broadleaf [B] or conifer [C]) and mean elevations calculated based on elevation data from wide network of permanent plots established by Forest Research and Training Centre (then Department of Forest Research and Survey), Nepal (DFRS, 2015) are shown.

Species name	Family	Leaf habit	Leaf hair	Leaf type	Mean elevation (m a.s.l.)
Abies spectabilis (D.Don) Mirb.	Pinaceae	E	N	C	2821.60
Aegle marmelos (L.) Corrêa	Rutaceae	D	N	B	344.17
Alnus nepalensis D.Don	Betulaceae	D	N	B	1741.72
Bombax ceiba L.	Bombacaceae	D	N	B	726.52
Dalbergia latifolia Roxb.	Fabaceae	D	N	B	303.59
Dalbergia sissoo DC.	Fabaceae	D	N	B	353.97
Eurya acuminata DC.	Theaceae	E	Y	B	1989.03
Ficus semicordata Buch.-Ham. ex Sm.	Moraceae	E	Y	B	921.01
Haldina cordifolia (Roxb.) Ridsdale	Rubiaceae	D	Y	B	377.49
Juniperus recurva Buch.-Ham. ex D.Don	Cupressaceae	E	N	C	3162.60
Lagerstroemia parviflora Roxb.	Lythraceae	D	N	B	556.37
Litsea monopetala (Roxb.) Pers.	Lauraceae	E	Y	B	818.79
Lyonia ovalifolia (Wall.) Drude	Ericaceae	D	N	B	1972.20
Mallotus philippensis (Lam.) Müll.Arg.	Euphorbiaceae	E	Y	B	501.63
Myrica esculenta Buch.-Ham. ex D.Don	Myricaceae	E	N	B	1720.48
Pieris formosa (Wall.) D.Don	Ericaceae	E	N	B	2644.88
Pinus roxburghii Sarg.	Pinaceae	E	N	C	1398.54
Pinus wallichiana A.B.Jacks.	Pinaceae	E	N	C	2518.70
Quercus lamellosa Sm.	Fagaceae	E	Y	B	2019.27
Quercus lanata Sm.	Fagaceae	E	Y	B	1978.08
Quercus semecarpifolia Sm.	Fagaceae	E	Y	B	2538.39
Rhododendron arboreum Sm.	Ericaceae	E	N	B	2272.32
Rhododendron arboreum var. *cinnamomeum* (Wall. ex G.Don) Lindl.	Ericaceae	E	N	B	2781.73
Rhododendron arboreum variety1	Ericaceae	E	N	B	3242.95
Rhododendron barbatum Wall. ex G.Don	Ericaceae	E	Y	B	3257.07
Rhododendron campanulatum D.Don	Ericaceae	E	N	B	3264.10
Schima wallichii (DC.) Korth.	Theaceae	E	Y	B	1163.38
Shorea robusta Gaertn.	Dipterocarpaceae	D	N	B	511.26
Syzygium cumini (L.) Skeels	Myrtaceae	E	N	B	609.22
Terminalia alata Roth	Combretaceae	D	Y	B	488.56
Tsuga dumosa (D.Don) Eichler	Pinaceae	E	N	C	2786.18

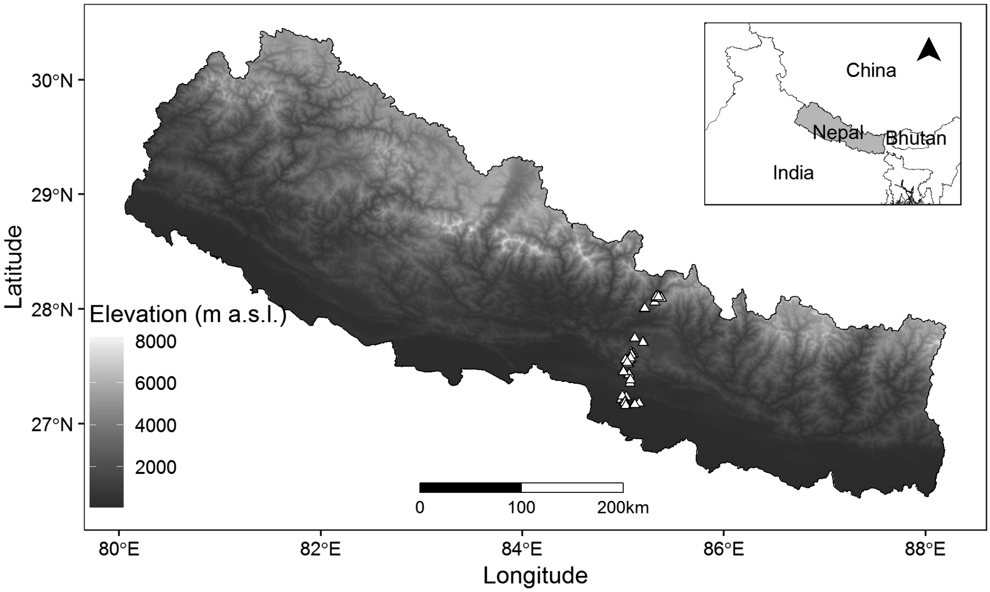

Figure S3.1. Map of the study area. Grey shades represent elevation of the study area, lighter the shade higher the elevation. White triangles represents the locations of sample trees. The inset shows the location of Nepal amongst the neighbouring countries. The black line indicates national boundary of Nepal. The Government of Nepal published on 20th May 2020 a new political map including Kalapani, Lipulekh and Limpiyadhura inside the Nepal borders. As our research started in 2016, in our research, we used the previous version of the map without these territories.

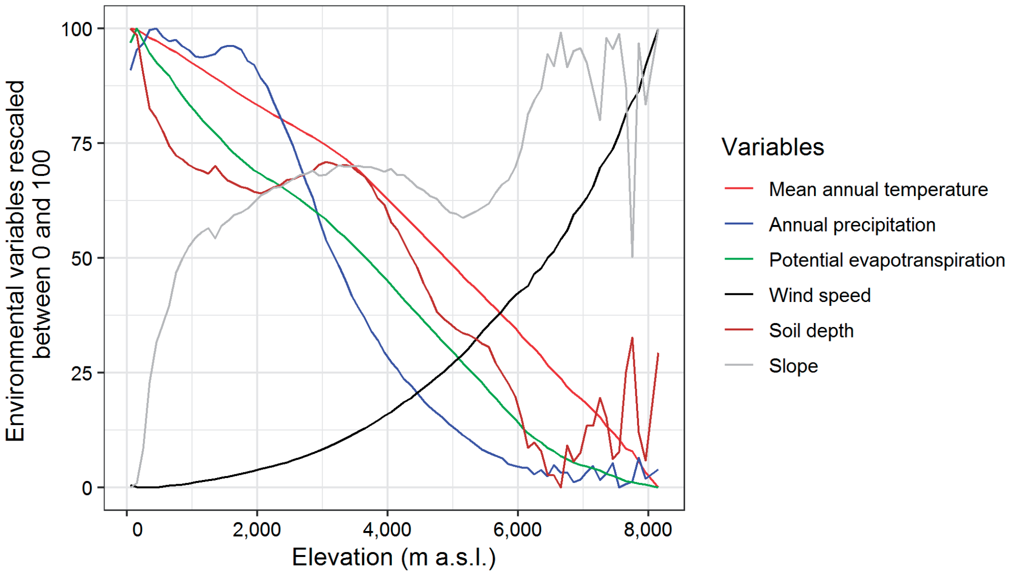

Figure S3.2. Changes in mean annual temperature, annual precipitation, potential evapotranspiration, wind speed, soil depth and slope along the elevational gradient. The graph indicates changes along the entire Himalayan elevational gradient. The study gradient is subset of the Himalayan elevational gradient. Here mean values of environmental variables for 100 m elevational belts rescaled between 0-100 are plotted against elvation (for data sources see Chapter 2).

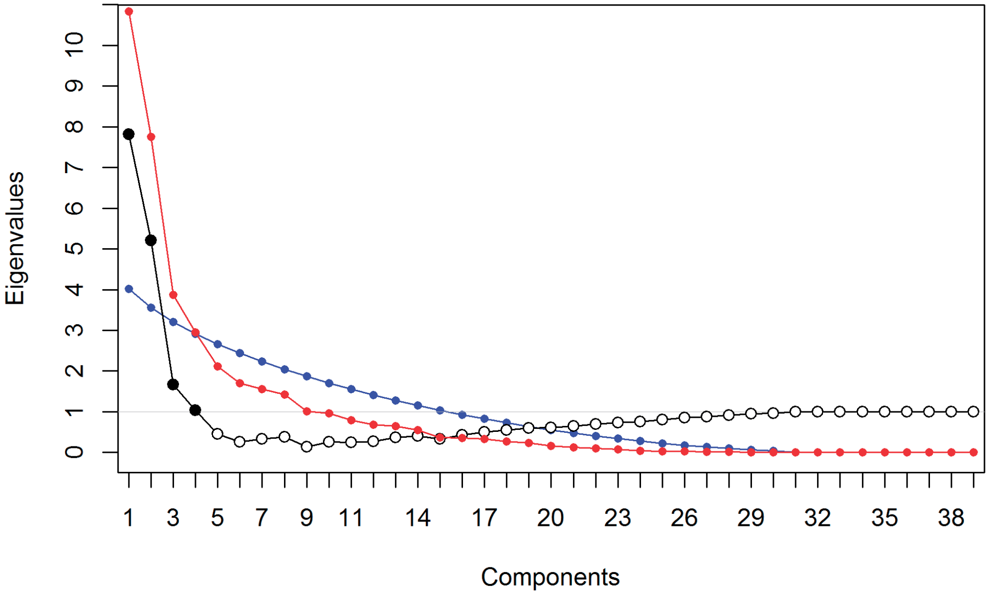

Figure S3.3. Number of components to retain in a categorical principal component analysis (CatPCA) analysed using Horn's parallel analysis. Colours of eigenvalue curves indicate methods used for their calculation (red: eigenvalues calculated based on 39 plant functional traits of 31 Himalayan tree species; black: aforementioned eigenvalues adjusted to their sample size; and blue: mean eigenvalues of the components calculated based on random datasets). Horizontal grey line indicate threshold of 1 and components with eigenvalues lower than threshold value are marked with open circles in black eigenvalue curve. Components with eigenvalues greater than mean eigenvalues i.e. two components in black eigenvalue curve above blue eigenvalue curve are retained in the CatPCA.

CHAPTER

4

Climate change induced elevational range shifts of Himalayan tree species

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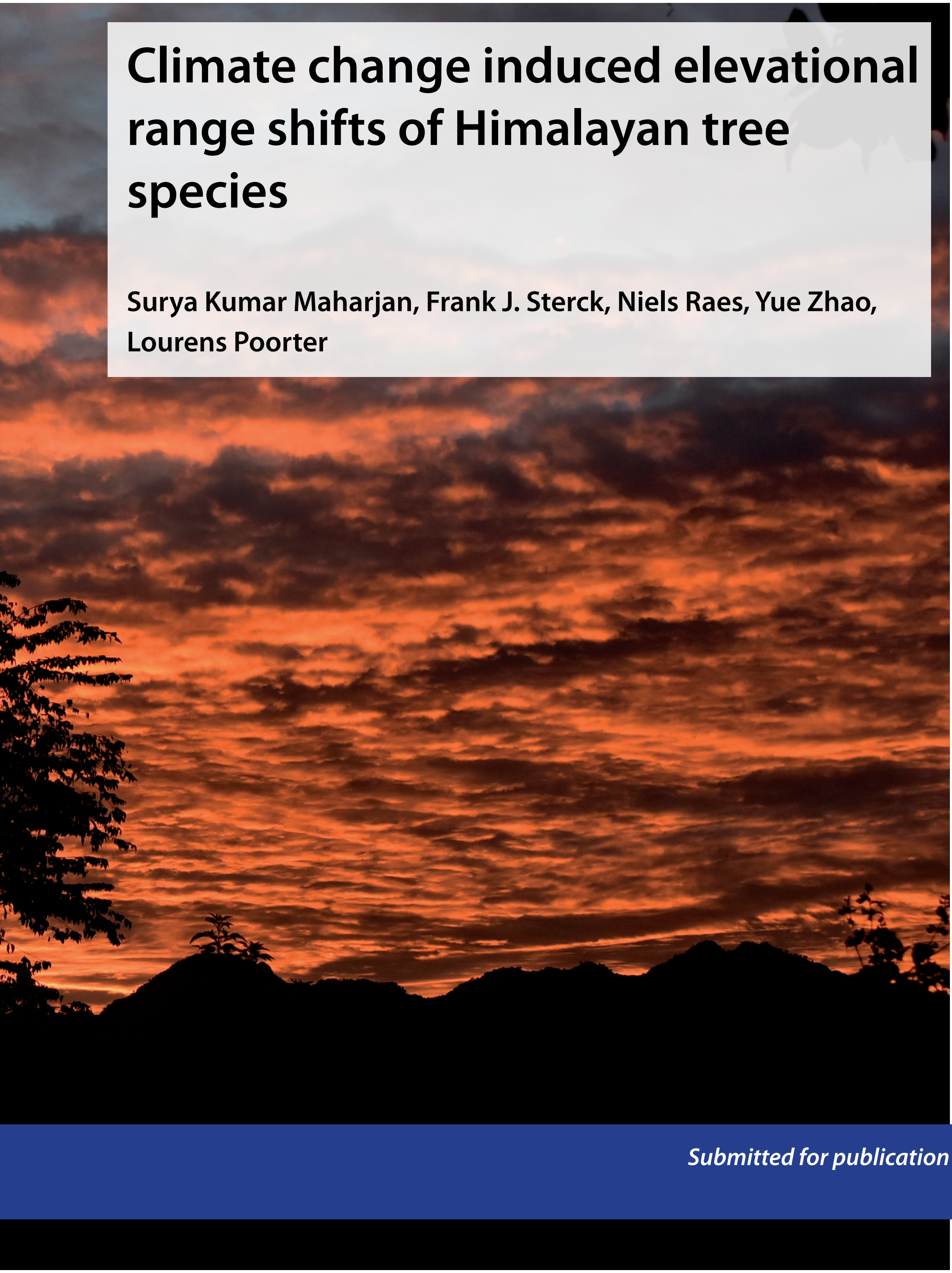

Submitted for publication

Abstract

Global warming may force montane tree species to shift upward to keep pace with their shifting climate niche. How species differences in such distribution shifts depend on their elevational positions, elevation-dependent warming rates and other environmental constraints or plant functional traits is poorly understood. Here we analysed for 137 Himalayan tree species how distribution shifts vary with elevational niche positions, environmental constraints and their functional traits. We developed ecological niche models using MaxEnt by combining species survey and botanical collections data with 19 environmental predictors. Species distributions were projected to 1985 and 2050 conditions, and elevational range parameters and distribution areas were derived from these maps. On average, species are predicted to shift 3 m yr^{-1} in optimum elevation, and have a 33% increase in distribution area. Highland species showed faster predicted elevational shifts than lowland species. Lowland and highland species are predicted to expand in distribution area unlike mid-elevation species that are predicted to contract in distribution area. Tree species for which species distribution models are driven by responses to temperature, precipitation (specifically aridity) or soil clay content showed the strongest predicted upslope shifts. Tree species with conservative trait values (i.e. narrow conduits) showed larger predicted upslope shifts than species with wide conduits. The predicted average upslope shift in maximum elevation (8 m yr^{-1}) is >2 times faster than the current observations indicating that many species will not be able to track climate change and potentially go extinct, unless they are supported by active conservation measures, such as assisted migration.

Keywords: assisted migration, climate change velocity, elevational gradient, elevation dependent warming, plant functional traits, MaxEnt, Nepal, species distribution modelling

4.1 Introduction

The global climate is changing at an unprecedented rate, with adverse effects on species, their interactions and entire ecosystems (IPCC, 2014; Nunez et al., 2019). Species are expected to track their preferred climatic niches and shift their distribution ranges (i.e. climate change induced species range shift, Bellard et al., 2012; Lenoir & Svenning, 2015; Tingley et al., 2009). With rising temperatures, species are bound to shift either upslope to higher elevations or poleward to higher latitudes (Lenoir et al., 2008; Morueta-Holme et al., 2015). Studies from the Himalayas (He et al., 2019), Andes (Feeley et al., 2011), Alps (Geppert et al., 2020) and Pyrenees (Marshall et al., 2020) have shown that many species are indeed shifting upslope to cooler elevations in response to rising temperatures. However, relatively few studies have assessed how shifts in distribution ranges of species vary with their niche positions along the elevational gradient and whether this is associated with plant functional traits (Estrada et al., 2016; Pacifici et al., 2017; Zu et al., 2021). Understanding the influence of species niche positions and traits on species elevational range shift potentials will be crucial to predict the future of species under climate change and to design appropriate conservation and climate adaptation measures.

With rising temperatures, species survival ultimately will depend on species' ability to keep pace with their shifting climate niche. To represent an instantaneous local velocity along Earth's surface needed to keep pace with rising temperatures, Loarie et al. (2009) introduced a new index called "the velocity of temperature change" or more generally "the velocity of climate change". It is calculated by dividing temporal change in temperature (°C yr^{-1}) by spatial change in temperature (°C km^{-1}) and is expressed in km yr^{-1}. Observations below 5,000 m a.s.l.–the elevation up to which trees can be found growing (Miehe et al., 2007)–suggest that high elevation areas are experiencing faster temporal rates of warming (0.05 °C yr^{-1}) than low elevation areas (0.02 °C yr^{-1}, elevation-dependent warming [EDW], Gao et al., 2018; Luitel et al., 2020; Pepin et al., 2015). Studies have indicated that EDW occurs partly because of increases in downward longwave radiation in response to increases in water vapour and partly because of increases in positive snow albedo feedback in response to increases in surface absorption of solar radiation owing to a reduced snow albedo (Minder et al., 2018; Rangwala et al., 2013). This implies that the velocity of temperature change may change with elevation. However, since upslope movements along steep slopes result in rapid changes in temperature, it is likely that small geographic displacements will be enough to keep pace with climate warming in the highlands despite the EDW. In contrast, in flatter areas such as valleys and lowland plains, larger geographic displacements will be required to track temperature increase. Mamantov et al. (2021), in a meta-analysis from 16 montane regions world-wide including Eastern Himalayas, showed that rates of species range shift indeed decrease with increase in elevation.

Plant functional traits are important to understand and predict species' potential responses to climate change. Plant functional traits are defined as morphological, physiological or phenological characteristics that affect plant physiological performance and their spatial distribution (Poorter & Bongers, 2006; Violle et al., 2007). Although plant traits can reflect the ability of species to disperse, establish, grow and colonize new sites (Estrada et al., 2016), little is known about how the variation in plant traits with elevation affect the capacity of species to shift their elevational ranges. Neither is there a consensus on how different plant traits contribute to species range shifts (MacLean & Beissinger, 2017). For instance, higher competitive ability may facilitate establishment and proliferation, and in plants, competitive ability are regulated by leaf-economic traits (Estrada et al., 2016). In the Himalayas, traits related to plant size, hydraulic efficiency and light competition determine species distribution along the elevational gradient (Chapter 3). These traits that are advantageous in closed vegetations associated with warm low elevations (Chapter 3) may also be important to colonize new sites that become available because of increased warming, as a large stature, wide conductive conduits and large leaf area per xylem area allow plant to be competitive, acquire more resources and attain a faster growth (cf. Estrada et al., 2016; Chapter 3). Here we ask whether such simple easy to measure traits can serve as proxies to predict temperature-induced range shifts.

The Himalayas in Nepal provide an excellent opportunity to investigate the effects of climate change on plant species distribution because within a 200 km distance elevation increases from ca. 60 m a.s.l. in the south to > 8 km in the north (HMGN/MFSC, 2002). Along this gradient, the vegetation changes from wet and warm tropical forests in the lowland plains, via temperate and sub-alpine forests to dry and cold alpine meadows above the treeline (Lillesø et al., 2005). The Himalayas experience substantial warming (0.2 °C decade^{-1} from 1951–2014, Ren et al., 2017), particularly at higher elevations (0.5 °C decade^{-1}, Gao et al., 2018; Luitel et al., 2020; Pepin et al., 2015) and climatic projections suggest that by 2050 the average temperature will increase with 2-5 °C (Rajbhandari et al., 2016; Shrestha et al., 2015). Average annual precipitation in the Himalayas is predicted to increase by 2–6% by 2030 and by 8–12% by 2050 (MoFE, 2019). Predicted climate warming and increase in precipitation should therefore have a pronounced effect on the distribution of Himalayan plant species and empirical studies show that species are shifting their upper elevation limits upslope at a rate as high as 27 m decade^{-1} (Bhatta et al., 2018; Gaire et al., 2014; Suwal et al., 2016; Telwala et al., 2013).

In this study, we assessed the potential effects of rising temperature on the distribution of 137 common tree species that partition the elevational gradient of the Himalayas in Nepal. For each of these species we compared near current (1985) climatic niche models (as quantified using MaxEnt) with future climatic projections for 2050, and relate that to traits that are considered to be important for shaping tree species distribution ranges in the Himalayas. We addressed the following four research questions and corresponding hypotheses:

First, how does climate warming affect the elevational range shift of low and high elevation species? Because in montane landscapes, upslope movements along steep slope result in large changes in temperature on short spatial distance, it is likely that small geographic displacements will be enough to keep pace with climate warming in the highlands despite the elevation dependent warming, whereas in flatter areas such as valleys and lowland plains, larger geographic displacements will be required to compensate for temperature increase. Mamantov et al. (2021), in a meta-analysis from 16 montane regions world-wide including Eastern Himalayas, showed that rates of species range shift indeed decrease with increase in elevation. Here, we tested whether the same relationship holds for the (Central) Himalayan elevational gradient, meaning that species with an optimum at low elevation shift their geographic ranges upslope at faster rates than species with an optimum at high elevation to track the environmental changes.

Second, how does climate warming affect the distribution area of low and high elevation species? Because climate warming is expected to force species to shift their distribution ranges to smaller upslope surface areas, we hypothesized that all species have a reduced distribution area under future climatic conditions, and that species with an optimum at low elevation show the largest predicted reductions in distribution area.

Third, which environmental variable controls the species range shifts? Because the Himalayas are already experiencing substantial warming and are predicted to experience even faster rates of warming in the future, particularly at higher elevations (Luitel et al., 2020; Rajbhandari et al., 2016; Shrestha et al., 2015) additional to predicted increase in precipitation throughout the Himalayas (MoFE, 2019), we hypothesized that species for which species distribution models are driven by responses to temperature and precipitation will show upslope shifts in their optimum elevation resulting in a reduction of their distribution area.

Fourth, can plant traits predict species range shifts and changes in distribution area? Because acquisitive trait values (e.g. wide conductive conduits) allow species to acquire resources faster and attain faster growth (Estrada et al., 2016; Chapter 3), we hypothesized that species with acquisitive trait values have large predicted range shifts and changes in distribution area.

4.2 Materials and methods

4.2.1 Study area

Our research focused on the Himalayan elevational gradient in Nepal (Figure 4.1a). Within a horizontal span of 200 km, elevation increases from ca. 60 m a.s.l. in the south to > 8 km a.s.l. in the north (HMGN/MFSC, 2002, Figure 4.1a). In the south of the gradient, is the Gangetic plain called Terai (60-300 m a.s.l.) and north of this plain is the range of round hills called the Siwalik Hills (300-1,500 m a.s.l.). North of the Siwalik Hills is the Lesser Himalayas or the Mahabharat range (1,500-2,700 m a.s.l.) with some valleys in-between called Inner Terai. North of the Mahabharat range is the Himalayas (> 4,000 m a.s.l.) with some valleys in-between called Midlands (600-3,500 m a.s.l.). Amid the Himalayas are several inner Himalayan valleys (valleys at elevations > 3,600 m a.s.l.). Finally, north of the Himalayas are plateaus that are part of the Tibetan Plateau (HMGN/MFSC, 2002, Figure 4.1a). Because of this unique topography, a rapid decline in surface area with small increase between 4,000-5,000 m a.s.l. can be observed as one climbs up from the Terai towards the Himalayas, (Figure 4.1a) and the majority of surface area falls under slope class 20-30 degrees (Figure 4.1b). Along this gradient, temperature approximately decreases linearly (Table S4.1a), precipitation peaks around 1,000 m a.s.l. and then decreases rapidly (Table S4.1e), and aridity (Table S4.1h) follows the inverse precipitation patterns. Cloud cover increases with increasing elevation (Table S4.1i, j). Soils become dry (Table S4.1k) and coarse (Table S4.1l-n) with increase in elevation with exception for intermountain valleys. Soil organic carbon content increases with increasing elevation (Table S4.1o). The soils in the Trans-Himalayan valleys are slightly alkaline while the rest of the country has neutral to acidic soils (Table S4.1p). Vegetation follows changes in temperature and precipitation patterns and changes from wet (1,738 mm yr-1) and warm (24.1 °C) tropical deciduous *Shorea robusta* forests to intermediate temperate moist forests of oaks and conifers to comparatively drier (1,132 mm yr-1) and colder (6.9 °C) sub-alpine forests of birchs, Rhododendrons and Junipers (HMGN/MFSC, 2002; Lillesø et al., 2005; Shrestha et al., 2015).

4.2.2 Study species

To show how species' responses to climate change may vary with climatic niche, we selected 137 common tree species that occupy different elevational zones along the Himalayas (a subset of 277 plant species used in Chapter 2; Table S4.2).

4.2.3 Near current environmental conditions

To model the near current (1970-2000) distributions of the study species we initially selected 53 environmental variables: climate variables from WorldClim (http://worldclim.org/version2, Fick & Hijmans, 2017), irradiance variables from EarthEnv (http://www.earthenv.org/cloud, Wilson & Jetz, 2016), soil related variables from ISRIC-SoilGrids (ftp://

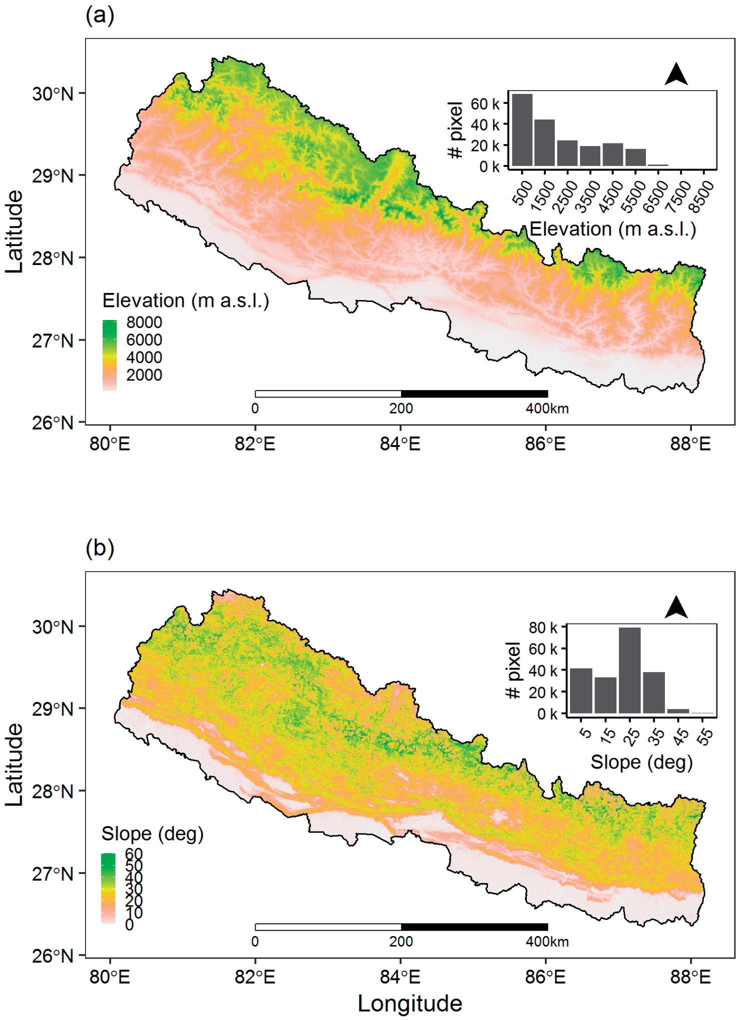

Figure 4.1. Map of the study area. (a) Elevation and (b) Slope map of the study area. Pixel count per 1,000 m elevation class in case of elevation map and that per 10 degree slope class in case of slope map are shown in the insets. The black line indicates national boundary of Nepal. The Government of Nepal published on 20th May 2020 a new political map including Kalapani, Lipulekh and Limpiyadhura inside the Nepal borders. As our research started in 2016, in our research, we used the previous version of the map without these territories.

ftp.soilgrids.org/data/aggregated/1km/, Hengl et al., 2017), topographic variables from CGIAR-CSI (https://cgiarcsi.community/data/srtm-90m-digital-elevation-database-v4-1/), river network data from HydroSHEDS (http://www.hydrosheds.org/) and global lakes and wetlands data from WWF (https://www.worldwildlife.org/pages/global-lakes-and-wetlands-database) that are known to potentially affect species distributions (Table S4.3; for details see also Chapter 2). To meet statistical assumptions and to avoid multicollinearity, we selected 19 environmental variables that were least correlated ($r < 0.7$, Dormann et al., 2013; Table S4.3). The variables were related to temperature (mean annual temperature, isothermality, temperature diurnal range and temperature annual range), water availability (annual precipitation, precipitation of driest quarter, precipitation seasonality and (Thornthwaite's aridity index), irradiance (cloud cover seasonality and mean annual cloud frequency), topography (slope, aspect and distance to water), soil texture (clay content, coarse fragments content and silt content), and soil conditions (organic carbon content, pH and available water capacity until wilting point). The spatial maps of these near current environmental variables are presented in Table S4.1.

4.2.4 Future environmental conditions

To correctly predict the effects of predicted climate change on plant species in the Himalayas, it is essential that the Global Climate Models (GCMs) that are used represent the monsoonal climate. A study by Jourdain et al. (2013) reported that five CMIP5 GCMs best reflect the monsoon in South Asia, namely, CCSM4, HadGEM2-AO, HadGEM2-ES, MIROC5 and NorESM1-M. At present, WorldClim version 2 (WC2) does not include future predictions for the five selected GCMs. Therefore, these future data were constructed using the WorldClim version 1.4 (WC1.4) data. We subtracted the near current WC1.4 data (average for 1960-1990) from the future WC1.4 data (average for 2041-2060) for the worst-case RCP8.5 scenario to derive the predicted differences between present and future for 19 bioclimatic variables, monthly minimum, maximum and mean temperature and monthly precipitation for each of the five selected GCMs. The future differences for the five GCMs were then averaged to obtain multi-model mean differences. These multi-model mean differences were then added to near current climate data of WC2 to calculate WC2 future climate data. Future aridity (Thornthwaite's aridity index), climatic moisture index, growing degree days (base temperature = 10 °C) and potential evapotranspiration (annual PET, PET extremes and PET seasonality) were computed using future WC2 monthly minimum, maximum and mean temperature and monthly precipitation data using ENVIREM R-package (Title & Bemmels, 2018). Future maximum climatic water deficit (MCWD) was computed using future WC2 monthly precipitation data based on (Malhi et al., 2009; see also Chapter 2). The spatial maps of the calculated future environmental variables are presented in Table S4.1.

4.2.5 Modelling near current and future species distributions

As our study species are subset of 277 species used in Chapter 2, we used the species distribution models developed in Chapter 2 to project their spatial distributions using 'near current' (1985) and future (2050) predicted environmental conditions. In Chapter 2, the near current (1970-2000) species distribution models for 277 species were developed using samples with data (SWD, in our case occurrence data combined with 19 climatic, soil and topographic predictor variables) format of MaxEnt version 3.3.3k (Phillips, 2010) within the R-package DISMO (Hijmans et al., 2017). To comply with the ecological theory that species responses to environmental gradients are often unimodal (Austin, 2007), MaxEnt was restricted to use only linear and quadratic features (Boucher-Lalonde et al., 2012; Merow et al., 2013), where linear features represent one side of a unimodal response due to partial representation of the entire gradient. The study area was defined by the country border of Nepal plus a 200 km buffer to avoid truncated niche predictions (Raes, 2012). We used 10,775 spatially unique observed species presence records at 30 arc seconds (~1km) raster resolution from forest inventories, online floral databases (Global Biodiversity Information Facility: http://www.gbif.org, Integrated Digitized Biocollections: http://www.idigbio.org and iNaturalist: http://www.inaturalist.org) and supplementary fieldwork (undertaken in Oct-Dec 2017) for the modelling (for details on sources of collection, processing and cleaning of species presence records, and MaxEnt modelling see Chapter 2).

For each of our 137 tree species, we prepared near current and future probability of occurrence maps by projecting the near current “species.lambdas” files to the near current and the future environmental conditions respectively using MaxEnt’s ‘density.Project’ function. Since collection localities cover the entire gradient of Nepal, species were interpolated for the near current projections whereas they were allowed to be extrapolated to non-analogue or novel future climatic conditions for the future projections. Since future projections for irradiance (i.e. cloud cover seasonality and mean annual cloud frequency) were not available these were kept unchanged. As topographic variables (i.e. aspect, slope and distance to water) and edaphic variables (i.e. soil organic carbon content, soil pH, available soil water capacity until wilting point, soil clay content, soil coarse fragments content and soil silt content) change little with time, these were also kept unchanged. For the further analyses, all near current and future probability of occurrence maps were cropped to the country border of Nepal. Then, we prepared discrete presence-absence maps i.e. species distribution maps by thresholding probability of occurrence maps using ‘10 percentile training presence logistic threshold’ (one of the most conservative and absence independent thresholds for presence-only species distribution models, Liu et al., 2011).

4.2.6 Data analysis

To evaluate whether climate warming results into different rates of elevational range shift among low and high elevation species, we compared the near current (1970-2000 i.e. ‘1985’) minimum, maximum and optimum elevations of species with their future (2041-2060 i.e. ‘2050’) values using linear regression. For this, we used the near current and the future species distribution maps to compute respective species’ minimum, maximum and optimum elevations. We used 5th and 95th percentile elevation values as conservative estimates of species’ minimum and maximum elevations. To quantify species’ optimum elevation we used the mid-value of the 100 m elevation band with the highest proportion of pixels predicted to be occupied. This procedure effectively corrects for the smaller available surface area at higher elevational bins (also see Chapter 2).

To evaluate whether climate warming results in differential changes in distribution area among low and high-elevation species, we regressed percentage changes in species distribution area relative to the near current distribution against the optimum elevation of the species using linear regression. For this, we used the abovementioned species distribution maps to compute species distributions areas for period 1985 and 2050. Then, we calculated percentage changes in species distribution area relative to the near current distribution as the species distribution area for 2050 minus the species distribution area for 1985 divided by species distribution area for 1985 whole multiplied by 100.

To evaluate which environmental variable controls the species range shifts, we grouped the species by the environmental variables contributing the most to the species distribution models (variables with the highest relative percentage contribution) and used a one-way ANOVA with a post-hoc Tukey test to analyse the differences in optimum shifts and the changes in distribution area among the species groups. Only the environmental variables that contributed the most to at least five species distribution models were considered for ANOVA.

To evaluate whether traits can be used as proxies to predict species range shifts and distributional area changes, we regressed shifts in species elevation and changes in species distribution area against species conduit diameter–one of the easy to understand traits that best explain tree species positions along Himalayan elevational gradient (for details see Chapter 3)–using a linear regression. Conduit diameter (average diameter of the 100 randomly sampled conduits, in mm) relates to hydraulic efficiency. At low elevations with benign environmental conditions, wide conduits facilitate water transport and growth whereas at high elevations with harsh environmental conditions, narrow conduits reduce freezing-induced cavitation and enhance species persistence. For this analysis, we used subset of 28 tree species for which we had both range shift data and conduit diameter data (species in bold in Table S4.2).

4.3 Results

4.3.1 Climate change predictions for Nepal for 2050

By 2050, the mean annual temperature is predicted to increase with 2-3 °C and particularly the north western region is predicted to experience substantial warming (Table S4.1a). Both the annual (Table S4.1b) and diurnal (Table S4.1c) ranges of temperature are predicted to decrease for the major parts of the country. However, the isothermality (Table S4.1d) is predicted to increase indicating that rate of decrease in annual temperature range will be higher than rate of decrease in diurnal temperature range for the major parts of the country. Annual precipitation is predicted to increase and particularly in the central and western lowlands and mid-hills, it is predicted to increase by more than 200 mm (Table S4.1e). Whereas the dry season precipitation is predicted to decrease (Table S4.1f) consequently leading to the increase in precipitation seasonality (Table S4.1g). Overall, the country is predicted to become warmer (Table S4.1a) and wetter (increase in annual precipitation, Table S4.1e; and decrease in aridity index, Table S4.1h).

4.3.2 Rates of shift amongst low and high elevation species

To evaluate whether climate warming results in different rates of elevational range shift among low and high elevation species, the estimated species' minimum, optimum and maximum elevations for 1985 were compared with their predicated values for 2050 using a linear regression. For all three species elevation values, the slopes of regression lines are significantly larger than 1 (Figure 4.2) indicating that highland species are predicted to shift their minimum, optimum and maximum elevations faster than the lowland species. In order to maintain their climatic niches, species are (on average) predicted to shift their minimum elevations upslope with 125 m, the optimum elevations with 204 m, and the maximum elevations with 512 m in 65 years (Figure 4.2 insets), corresponding to the rates of respectively 2, 3 and 8 m yr^{-1}. Some of the mid-elevation species show large (>2,000 m) shifts in their optimum and maximum elevation (e.g. species labelled with their name abbreviations in Figure 4.2). However, the intercepts of regression lines for each of the three species elevation values are not significantly different from zero indicating that some of the species at lower elevations are predicted to maintain their elevations or even shift their minimum (42 species) and optimum (5 species) elevations slightly downslope (Figure 4.2).

4.3.3 Changes in distribution area amongst low and high elevation species

To evaluate whether climate warming results in differential changes in distribution area among low and high-elevation species, changes in distribution area of species were regressed against the optimum elevation of the species. Twenty-nine percent (i.e. 40 species) of the tree species are predicted to reduce their distribution area whereas the other 71% (97 species) are predicted to gain distribution area (Figure 4.3). Particularly, lowland and highland species are predicted to gain distribution area, but mid-elevation species are predicted to lose distribution area (Figure 4.3, Figure 4.4). The results are similar when regression analysis was carried out by excluding *Larix griffithii* with the largest predicted gain in distribution area (R^2=0.36, see Figure S4.1a) or by log-transforming percentage change in distribution area (R^2=0.44, see Figure S4.1b). Some lowland and highland species (e.g. species labelled with their name abbreviations in Figure 4.3) are predicted to more than double their distribution area by 2050. On average, species are predicted to gain

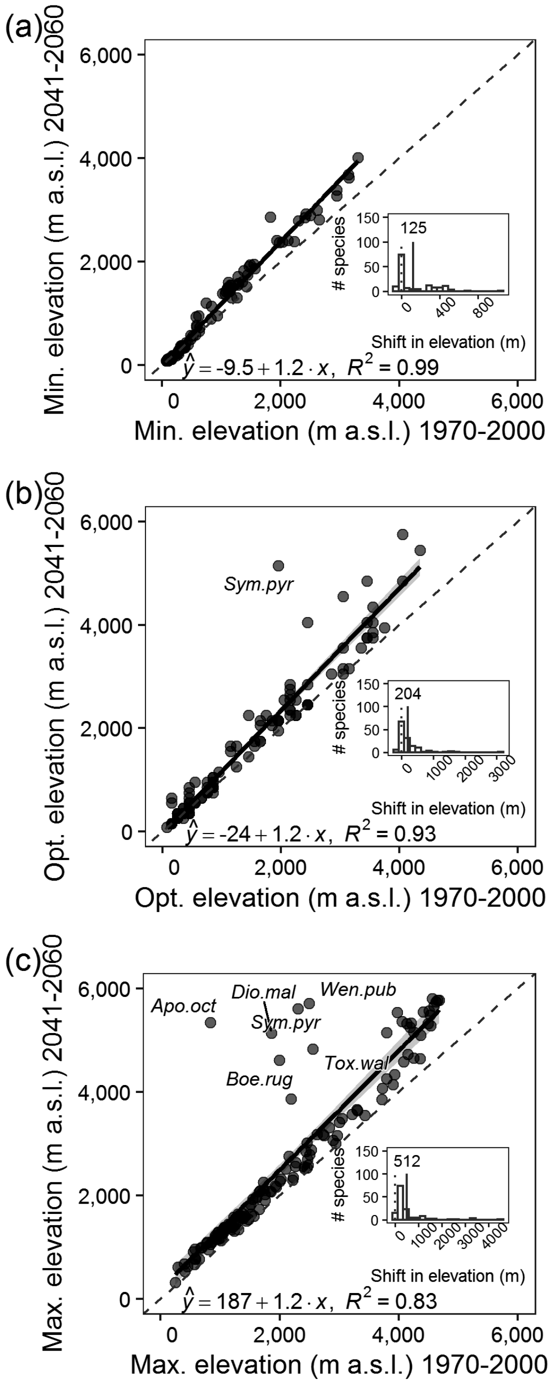

Figure 4.2. Scatterplots comparing the elevational distributions of 137 Himalayan tree species between periods 1985 and 2050. Each circle represents one species. The dashed line indicates the 1:1 line (no change in distribution). Solid regression lines are significant at $p < 0.05$. Grey shade around regression line indicates 95% confidence interval. The 95% confidence intervals of slopes of regression lines range between for a) 1.17-1.22, b) 1.13-1.24 and c) 1.07-1.24 indicating that the slopes of regression lines are significantly larger than 1. The 95% confidence intervals of intercepts of regression lines range between for a) -34.44-15.42, b) -113.48-66.13 and c) -29.69-403.13 and in all cases do not differ from zero. Insets show the frequency distributions of elevational shifts over the 65 years. The vertical dashed line indicates zero or no shift, the vertical solid line indicates the mean elevational shift, and number on the top indicates the magnitude of the mean elevational shift. Species with elevational shifts >2,000 m are labelled with their names. Species name abbreviations are based on the first three letters of their genus and species names. For the complete list of study species see Table S4.2.

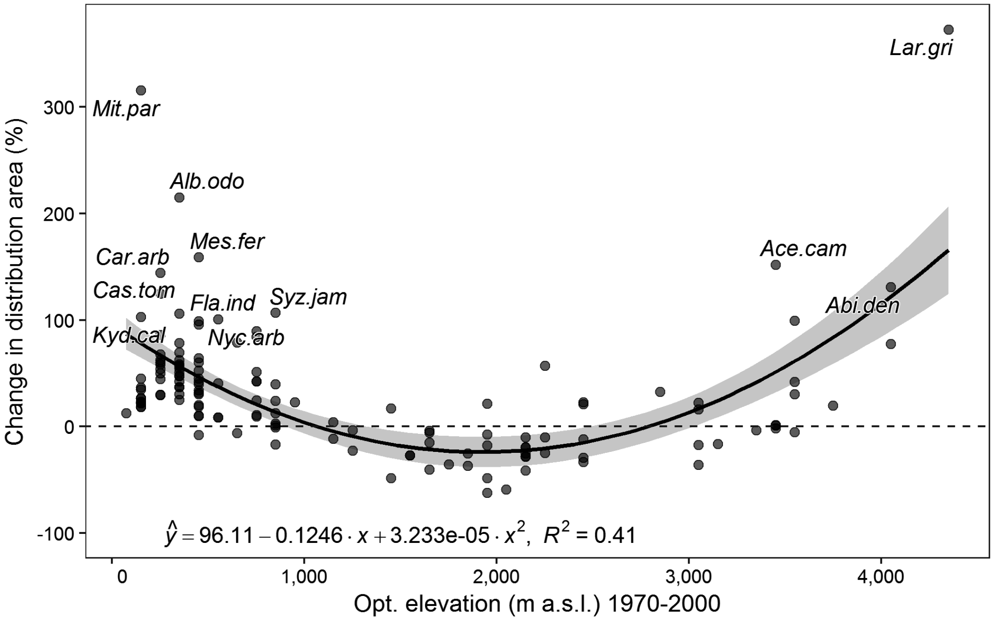

Figure 4.3. Relationship between change in distribution area between periods 1985 and 2050 expressed as percentage change relative to 1985 distribution area and optimum elevation for 137 Himalayan tree species. Each circle represents one species. The horizontal dashed line indicates zero or no change in distribution area. The solid black regression line is significant at p <0.05. Species with distribution area gain >100% are labelled with their names. Species name abbreviations are based on the first three letters of their genus and species names. For the complete list of study species see Table S4.2. The evaluated distribution area refers to Nepal.

33% of their distribution areas ranging from -62 to 373% (Figure 4.3). Additionally, to confirm whether predicted change in distribution area is also influenced by species range shift parameters, a stepwise multiple regression analysis was carried out. This shows that change in distribution area not only depends on optimum elevation but also declines with shift in minimum elevation (*change in distribution area* = 91.54 – 0.113 x *species optimum elevation* + 0.00003 x (*species optimum elevation*)^2 – 0.063 x *species shift in minimum elevation*, $R^2 = 0.42$, $N = 137$, all coefficients were significant at $p < 0.1$).

4.3.4 Which environmental variable controls species range shifts?

To evaluate which environmental variable controls the species range shifts, we grouped the species by the environmental variables contributing the most to the species distribution models (variables with the highest relative percentage contribution) and used a one-way ANOVA with a post-hoc Tukey test to analyse the differences in optimum shifts and the changes in distribution area among the species groups. Species that show significant and strongest upslope shifts are species whose distribution models are driven by responses to the aridity index, soil clay content and mean annual temperature. The 95% confidence

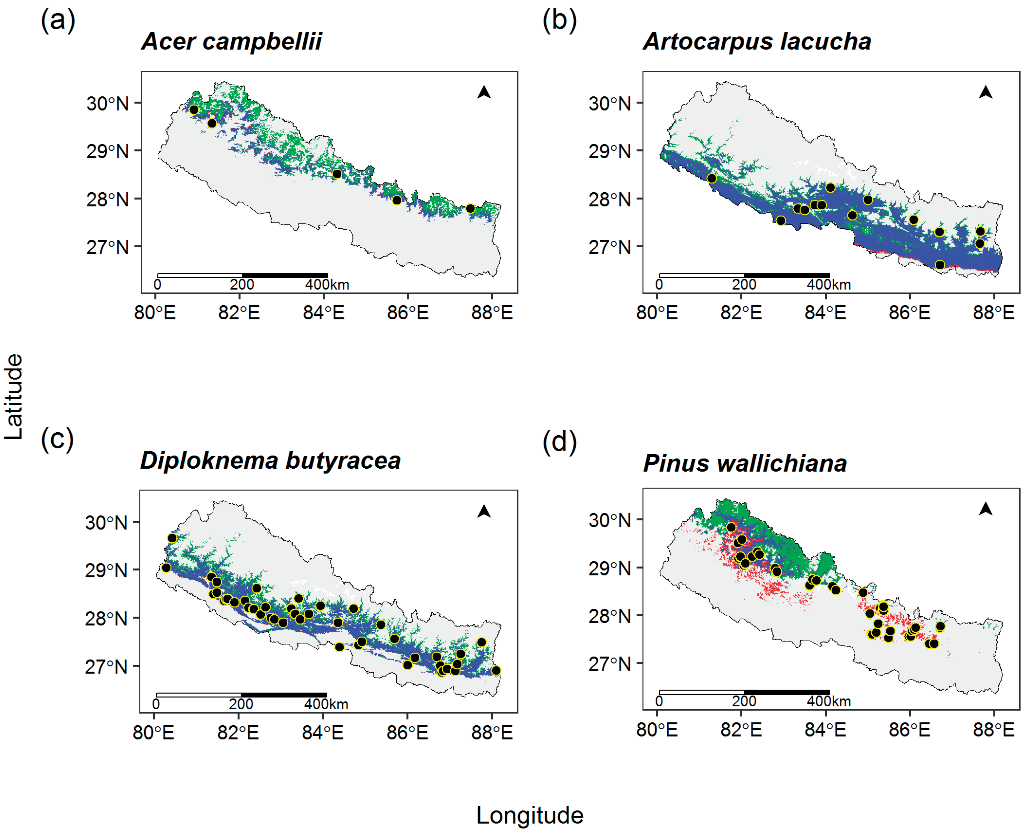

Figure 4.4. Maps showing changes in distribution area between 1985 and 2050 for four tree species: (a) *Acer campbellii*, (b) *Artocarpus lacucha*, (c) *Diploknema butyraceae* and (d) *Pinus wallichiana*. The black line indicates national boundary of Nepal. The Government of Nepal published on 20th May 2020 a new political map including Kalapani, Lipulekh and Limpiyadhura inside the Nepal borders. As our research started in 2016, in our research, we used the previous version of the map without these territories. Colours indicate distribution areas that are predicted to be lost (red), maintained (blue) or gained (green). The areas in white represent areas with missing environmental data. Black circles indicate spatially unique observed species presence records at 30 arc seconds (~1km) raster resolution from forest inventories, online floral databases and field survey for Nepal used for modelling the species distribution.

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intervals of upslope shifts for species whose distribution models are driven by responses to other environmental variables such as available soil water capacity until wilting point, soil organic carbon content and slope overlap with zero indicating that these environmental variables are not associated with upslope shifts (Figure 4.5a). Similarly, species that show significant gains in distribution area are species whose distribution models are driven by responses to mean annual temperature whereas species that show significant losses in distribution area are species whose distribution models are driven by responses to aridity index. The 95% confidence intervals of changes in distribution area for species

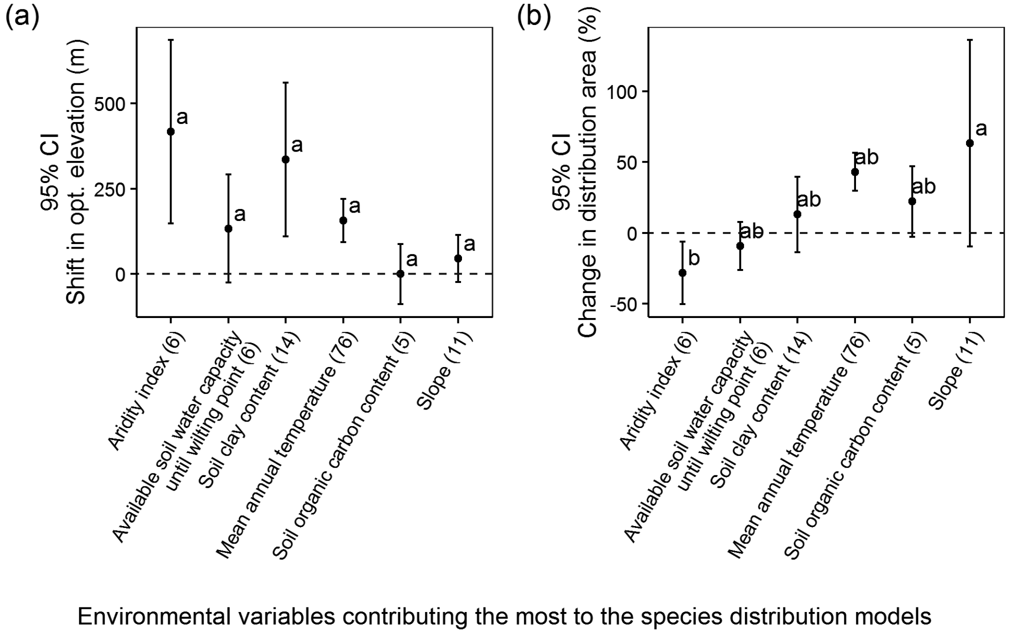

Figure 4.5. Relationships between species range shifts: (a) shifts in species optimum elevation and (b) changes in species distribution area and environmental variables. Species are grouped by environmental variables contributing the most to the species distribution models (variables with the highest relative percentage contribution). Differences between the species groups are tested using ANOVA. Error bars with same letters are not significantly different while those with different letters are significantly different (post-hoc Tukey test, p <0.05). Black circles indicate group means and error bars indicate 95% confidence interval. Horizontal dashed line indicate no shift/change. Numbers in parenthesis next to environmental variable names indicate the number of species in the group.

whose distribution models are driven by responses to other environmental variables such as available soil water capacity until wilting point, soil clay content, soil organic carbon content and slope overlap with zero indicating that these environmental variables are not associated with changes in distribution area (Figure 4.5b).

4.3.5 Can traits predict species range shifts and changes in distribution area?

To evaluate whether traits (in our case conduit diameter) can be used as proxies to predict species range shifts and distributional area changes, we regressed shifts in species elevation and changes in species distribution area against species conduit diameter using a linear regression. Species that show large predicted upslope shifts in minimum, optimum and maximum elevation have small trait values and vice versa (Table 4.1, Figure 4.6a-c). The association between changes in distribution area and trait values is positive but not significant (Table 4.1, Figure 4.6d).

Table 4.1. Bivariate relationships between current optimum elevation, four species range shift parameters and conduit diameter. Pearson's correlation coefficients in bold are significant at p <0.05, those in bold and italic are significant at p <0.01, and those in bold and underline are significant at p <0.001. N indicates number of tree species included in the analysis.

	Shift in min. elevation (m)	Shift in opt. elevation (m)	Shift in max. elevation (m)	Change in distribution area (%)	Conduit diameter (mm)
	N = 137	*N* = 137	*N* = 137	*N* = 137	*N* = 28
Optimum elevation (m a.s.l.)	**0.82**	**0.50**	**0.28**	-0.16	**-0.77**
Shift in min. elevation (m)		**0.48**	0.13	***-0.24***	**-0.68**
Shift in opt. elevation (m)			**0.32**	-0.02	***-0.52***
Shift in max. elevation (m)				0.04	**-0.65**
Change in distribution area (%)					0.29

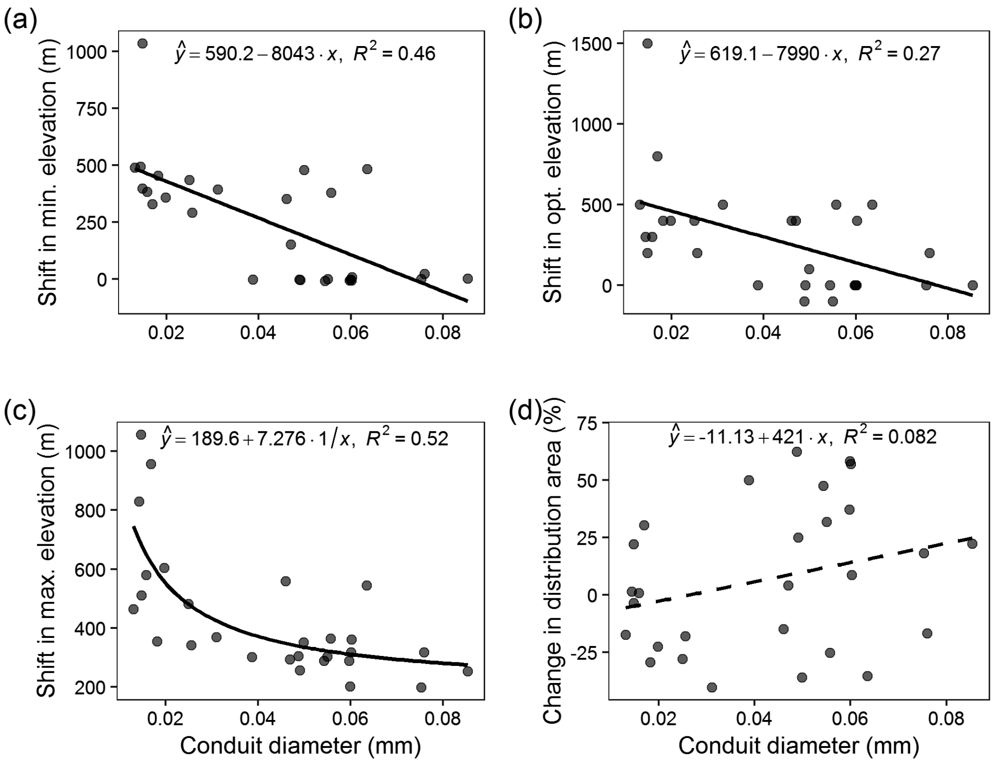

Figure 4.6. Relationships between predicted species elevational shifts (between 1985 and 2050) and conduit diameter for (a) minimum elevation, (b) optimum elevation and (c) maximum elevation, and (d) relationship between change in species distribution area and conduit diameter. Each circle represents one species (N=28). Solid regression lines are significant at p <0.05. Regression equations and coefficients of determination (R^2) are shown.

4.4 Discussion

We evaluated how climate warming affects the elevational ranges and the distribution areas of low and high elevation tree species, which environmental variable controls species range shifts, and how plant traits are associated with species range shifts. The modelling results indicate that highland species are predicted to show faster elevational shifts than lowland species. Lowland and highland species are predicted to enlarge their distribution area whereas mid-elevation species are predicted to reduce their distribution area. Tree species that show the largest upslope shifts are species for which species distribution models are driven by responses to aridity index, soil clay content and mean annual temperature, and have narrow conduits. Below, we discuss the underlying mechanisms.

4.4.1 Rates of shift amongst low and high elevation species

Our climatic niche models show that climate change predictions result in an upslope shift for all three elevational distribution parameters (minimum, optimum and maximum elevations) for the majority of species (Figure 4.2). This is in line with the findings of empirical studies from the Himalayas (Bhatta et al., 2018; Gaire et al., 2014; Suwal et al., 2016; Telwala et al., 2013) and other mountain ranges across the globe: Andes (Feeley et al., 2011), Alps (Geppert et al., 2020) and Pyrenees (Marshall et al., 2020). Because the lowlands are dominated by flat plains and the highlands by steep slopes (Figure 4.1), we expected that the required velocity for tracking climate change (i.e. rate of species range shift) to be higher for low elevation species than that for high elevation species. However, highland species were predicted to have faster range shifts than the lowland species (Figure 4.2). Such faster predicted range shifts of highland species suggest that along this extreme elevational gradient upslope range shifts are primarily controlled by the temporal rates of warming that is observed (Luitel et al., 2020) and predicted to be higher for the highland areas (elevation dependent warming, Gao et al., 2018; Pepin et al., 2015).

The average upslope shifts of the maximum elevation of the tree species are predicted to be as high as 8 m yr^{-1} (Figure 4.2c inset) which is more than 2 times larger than the observed average upward shifts of the upper distribution limit of highland tree species in the Himalayas (3 m yr^{-1}, Gaire et al., 2014; Telwala et al., 2013) and much larger than global average of 0.6 m yr^{-1} (Parmesan & Yohe, 2003). Furthermore, some of the mid-elevation species showed large (>2,000 m) predicted upslope shifts in their optimum and maximum elevations in 65 years (e.g. species labelled with their name abbreviations in Figure 4.2). This is again much larger than the observed maximum upslope shift of 998 m between 1850 & 2010 in the Himalayas (Telwala et al., 2013). This suggests that large areas with novel bioclimatic conditions at the upper limits of the species are predicted to become suitable for these species. The question remains whether these species are capable of migrating to potentially suitable future highland habitats on their own or that dispersal limitations will prevent colonization of suitable habitats. Therefore, to enable species to track climate change, it should be considered to establish migration corridors through the fragmented landscapes or even assist species to migrate to potentially suitable future highland habitats through direct seeding or planting (cf. Yan & Tang, 2019).

4.4.2 Changes in distribution area amongst low and high elevation species

Because climate warming is expected to force species to shift their distribution ranges to smaller upslope surface areas, we hypothesized that all tree species will reduce their distribution area, and that low elevation species will show the largest reductions in distribution area. In contrast, the majority (71%) of the tree species are predicted to enlarge their distribution area: these are particularly species from the lowlands or highlands whereas species from mid-elevations may reduce their distribution area (Figure 4.3, Figure 4.4). All else being equal, an upslope shift in minimum elevation should lead to a reduction in distribution area (as there is less surface area at higher elevations, Figure 4.1; Körner, 2007) and an upslope shift in maximum elevation should lead to an increase in distribution area. However, the actual change depends on the Himalayan topography and the area of each elevational belt (cf. Elsen & Tingley, 2015).

The prediction that lowland species expand their distribution area (Figure 4.3) is partly explained by the possibility that the Himalayan lowland species extend their upper limits upslope and partly by the ability of these species to persist at their lower limits, despite warming (Figure 4.2, Figure 4.4). This is consistent with observation from the French Alps, where the cosmopolitan and thermophilous nature of the lowland species are reported to contribute to their higher local persistence (Bertrand et al., 2011). However, in long run, further increase in temperature at lowlands may surpass species' thermal maximums and could lead to lowland biotic attrition (Colwell et al., 2008; Feeley & Silman, 2010), which should be noted and monitored. The prediction that many mid-elevation species (between 1,000 and 2,500 m) reduce their distribution area (Figure 4.3) suggests that the mid-elevation species may face smaller upslope surface areas above 1,000 m a.s.l. (see Figure 4.1a), while their lower limits become unsuitable for them. The prediction that highland species expand their distribution areas (Figure 4.3) is in line with the findings of other studies in the Himalayas (Anderson et al., 2020; He et al., 2019; He et al., 2020; Yan & Tang, 2019) and in alpine ecosystems in general (Rew et al., 2020). This suggests that warming is likely to make a large area of intermountain valleys and highland plateaus situated around 4,500 m a.s.l. (Figure 4.1; Figure 4.2c; Elsen & Tingley, 2015) suitable for the upslope shifting highland species. Given their limited dispersal ability, the question remains whether the tree species will be able to get up to those distant plateaus timely. This is especially the case for species with future modelled disjunct distributions, such as *Aporosa octandra*, *Boehmeria rugulosa*, *Diospyros malabrica*, *Symplocos pyrifolia*, *Toxicodendron wallichii* and *Wendlandia puberula* (Figure S4.2). These distributions are disjunct because the highland plateaus are intersected by mountain ranges, and because the valleys have different soil conditions, such as clayey deposits (Table S4.1m) and a higher organic carbon content (Devi & Sherpa, 2019; Table S4.1o). For these species with predicted disjunct future distributions or for species with continuous distributions for which new remote areas become available, species shifts could be assisted through direct seeding or planting in new potentially suitable highland habitats (cf. Yan & Tang, 2019).

4.4.3 Environmental variables controlling species range shifts

Because the Himalayas are already experiencing substantial warming and are predicted to experience even faster rates of warming in the future, particularly at higher elevations (Table S4.1a), additional to predicted increase in precipitation throughout the Himalayas (Table S4.1e), we hypothesized that species for which the species distribution models are driven by responses to temperature and precipitation would show upslope shifts in their optimum elevations resulting in reduction of their distribution areas. Indeed, the species for which their species distribution models are determined by temperature (i.e. mean annual temperature) showed significant and strongest predicted upslope shifts. But in contrast, they showed significant expansion in their predicted distribution areas (Figure 4.5). This suggests that for warm-adapted lowland species such increase in temperature may facilitate range expansion in the Himalayas. As predicted climate change also leads to increased precipitation and consequent decrease in aridity–another important environmental factor that controls the magnitude of predicted upslope shifts and changes in distribution area. Species for which their species distribution models are determined by aridity indeed showed significant and strongest predicted upslope shifts and significant contraction in their predicted distribution areas (Figure 4.5). Several studies from the Himalayas (Gaire et al., 2014; Telwala et al., 2013) and other mountain ranges (Crimmins et al., 2011; Feeley et al., 2011; Lenoir et al., 2008; Pauli et al., 2012; Zhang et al., 2020) have highlighted such important roles of precipitation–in addition to warming–in controlling species range shifts. This suggests that for the species that prefer dry to moist sites such increase in temperature and precipitation may lead to range contraction.

Interestingly, soil clay content (ClayC) appeared as another important environmental variable (Figure 4.5) suggesting that species responses to climate change are also strongly modified by soil clay content. As species, particularly high-elevation species, shift upslope, they are likely to spill over to large clayey intermountain valleys and highland plateaus situated around 4,500 m a.s.l. (Figure 1; Figure 2c; Table S4.1m; Elsen & Tingley, 2015) that are presently not suitable as result of present bioclimatic conditions. Hence, fixed soil properties in combination with changing bioclimatic conditions may strongly constrain and modify species responses to climate change along the Himalayan elevational gradient. Other studies – but from Andes – also found that responses of tree species and communities to global warming are highly heterogeneous (cf. Figure 4.5a; Duque et al., 2015; Fadrique et al., 2018), and depend not only on the magnitude of temperature change at that specific elevation (Fadrique et al., 2018), but also on local soil conditions that can constrain the immigration and establishment of non-specialists (Duque et al., 2015). This suggests that soil effect is not Himalaya specific, but generic.

4.4.4 Traits as proxies to predict species range shifts and changes in distribution area

Because acquisitive trait values allow species to acquire resources faster and attain faster growth (Estrada et al., 2016; Chapter 3), we hypothesized that species with predicted large range shifts and changes in distribution area have acquisitive trait values. However, the modelling results indicate that species with small predicted upslope shifts have large trait values i.e. acquisitive trait values (Table 4.1, Figure 4.6). This suggests that acquisitive trait values are negatively associated with magnitude of species range shifts.

Particularly in the Himalayas, species with acquisitive trait values (wide conduits) dominate lowland areas (Chapter 3), probably because wide conduits facilitate water transport and growth, and consequently enhance competitive ability in dense stands in moist and productive lowland environmental conditions (cf. Venturas et al., 2017). The majority of these warm-adapted lowland species with acquisitive trait values are predicted to maintain their current lower distribution limits while they are predicted to shift their upper distribution limits upslope (Figure 4.2). When they shift their upper distribution limits upslope to higher elevations while maintaining their lower distribution limits, this will lead to increase in their distribution areas. This must have resulted into positive but non-significant association between acquisitive trait values and changes in distribution area. Hence, an easily measurable trait, such as conduit diameter, can be used as a proxy to predict species' range shifts and distributional area changes. Although not for conduit diameter, but traits like fruit type, dispersal mode and life form have been shown to be useful in predicting species range shifts among the subtropical mountain plants in the Hengduan Mountains in China (Zu et al., 2021). Given that the environmental conditions of Nepal are predicted to be warmer and wetter (MoFE, 2019; Table S4.1a; Table S4.1e), the tree species with wide conduits i.e. species with high hydraulic efficiency (Olson et al., 2018; Pittermann & Sperry, 2006) are likely the ones going to benefit the most in terms of expansion of their distribution areas. Such wide conduits may also make trees species more competitive under the predicted warmer and wetter environmental conditions.

4.4.5 Management recommendations

The average upslope shifts of the maximum elevation of the tree species are predicted to be more than 2 times larger (8 m yr^{-1}, Figure 4.2c inset) than the observed average upward shifts of the upper distribution limit of highland tree species in the Himalayas (3 m yr^{-1}, Gaire et al., 2014; Telwala et al., 2013). Therefore, to enable species to track climate change, it should be considered to establish migration corridors through the fragmented landscapes or even assist species to migrate to potentially suitable future highland habitats through direct seeding or planting (cf. Yan & Tang, 2019). Further, the prediction that lowland species expand their distribution area (Figure 4.3) suggest that lowland species may extend their upper limits upslope and at the same time persist at their lower limits, despite warming. However, in long run, further increase in temperature at lowlands may surpass species' thermal maximums and could lead to lowland biotic attrition (Colwell et al., 2008; Feeley & Silman, 2010). It is thus recommended to monitor lowland species for lowland biotic attrition. Furthermore, the prediction that highland species expand their distribution area (Figure 4.3) suggest that with climate warming large area of intermountain valleys and highland plateaus situated around 4,500 m a.s.l. (Figure 4.1) will become potentially suitable for the upslope shifting highland species. Particularly for the species with disjunct distributions (e.g. *Aporosa octandra*, *Boehmeria rugulosa*, *Diospyros malabrica*, *Symplocos pyrifolia*, *Toxicodendron wallichii* and *Wendlandia puberula,* Figure S4.2) or for the species with continuous distributions for which new remote areas become available, upslope shifts should be assisted through direct seeding or planting in new potentially suitable highland habitats (cf. Yan & Tang, 2019). A significant proportion of the species (29%) are predicted to show decrease in their distribution areas. Especially for those species with the largest contractions in distribution areas (e.g. *Betula alnoides*, *Prunus cerasoides*, *Pyrus pashia* and *Quercus floribunda*, Table S4.2), it is recommended to monitor whether they are able to maintain a viable population size. Our findings may be used in numerous additional ways such as locating currently undocumented species locations, potential locations where species may occur in the future, or potential locations where the species could be seeded or planted to enable species to track their climatic niches, thus contributing to the species conservation and management.

Acknowledgements

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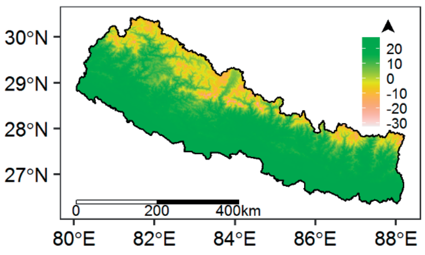
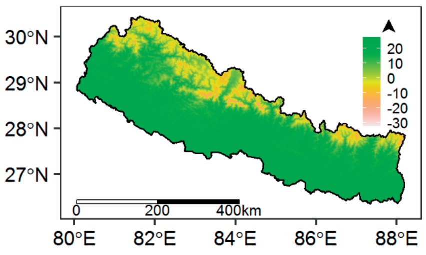
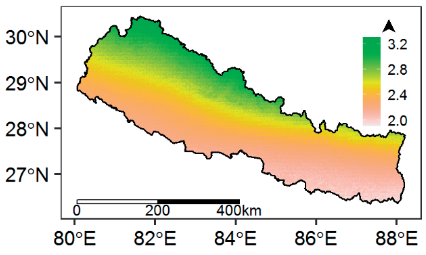
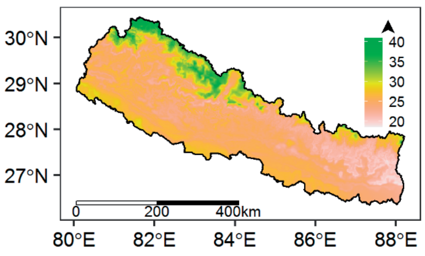
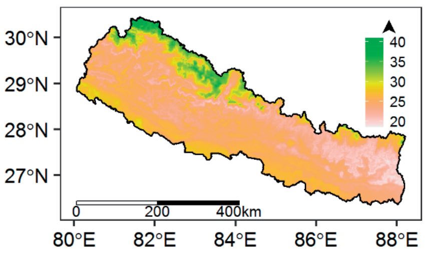
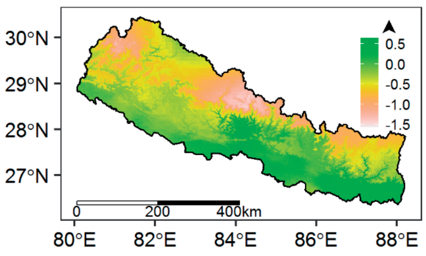
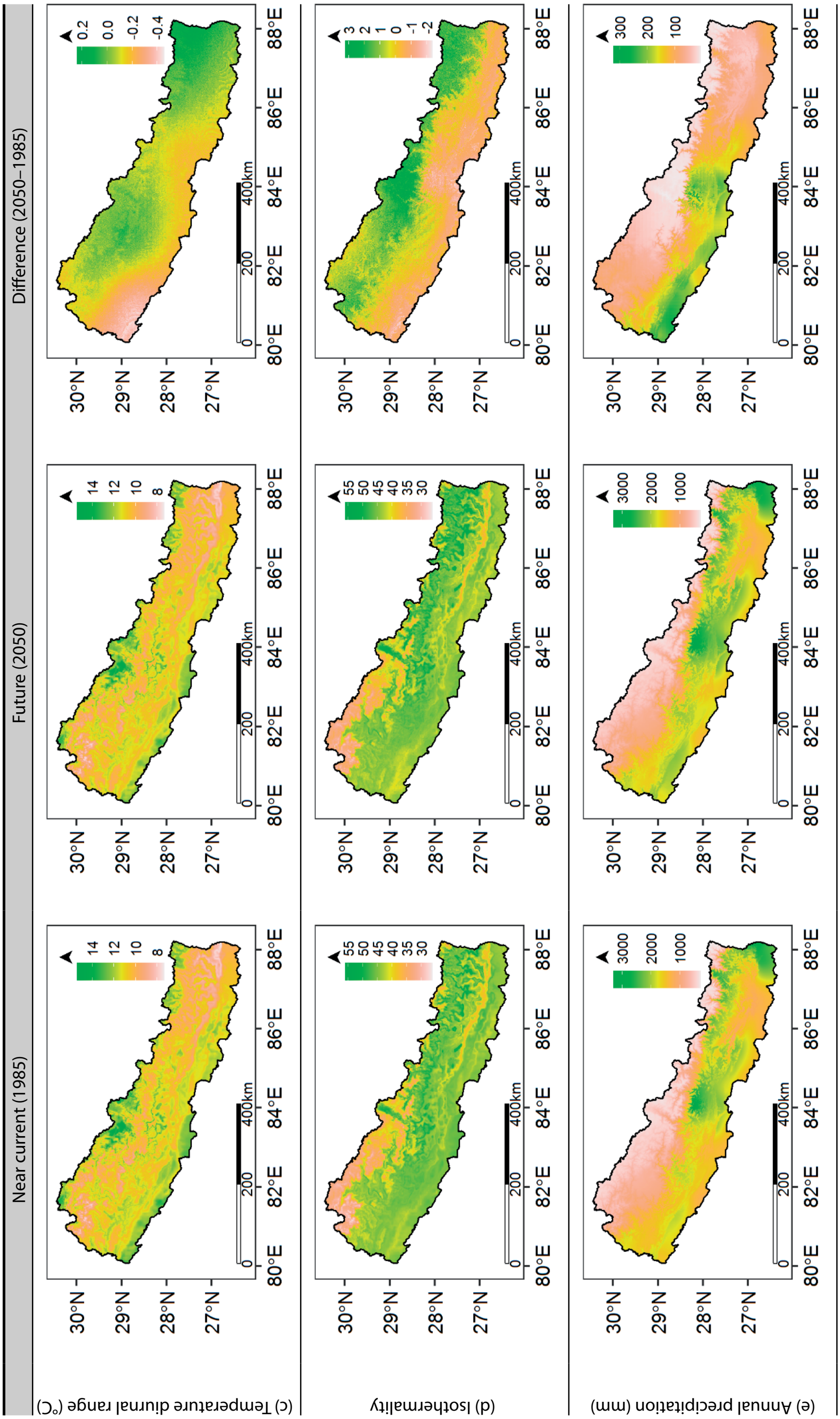
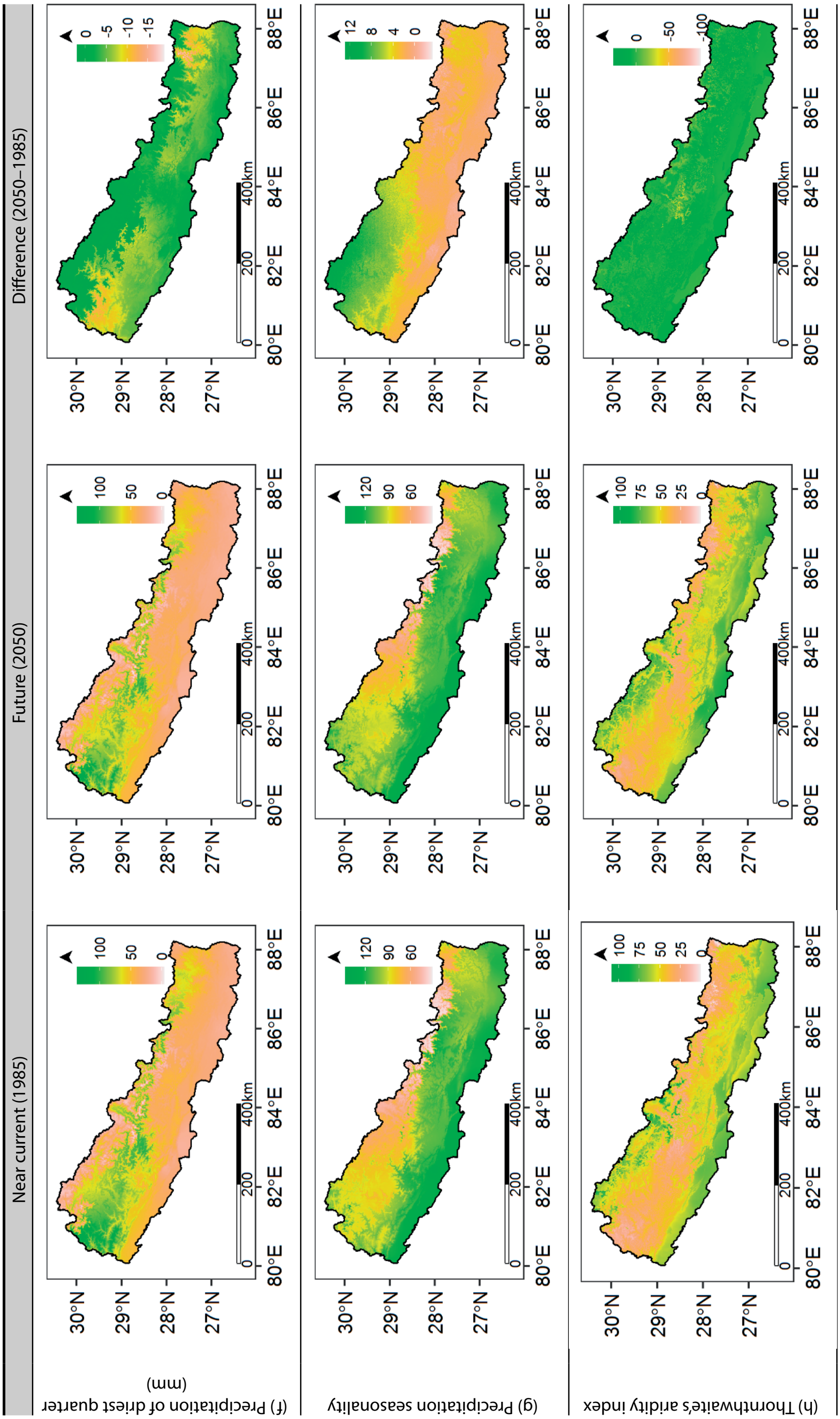
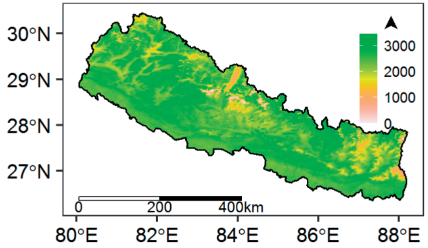
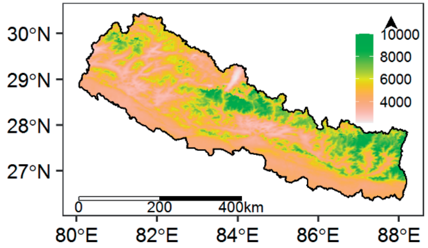
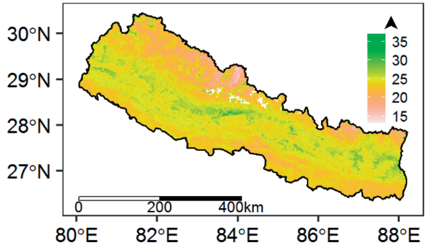
Supplementary information

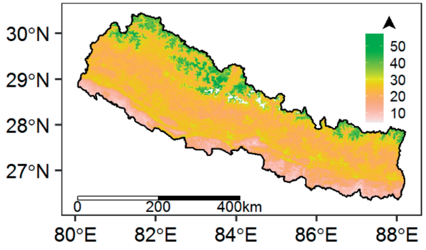
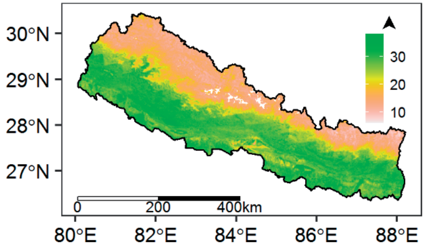
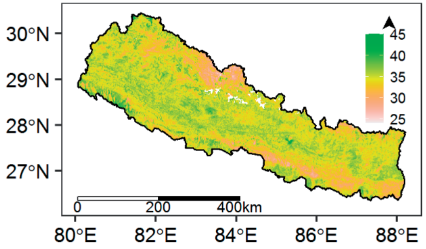
Table S4.1. Spatial maps of selected 19 environmental variables namely, a) mean annual temperature, b) temperature annual range, c) temperature diurnal range, d) isothermality, e) annual precipitation, f) precipitation of driest quarter, g) precipitation seasonality, h) Thornthwaite's aridity index, i) cloud cover seasonality, j) mean annual cloud frequency, k) available soil water capacity until wilting point, l) soil coarse fragments content, m) soil clay content, n) soil silt content, o) soil organic carbon content, p) soil pH x 10 in water, q) aspect, r) slope and s) distance to water for period 1985, 2050, and difference between 2050 and 1985. For the variables for which future projections are not available and for the variables that change little with time, only spatial maps for period 1985 are shown. The black line indicates national boundary of Nepal. The Government of Nepal published on 20th May 2020 a new political map including Kalapani, Lipulekh and Limpiyadhura inside the Nepal borders. As our research started in 2016, in our research, we used the previous version of the map without these territories. The areas in white, if any, represent areas with missing environmental data.

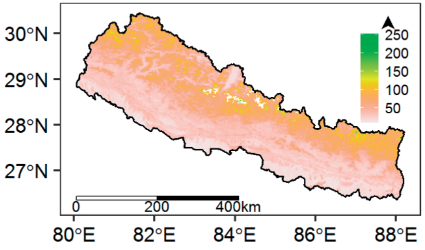
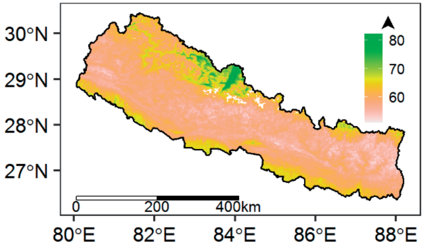
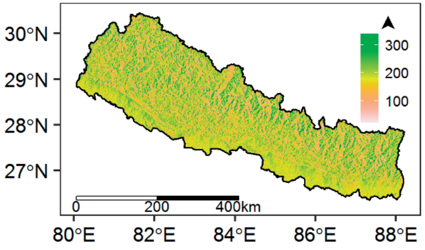
	Near current (1985)	Future (2050)	Difference (2050–1985)
(a) Mean annual temperature (°C)			
(b) Temperature annual range (°C)			


Near current (1985)
Future (2050)
Difference (2050–1985)
(c) Temperature diurnal range (°C)
(d) Isothermality
(e) Annual precipitation (mm)
14
12
10
8
0.2
0.0
-0.2
-0.4
55
50
45
40
35
30
3
2
1
0
-1
-2
3000
2000
1000
300
200
100
0
200
400km
30°N
29°N
28°N
27°N
80°E
82°E
84°E
86°E
88°E


Near current (1985)
Future (2050)
Difference (2050–1985)
(f) Precipitation of driest quarter (mm)
(g) Precipitation seasonality
(h) Thornthwaite's aridity index
100
50
0
-5
-10
-15
120
90
60
12
8
4
75
25
-50
-100
0
200
400km
30°N
29°N
28°N
27°N
80°E
82°E
84°E
86°E
88°E

	Near current (1985)	Future (2050)	Difference (2050–1985)
(i) Cloud cover seasonality			
(j) Mean annual cloud frequency			
(k) Available soil water capacity until wilting point (%)			

	Near current (1985)	Future (2050)	Difference (2050–1985)
(l) Soil coarse fragments content (%)			
(m) Soil clay content (%)			
(n) Soil silt content (%)			

	Near current (1985)	Future (2050)	Difference (2050–1985)
(o) Soil organic carbon content (gm/kg)			
(p) Soil pH x 10 in water			
(q) Aspect (degree)			

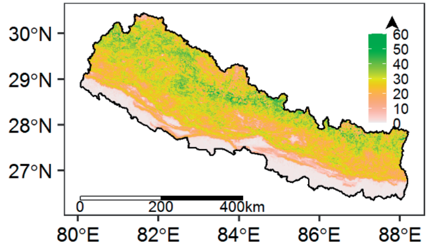
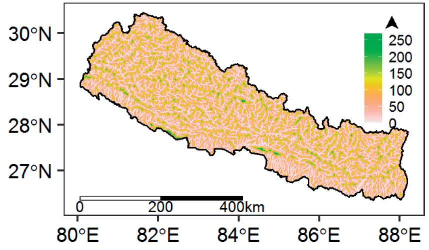
	Near current (1985)	Future (2050)	Difference (2050–1985)
(r) Slope (degree)			
(s) Distance to water (arc second)			

Table S4.2. Complete list of 137 tree species selected for this study. Species names, their respective families, number of spatially unique presence records used for MaxEnt modelling, and their near current and predicted future elevational distributions (minimum, optimum and maximum elevations and distribution areas) and changes in distribution area are shown. Species names in bold mark species with traits data.

Species name	Family	Presence record	1985				2050				Change in dist. area (%)
			Elevation (m a.s.l.)			Dist. area (pixels)	Elevation (m a.s.l.)			Dist. area (pixels)	
			Min	Opt	Max		Min	Opt	Max		
Abies densa Griff.	Pinaceae	9	3144	4050	4655	16402	3677	4850	5775	37859	130.82
Abies pindrow (Royle ex D.Don) Royle	Pinaceae	25	2410	3550	4413	28441	2854	3750	5545	40325	41.78
***Abies spectabilis* (D.Don) Mirb.**	Pinaceae	40	2493	3350	4079	18044	2892	3550	4590	17408	-3.52
Acacia catechu (L.f.) Willd.	Fabaceae	66	80	150	867	41580	83	150	1103	56789	36.58
Acer campbellii Hook.f. & Thomson ex Hiern	Aceraceae	11	2650	3450	4591	13933	2813	4850	5662	35087	151.83
Acer oblongum Wall. ex DC.	Aceraceae	23	135	450	2106	59851	135	450	2512	71837	20.03
***Aegle marmelos* (L.) Corrêa**	Rutaceae	38	87	250	692	35365	85	250	994	53056	50.02
Aesculus indica (Wall. ex Cambess.) Hook.	Hippocastanaceae	9	1170	2150	3796	15587	1300	2350	5146	12513	-19.72
Albizia chinensis (Osbeck) Merr.	Fabaceae	21	94	750	1756	50583	90	850	2022	95818	89.43
Albizia lebbeck (L.) Benth.	Fabaceae	9	82	250	1051	35980	83	350	1337	60333	67.68
Albizia odoratissima (L.f.) Benth.	Fabaceae	6	82	350	397	2279	84	350	678	7181	215.09
Albizia procera (Roxb.) Benth.	Fabaceae	45	95	350	1231	40465	95	450	1577	63572	57.1
***Alnus nepalensis* D.Don**	Betulaceae	133	1070	1650	2455	41384	1423	2050	3014	35202	-14.94
Anogeissus latifolia (Roxb. ex DC.) Wall. ex Guillem. & Perr.	Combretaceae	44	282	450	1241	20260	263	650	1308	27170	34.11
Aporosa octandra (Buch.-Ham. ex D.Don) Vickery	Euphorbiaceae	12	113	350	838	3652	125	350	5349	4763	30.42
Artocarpus lacucha Buch.-Ham.	Moraceae	16	83	150	1377	62244	86	150	1557	76745	23.3
Bauhinia malabarica Roxb.	Fabaceae	36	89	250	649	22547	82	250	770	36594	62.3
Bauhinia purpurea L.	Fabaceae	43	257	750	1547	46449	232	750	1923	66173	42.46
Bauhinia variegata L.	Fabaceae	40	97	150	1759	44742	95	650	1902	54437	21.67
Betula alnoides Buch.-Ham. ex D.Don	Betulaceae	24	1445	1950	2724	11032	1747	2150	3178	4177	-62.14
Betula utilis D.Don	Betulaceae	43	2945	3450	4358	21031	3380	4050	4646	20704	-1.55
Boehmeria rugulosa Wedd.	Urticaceae	23	385	750	1993	37136	336	750	4611	56110	51.09
***Bombax ceiba* L.**	Bombacaceae	56	85	150	1385	72809	88	150	1638	89092	22.36
Bridelia retusa (L.) A.Juss.	Euphorbiaceae	61	95	350	1064	43496	91	350	1388	67383	54.92
Brucea javanica (L.) Merr.	Simaroubaceae	32	1103	1850	2441	27875	1483	2150	2852	20800	-25.38
Buchanania cochinchinensis (Lour.) M.R.Almeida	Anacardiaceae	121	106	350	833	23515	99	350	1054	35486	50.91
Careya arborea Roxb.	Lecythidaceae	36	85	250	589	17804	81	250	762	43462	144.11
Casearia graveolens Dalzell	Flacourtiaceae	71	174	450	1483	50018	182	750	1787	65271	30.5
Casearia tomentosa Roxb.	Flacourtiaceae	28	99	250	553	23819	84	350	914	53487	124.56
Cassia fistula L.	Fabaceae	73	84	250	785	35116	84	250	1098	55646	58.46

Species name	Family	Presence record	1985				2050				Change in dist. area (%)
			Elevation (m a.s.l.)			Dist. area (pixels)	Elevation (m a.s.l.)			Dist. area (pixels)	
			Min	Opt	Max		Min	Opt	Max		
Castanopsis indica (Roxb. ex Lindl.) A.DC.	Fagaceae	66	830	1550	2264	43213	1132	1750	2560	31583	-26.91
Castanopsis tribuloides (Sm.) A.DC.	Fagaceae	39	351	750	2412	48036	353	750	2525	53119	10.58
Catunaregam spinosa (Thunb.) Tirveng.	Rubiaceae	107	85	250	942	45156	86	250	1160	58468	29.48
Cinnamomum tamala (Buch.-Ham.) T.Nees & Eberm.	Lauraceae	22	335	850	2478	47139	362	850	2587	47624	1.03
Cotoneaster ellipticus (Lindl.) Loudon	Rosaceae	10	1141	2250	4139	9683	1433	2250	5324	8705	-10.1
***Dalbergia latifolia* Roxb.**	Fabaceae	33	83	350	573	16303	82	350	774	25823	58.39
***Dalbergia sissoo* DC.**	Fabaceae	29	83	150	1183	55138	84	150	1381	65215	18.28
Daphniphyllum himalense (Benth.) Müll.Arg.	Daphniphyllaceae	7	1424	2450	3973	10778	1517	2450	5543	13231	22.76
Desmodium oojeinense (Roxb.) H.Ohashi	Fabaceae	83	311	450	1417	28536	362	850	1595	33883	18.74
Diospyros malabarica (Desr.) Kostel.	Ebenaceae	39	363	750	1866	49705	336	750	5143	61826	24.39
Diploknema butyracea (Roxb.) H.J.Lam	Sapotaceae	54	401	850	1676	41669	426	1050	2093	58217	39.71
Dodecadenia grandiflora Nees	Lauraceae	18	1262	2450	3929	20401	1298	2450	4342	24649	20.82
Duabanga grandiflora (DC.) Walp.	Sonneratiaceae	13	164	450	1034	10458	150	350	1186	20780	98.7
Dysoxylum excelsum Blume	Meliaceae	6	108	350	1438	33231	108	450	1509	47282	42.28
Ehretia laevis Roxb.	Cordiaceae	14	80	150	579	40927	83	150	959	59423	45.19
Engelhardia spicata Lesch. ex Blume	Juglandaceae	68	584	1150	1925	47481	772	1650	2183	41969	-11.61
***Eurya acuminata* DC.**	Theaceae	81	1286	1950	2535	25726	1579	2150	2877	21120	-17.9
Falconeria insignis Royle	Euphorbiaceae	96	481	950	1607	44790	574	1150	1963	55047	22.9
Ficus auriculata Lour.	Moraceae	36	326	850	2225	68904	377	950	2349	68480	-0.62
Ficus benghalensis L.	Moraceae	15	177	450	1482	44920	172	450	1532	49569	10.35
Ficus glaberrima Blume	Moraceae	11	436	750	1857	17955	399	750	2066	33091	84.3
Ficus hispida L.f.	Moraceae	28	156	850	1732	43955	120	850	2253	45126	2.66
Ficus lacor Buch.-Ham.	Moraceae	21	358	850	1568	28172	325	750	1602	31657	12.37
Ficus neriifolia Sm.	Moraceae	55	1280	1850	2506	25298	1550	2050	2791	15922	-37.06
Ficus racemosa L.	Moraceae	15	133	450	1327	8771	127	550	1617	8095	-7.71
Ficus religiosa L.	Moraceae	29	85	150	1298	59005	86	150	1502	74510	26.28
***Ficus semicordata* Buch.-Ham. ex Sm.**	Moraceae	89	109	550	1739	69806	119	950	2100	75837	8.64
Flacourtia indica (Burm.f.) Merr.	Flacourtiaceae	15	150	350	799	15629	128	350	952	32222	106.17
Fraxinus floribunda Wall.	Oleaceae	18	637	1550	2460	49402	728	1650	2531	36109	-26.91
Garuga pinnata Roxb.	Burseraceae	39	256	450	1258	26118	246	450	1431	42930	64.37
Gmelina arborea Roxb.	Verbenaceae	9	82	150	1070	56416	86	150	1371	76093	34.88
Grevillea robusta A.Cunn. ex R.Br.	Proteaceae	19	281	750	1658	40308	296	750	1728	44125	9.47
Grewia asiatica L.	Tiliaceae	48	273	750	1656	53992	217	950	2069	76767	42.18

Species name	Family	Presence record	1985				2050				Change in dist. area (%)
			Elevation (m a.s.l.)			Dist. area (pixels)	Elevation (m a.s.l.)			Dist. area (pixels)	
			Min	Opt	Max		Min	Opt	Max		
Grewia optiva J.R.Drumm. ex Burret	Tiliaceae	17	115	550	1838	65810	116	550	2076	71451	8.57
***Haldina cordifolia* (Roxb.) Ridsdale**	Rubiaceae	85	86	350	679	34911	84	250	983	56750	62.56
Hymenodictyon orixense (Roxb.) Mabb.	Rubiaceae	18	74	74	249	20992	75	75	318	23608	12.46
Ilex dipyrena Wall.	Aquifoliaceae	16	2122	2850	3305	6576	2408	3050	3642	8708	32.42
Juglans regia L.	Juglandaceae	23	1465	2150	3002	24118	1902	2750	3413	19450	-19.35
Kydia calycina Roxb.	Malvaceae	9	82	150	969	25404	85	550	1244	51549	102.92
***Lagerstroemia parviflora* Roxb.**	Lythraceae	222	93	350	973	45705	87	350	1291	71817	57.13
Lannea coromandelica (Houtt.) Merr.	Anacardiaceae	102	82	250	964	50590	85	350	1278	73118	44.53
Larix griffithii Hook.f.	Pinaceae	10	3307	4350	4684	4589	4007	5450	5775	21698	372.83
Leucaena leucocephala (Lam.) de Wit	Fabaceae	11	86	650	1311	18334	86	650	1339	17217	-6.09
Lindera pulcherrima (Nees) Hook.f.	Lauraceae	24	620	3050	4054	50185	950	3050	5366	58275	16.12
Litsea doshia (D.Don) Kosterm.	Lauraceae	27	822	1650	2941	39087	892	1750	3006	36841	-5.75
***Litsea monopetala* (Roxb.) Pers.**	Lauraceae	104	89	850	1511	65513	113	1050	1829	54466	-16.86
***Lyonia ovalifolia* (Wall.) Drude**	Ericaceae	126	1275	2150	2832	35394	1710	2550	3314	25505	-27.94
Lyonia villosa (Wall. ex C.B.Clarke) Hand.-Mazz.	Ericaceae	7	2231	4050	4562	13155	2387	5750	5806	23369	77.64
Macaranga denticulata (Blume) Müll.Arg.	Euphorbiaceae	19	90	250	1940	51773	91	250	2165	83001	60.32
Machilus duthiei King	Lauraceae	47	1375	2150	3049	30061	1825	2850	3490	27062	-9.98
***Mallotus philippensis* (Lam.) Müll.Arg.**	Euphorbiaceae	219	87	450	1140	61701	87	350	1443	81377	31.89
Mangifera indica L.	Anacardiaceae	13	105	550	1014	19598	102	550	1122	27558	40.62
Melia azedarach L.	Meliaceae	28	84	150	1391	68439	86	150	1573	80934	18.26
Mesua ferrea L.	Clusiaceae	7	107	450	979	18873	93	450	1160	48851	158.84
Miliusa velutina (A.DC.) Hook.f. & Thomson	Annonaceae	60	76	250	450	26624	79	250	620	40985	53.94
Mitragyna parvifolia (Roxb.) Korth.	Rubiaceae	9	95	150	296	9877	80	150	612	41051	315.62
***Myrica esculenta* Buch.-Ham. ex D.Don**	Myricaceae	75	1152	1650	2270	32102	1546	2150	2639	19133	-40.4
Neolamarckia cadamba (Roxb.) Bosser	Rubiaceae	7	109	450	1229	26572	105	450	1375	42612	60.36
Neolitsea umbrosa (Nees) Gamble	Lauraceae	8	932	1950	3907	34555	954	1950	4146	31969	-7.48
Nyctanthes arbor-tristis L.	Oleaceae	22	90	550	1039	21831	92	550	1295	43835	100.79
Ocotea lancifolia (Schott) Mez	Lauraceae	9	182	450	1523	25691	151	450	1640	35839	39.5
Oroxylum indicum (L.) Kurz	Bignoniaceae	7	95	450	1613	65700	90	450	1943	93297	42
Persea odoratissima (Nees) Kosterm.	Lauraceae	30	326	1250	2214	60748	351	1250	2299	58509	-3.69
Phyllanthus emblica L.	Phyllanthaceae	143	105	350	1137	50946	98	350	1402	69701	36.81
Picea smithiana (Wall.) Boiss.	Pinaceae	13	1979	3750	4541	28388	2371	3950	5283	34025	19.86
***Pinus roxburghii* Sarg.**	Pinaceae	117	573	1250	2153	55733	932	1650	2757	43126	-22.62

Species name	Family	Presence record	1985				2050				Change in dist. area (%)
			Elevation (m a.s.l.)			Dist. area (pixels)	Elevation (m a.s.l.)			Dist. area (pixels)	
			Min	Opt	Max		Min	Opt	Max		
***Pinus wallichiana* A.B.Jacks.**	Pinaceae	59	1823	3050	4515	24363	2858	4550	5572	29752	22.12
Prunus cerasoides Buch.-Ham. ex D.Don	Rosaceae	34	1165	1950	2468	16899	1536	2150	2700	8730	-48.34
Prunus napaulensis (Ser.) Steud.	Rosaceae	17	1551	2250	4193	29314	1946	2550	5248	21988	-24.99
Prunus persica (L.) Batsch	Rosaceae	11	1114	2450	4371	26121	1414	4050	5095	17402	-33.38
Psidium guajava L.	Myrtaceae	8	148	650	1301	18866	151	650	1635	33741	78.85
Pyrus pashia Buch.-Ham. ex D.Don	Rosaceae	69	742	1450	2741	47167	1198	2250	3163	24339	-48.4
Quercus floribunda Lindl. ex A.Camus	Fagaceae	11	1567	2050	3714	12234	1868	2550	3856	5007	-59.07
Quercus glauca Thunb.	Fagaceae	36	622	1650	3431	74814	653	1750	3550	71984	-3.78
***Quercus lamellosa* Sm.**	Fagaceae	20	1122	2150	3297	40962	1502	2650	3661	30598	-25.3
***Quercus lanata* Sm.**	Fagaceae	78	1117	1750	2633	37597	1601	2250	3177	24319	-35.32
Quercus oblongata D.Don	Fagaceae	21	1017	2150	2967	31361	1388	2250	3155	18420	-41.26
Quercus oxyodon Miq.	Fagaceae	15	1147	2450	4209	44831	1444	2450	5338	39472	-11.95
***Quercus semecarpifolia* Sm.**	Fagaceae	121	1930	3050	3723	30490	2410	3150	4075	19536	-35.93
***Rhododendron arboreum* Sm.**	Ericaceae	171	1483	2450	3217	35812	1937	2850	3571	25321	-29.29
***Rhododendron arboreum* var. *cinnamomeum* (Wall. ex G.Don) Lindl.**	Ericaceae	12	2426	3450	4491	12908	2921	3750	5320	13098	1.47
***Rhododendron barbatum* Wall. ex G.Don**	Ericaceae	25	2616	3450	4152	15568	2999	3750	4732	15704	0.87
***Rhododendron campanulatum* D.Don**	Ericaceae	16	2945	3550	4530	16574	3274	4350	5487	21628	30.49
Saurauia napaulensis DC.	Actinidiaceae	17	565	1450	2416	40810	579	1450	2553	47805	17.14
***Schima wallichii* (DC.) Korth.**	Theaceae	138	582	1150	2022	37938	734	1550	2315	39491	4.09
Schleichera oleosa (Lour.) Merr.	Sapindaceae	15	78	250	405	12237	77	250	536	22750	85.91
Semecarpus anacardium L.f.	Anacardiaceae	127	98	350	923	35325	92	350	1202	52011	47.24
***Shorea robusta* Gaertn.**	Dipterocarpaceae	324	93	350	1032	53145	87	350	1320	72933	37.23
Sorbus cuspidata (Spach) Hedl.	Rosaceae	12	1064	3150	4250	27449	1372	3150	5158	23008	-16.18
Sorbus foliolosa (Wall.) Spach	Rosaceae	20	3154	3550	4626	20886	3621	4050	5747	41646	99.4
Sterculia villosa Roxb.	Malvaceae	9	98	350	775	30495	90	350	1070	54460	78.59
Stereospermum tetragonum DC.	Bignoniaceae	26	80	250	569	26929	81	250	662	35015	30.03
Symplocos pyrifolia Wall. ex G.Don	Symplocaceae	7	521	1950	2307	4672	562	5150	5610	5674	21.45
Symplocos ramosissima Wall. ex G.Don	Symplocaceae	29	1347	2150	2900	19995	1609	2350	3070	14329	-28.34
***Syzygium cumini* (L.) Skeels**	Myrtaceae	256	95	350	1228	64627	91	350	1484	80859	25.12
Syzygium jambos (L.) Alston	Myrtaceae	6	157	850	2196	13335	111	850	3862	27572	106.76
Syzygium nervosum A.Cunn. ex DC.	Myrtaceae	89	172	450	1202	32351	135	350	1342	49330	52.48
Taxus wallichiana Zucc.	Taxaceae	24	2029	3550	4255	20715	2374	3850	4654	19662	-5.08

Species name	Family	Presence record	1985				2050				Change in dist. area (%)
			Elevation (m a.s.l.)			Dist. area (pixels)	Elevation (m a.s.l.)			Dist. area (pixels)	
			Min	Opt	Max		Min	Opt	Max		
***Terminalia alata* Roth**	Combretaceae	261	96	350	1076	47659	89	350	1365	70343	47.6
Terminalia bellirica (Gaertn.) Roxb.	Combretaceae	44	241	450	1047	21638	184	450	1267	42338	95.67
Terminalia chebula Retz.	Combretaceae	90	88	350	915	39236	85	350	1223	66531	69.57
Toona ciliata M.Roem.	Meliaceae	36	278	850	2001	56095	268	950	2275	69502	23.9
Toxicodendron wallichii (Hook.f.) Kuntze	Anacardiaceae	42	121	450	2557	78969	130	450	4835	86713	9.81
***Tsuga dumosa* (D.Don) Eichler**	Pinaceae	52	2301	3050	3797	24656	2791	3550	4261	20374	-17.37
Wendlandia puberula DC.	Rubiaceae	7	484	2250	2491	11672	499	2250	5714	18356	57.27
Ziziphus jujuba Mill.	Rhamnaceae	22	88	450	1388	47325	90	550	1556	68731	45.23
Ziziphus rugosa Lam.	Rhamnaceae	8	96	150	866	23340	97	150	1096	29586	26.76

Table S4.3. Detailed list of 53 environmental variables compiled for this study. Variable categories, sub-categories, names and their respective units, abbreviations and sources or remarks on computation methods are presented. Environmental variables in bold mark 19 least correlated environmental variables selected for the MaxEnt modelling.

Category	Sub-category	Name and unit	Abbreviation	Source/remarks
Climatic	Temperature	**Isothermality (Mean temperature diurnal range/ Temperature annual range) * 100**	**IT**	WorldClim 2 data (www.worldclim.org/version2)
		Maximum temperature of warmest month (°C)	MaxTWaM	
		Mean annual temperature (°C)	**MAT**	
		Mean temperature diurnal range (Mean of monthly (maximum temperature–minimum temperature), °C)	**TDR**	
		Mean temperature of coldest quarter (°C)	TCQ	
		Mean temperature of driest quarter (°C)	TDQ	
		Mean temperature of warmest quarter (°C)	TWaQ	
		Mean temperature of wettest quarter (°C)	TWeQ	
		Minimum temperature of coldest month (°C)	MinTCM	
		Temperature annual range (Maximum temperature of warmest month–Minimum temperature of coldest month, °C)	**TAR**	
		Temperature seasonality (standard deviation * 100)	TS	
	Precipitation	**Annual precipitation (mm)**	**AP**	
		Precipitation of coldest quarter (mm)	PCQ	
		Precipitation of driest month (mm)	PDM	
		Precipitation of driest quarter (mm)	**PDQ**	
		Precipitation of warmest quarter (mm)	PWaQ	
		Precipitation of wettest month (mm)	PWeM	
		Precipitation of wettest quarter (mm)	PWeQ	
		Precipitation seasonality (coefficient of variation)	**PS**	
	Other climatic	Annual potential evapotranspiration (mm)	PET	Computed using WorldClim 2 monthly data
		Climatic moisture index (Annual precipitation/ Annual potential evapotranspiration–1 when Annual precipitation < Annual potential evapotranspiration and 1–Annual potential evapotranspiration/Annual precipitation when Annual precipitation ≥ Annual potential evapotranspiration)	CMI	
		Cloud cover seasonality (standard deviation * 100)	**CCS**	Global 1-km cloud cover data (www.earthenv.org/cloud)
		Growing degree days (sum of all monthly temperatures > 10 °C, multiplied by total number of days)	GDD10	Computed using WorldClim 2 monthly data
		Maximum climatological water deficit (the most -ve value of climatological water deficit (CWD) attained over a year, where CWD of a month = CWD of previous month + Precipitation of the month–Evapotranspiration of the month)	MCWD	
		Mean annual cloud frequency (% * 100)	**MACF**	Global 1-km cloud cover data (www.earthenv.org/cloud)
		Potential evapotranspiration of coldest quarter (mm)	PETCQ	Computed using WorldClim 2 monthly data
		Potential evapotranspiration of driest quarter (mm)	PETDQ	
		Potential evapotranspiration of warmest quarter (mm)	PETWaQ	
		Potential evapotranspiration of wettest quarter (mm)	PETWeQ	
		Potential evapotranspiration seasonality (standard deviation * 100)	PETseas	
		Solar radiation (Mean of monthly means, kJ/sq m/day)	Srad	
		Thornthwaite's aridity index	**AI**	
		Water vapour pressure (Mean of monthly means, kPa)	Vapr	
		Wind speed (Mean of monthly means, m/s)	Wind	

Category	Sub-category	Name and unit	Abbreviation	Source/remarks
Edaphic	Chemical	Soil cation exchange capacity (cmol/kg)	CEC	Computed using ISRIC-SoilGrids (ftp://ftp.soilgrids.org/data/aggregated/1km/)
		Soil organic carbon content (gm/kg)	**OCC**	
		Soil organic carbon stock (tonnes/ha)	OCS	
		Soil pH * 10 in water	**pH**	
	Physical	**Available soil water capacity until wilting point (%)**	**AWCWP**	
		Available soil water capacity with FC = pF 2.0 (%)	AWCh1	
		Available soil water capacity with FC = pF 2.3 (%)	AWCh2	
		Available soil water capacity with FC = pF 2.5 (%)	AWCh3	
		Bulk density (kg/cu m)	BD	
		Depth to bedrock (R horizon) up to 200 cm	D2BR	
		Saturated water content teta-S (%)	SWCtS	
		Soil clay content (%)	**ClayC**	
		Soil coarse fragments content (%)	**CFC**	
		Soil sand content (%)	SandC	
		Soil silt content (%)	**SiltC**	
Topographic		Elevation (m)	Elev	Computed using SRTM 90m digital elevation database v4.1 (www.cgiarcsi.community/data/srtm-90m-digital-elevation-database-v4-1)
		Aspect (deg)	**Aspect**	
		Distance to water (arc sec)	**D2W**	Computed using river network data (http://www.hydrosheds.org/) and global lakes and wetlands data (www.worldwildlife.org/pages/global-lakes-and-wetlands-database)
		Slope (deg)	**Slope**	Computed using SRTM 90m digital elevation database v4.1 (www.cgiarcsi.community/data/srtm-90m-digital-elevation-database-v4-1)

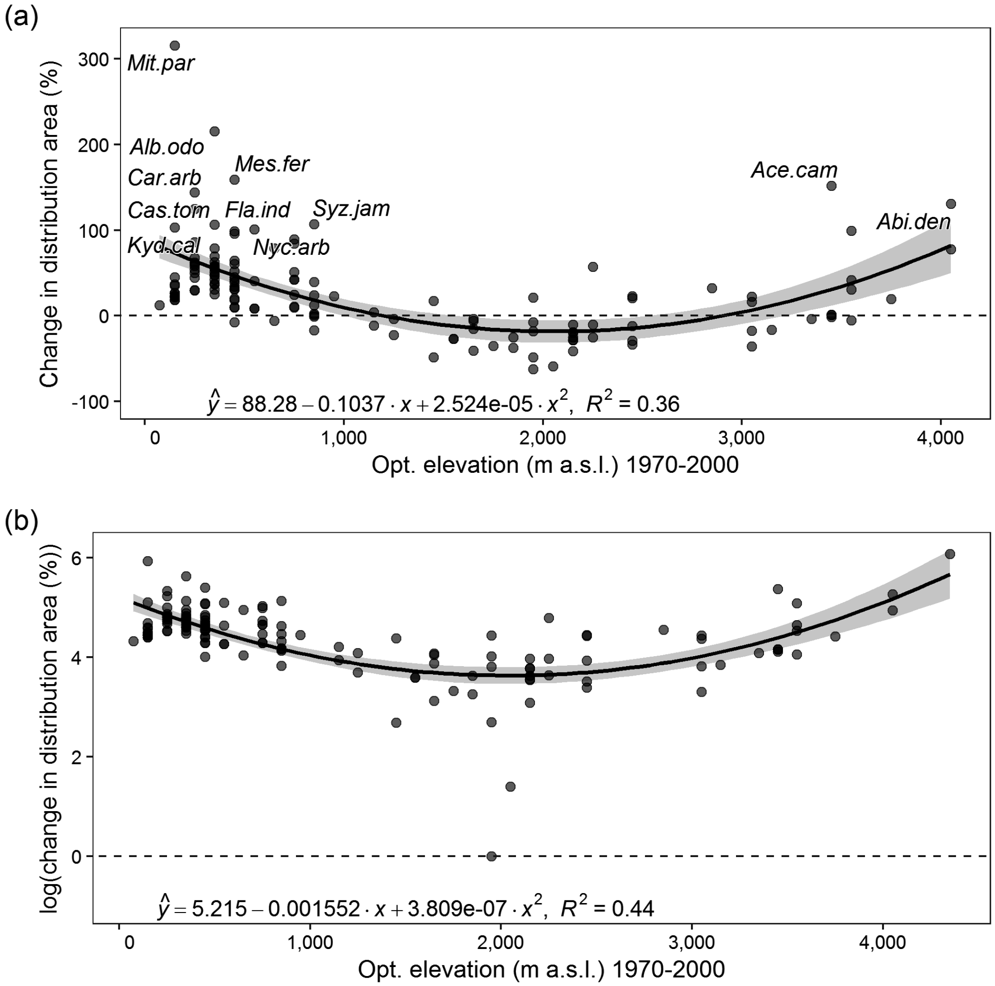


Figure S4.1. Relationship between (a) percentage change in distribution area between periods 1970-2000 ('1985') and 2041-2060 ('2050') relative to 1985 distribution area and optimum elevation for 136 Himalayan tree species excluding *Larix griffithii* and (b) log-transformed percentage change in distribution area between periods 1970-2000 ('1985') and 2041-2060 ('2050') relative to 1985 distribution area and optimum elevation for 137 Himalayan tree species. Each circle represents one species. The horizontal dashed line indicates zero or no change in distribution area. The solid black regression line is significant at $p < 0.05$. Species with distribution area gain >100% are labelled with their name abbreviations. Species name abbreviations used in the plot refer to first three letters of their genus and species. The complete list of study species is shown in Table S4.2. The evaluated distribution area refers to Nepal.

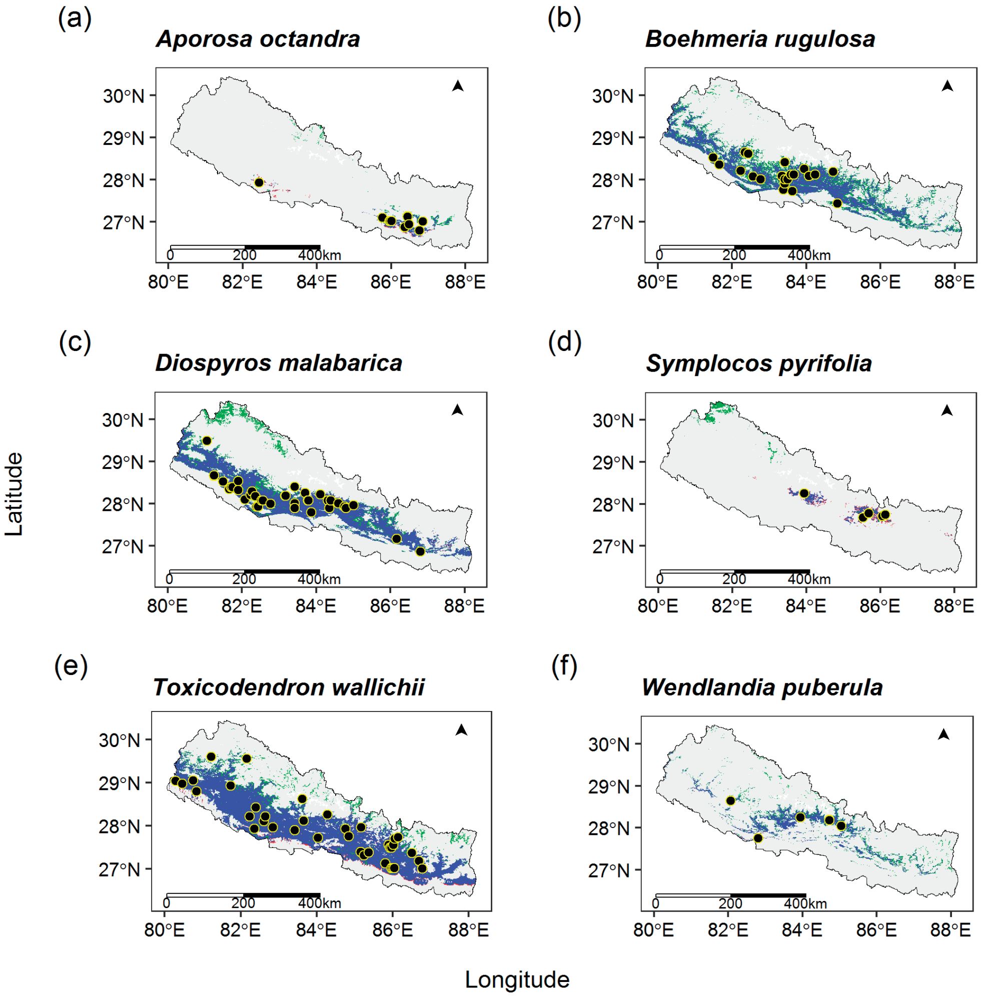


Figure S4.2. Maps showing changes in distribution area between 1985 and 2050 for six tree species: (a) *Aporosa octandra*, (b) *Boehmeria rugulosa*, (c) *Diospyros malabarica*, (d) *Symplocos pyrifolia*, (e) *Toxicodendron wallichii* and (f) *Wendlandia puberula*. The black line indicates national boundary of Nepal. The Government of Nepal published on 20th May 2020 a new political map including Kalapani, Lipulekh and Limpiyadhura inside the Nepal borders. As our research started in 2016, in our research, we used the previous version of the map without these territories. Colours indicate distribution areas that will be lost (red), maintained (blue) or gained (green). The areas in white represent areas with missing environmental data. Black circles indicate spatially unique observed species presence records at 30 arc seconds (~1km) raster resolution from forest inventories, online floral databases and field survey for Nepal used for modelling the species distribution.

CHAPTER

5

General discussion

5.1 Introduction

The Himalayas are amongst the global hotspots of biodiversity (Mittermeier et al., 2004) because they present one of the longest and steepest elevational gradients in the world, supporting a diversity of vegetation types and plant species (Figure 1.2; Lillesø et al., 2005; Shrestha et al., 2015). The Himalayas are experiencing substantial warming (0.2 °C decade^{-1} from 1951–2014, Ren et al., 2017), particularly at higher elevations (0.5 °C decade^{-1}, Luitel et al., 2020), forcing species to shift their upper elevation limits upslope at a rate as high as 27 m decade^{-1} (Bhatta et al., 2018; Gaire et al., 2014; Suwal et al., 2016; Telwala et al., 2013). Such elevational shifts will be particularly problematic for plant species with narrow elevational ranges; if they cannot acclimate or migrate sufficiently rapid, their whole population may drop outside their climatic niche, leading to suboptimal performance, strong competitive suppression by better-adapted species, and possibly extinction. The Himalayas present an ideal system to study how environmental conditions and species properties (species' elevational positions and functional traits) shape species' distributions along an elevational gradient and, from this, to project how future climate warming will affect species' elevational distributions. In this thesis, I quantified species' distributions in terms of their elevational ranges defined by lower, optimal (i.e. the 100 m elevation belt with the highest proportion of area predicted to be occupied by a target species) and upper elevational limits, and of distribution areas defined by the size of the occupied area. In this thesis, I analysed the patterns of plant species distribution along the Himalayan elevational gradient in Nepal and addressed the following questions: 1) which environmental factors best predict species' elevational distributions and do highland species occupy wider elevational ranges than species from the lowlands (*Chapter 2*)?, 2) how do functional traits shape species' elevational positions and lead to species partitioning of the elevational gradient (*Chapter 3*)? and 3) how will predicted future global warming affect species' elevational ranges and distribution areas (*Chapter 4*)? In this chapter (*Chapter 5*), I combine the results of this thesis and discuss the importance of understanding the mechanisms that shape current and predicted future species' elevational distributions to inform conservation measures for the Himalayan forests, designing climate change adaptation measures, and to select plant species that will require assisted migration for their future survival. I will also discuss the role of science and its research priorities and the society in general for safeguarding the diversity and functioning of tropical montane landscapes.

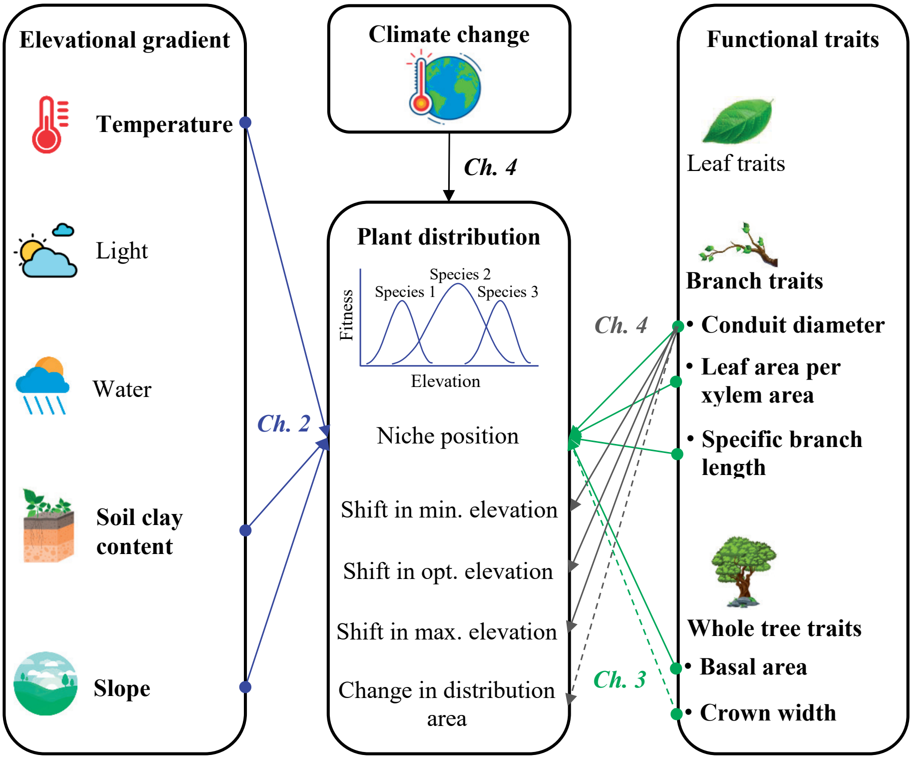


Figure 5.1. Conceptual diagram showing interlinkage among the three chapters (Ch.). Ch. 2 focuses on roles of environmental factors on controlling present-day species elevational distributions; Ch.3 focuses on roles of plant traits in shaping present-day species elevational distributions; and Ch.4 focuses on effects of climate change and plant traits on change in species elevational distributions i.e. species elevational range shifts. Environmental factors in bold indicate key environmental factors predicting present-day species elevational distributions. Arrows in blue indicate the relationships between environmental factors and present-day species elevational distributions. Traits in bold indicate key traits shaping present-day species elevational distributions. Arrows in green (solid – significant negative at p <0.05 and dashed non-significant positive) indicate the relationships between traits and present-day species elevational distributions. Arrows in grey (solid – significant negative at p <0.05 and dashed non-significant positive) indicate the relationships between conduit diameter and species range shift parameters.

5.2 Species' distributions along elevational gradient (*Chapter 2*)

In the Himalayas, the presence of steep mountain ranges are likely to leave plant species with only one option to respond to climate warming – to shift their distribution ranges upward. To accurately predict how montane plant species are likely to respond to climate change, it is urgently needed to understand what controls their distribution and how species are spatially distributed in montane landscapes. In *Chapter 2*, I asked which environmental factors best predict species' elevational distributions, and whether highland species occupy wider elevational ranges than lowland species?

5.2.1 Environmental factors that best predict species' elevational distributions

I found that mean annual temperature followed by soil clay content and slope are the key environmental factors that best predict species' elevational distributions in the Himalayas (Figure 2.3; Figure 5.1). The important role of the temperature was expected because temperature decreases approximately linearly with elevation (Figure 1.2) and directly influences plant metabolic rates and physiological processes, and is associated with growing season length (Table S2.3). Soil clay content and slope appeared as next important environmental factors probably because, along this gradient, the Himalayas become steeper and soils become shallower and coarser with elevation (Figure 1.2; Table S2.3) reducing the opportunity for rooting and water and nutrient uptake. Along this elevational gradient, mean annual temperature is highly correlated with a suite of other environmental variables (Figure 2.1). The majority of these variables are closely related to temperature, such as mean temperatures of different quarters, temperature extremes and growing degree-days whereas other meteorological variables (such as solar radiation, wind speed, maximum climatological water deficit and potential evapotranspiration) and edaphic variables (such as available soil water content and bulk density) are not directly related to temperature. Such strong associations among environmental variables allow for highlighting the relative importance of an environmental variable (such as mean annual temperature) and its associated covariates in shaping species niches, but not for teasing apart a single ecological mechanism regulating species niches along the elevational gradient. Nevertheless, my study shows that apart from the obvious changes in temperature and its associates with elevation, both soil conditions and slope play a major role in shaping species distributions along lowland to highland gradient in the Nepalese Himalayas.

5.2.2 Elevational ranges are widest for plant species from intermediate elevations

Because environmental conditions become harsher, more stressful and variable with increase in elevation, I hypothesized, in line with the climatic variability hypothesis, that species living at high elevations would have wider physiological tolerances to environmental conditions and therefore occupy wider elevational ranges. However, I found that species at both ends of the Himalayan elevational gradient have narrow elevational ranges and species in the middle (2,000-3,000 m a.s.l.) have relatively wide elevational ranges (Figure 2.5). Earlier Himalayan studies (Bhattarai & Vetaas, 2006; Vetaas & Grytnes, 2002) suggested that in the lowlands and highlands, high species richness might lead to stronger interspecific competition and narrower species ranges. Since the majority of the study species have their elevational optimum towards the lowlands (Figure 2.5), the narrow elevational ranges at lower end of the gradient could indeed result from stronger interspecific competition (Bhattarai & Vetaas, 2006; Schellenberger Costa et al., 2018; Vetaas & Grytnes, 2002) or from niche partitioning amongst tropical species (Stevens, 1992). Maximum richness of endemic species at higher elevations was identified as a reason for narrow elevational ranges at high elevations by Vetaas & Grytnes (2002). But in my case I don't have enough endemic species to support this. Thus, it could be an artefact that interpolation close to the upper end of the gradient created artificially narrow ranges due to low sampling intensity. Alternatively, wide elevational ranges at the middle of the gradient could be the result of a mid-domain effect (Colwell & Hurtt, 1994), which suggests that species with wide elevational ranges have their elevational optima closer to the centre of the domain (cf. Bhattarai & Vetaas, 2006; Colwell & Lees, 2000). With predicted climate warming, tracking suitable climatic ranges could probably be the best long-term survival strategy. In doing so, it is likely that the distributions of mid-elevation species might be less affected than the distributions of warm-adapted and cold-adapted species at both ends of the elevational gradient since their wider elevational ranges may partially buffer against climate change induced range shifts.

5.3 Roles of functional traits in shaping plant species distribution (*Chapter 3*)

Plant functional traits determine plant performance (Poorter & Bongers, 2006) and have therefore the potential to shape and predict species distributions (Violle et al., 2007). In several studies (Mao et al., 2018; Yang et al., 2020), it was shown that there are differences in plant growth and traits between low and high elevation plant communities, however, the directions and strengths of such relationships are poorly understood. In *Chapter 3*, I asked how functional traits shape species' elevational positions and lead to species partitioning of the elevational gradient?

5.3.1 Key plant strategies among Himalayan tree species

I hypothesized that the harsher environmental conditions at higher elevations select for species with more conservative trait values and vice versa. Indeed, I found that the highland species have a small stature, small and thick leaves with low nutrient concentrations, and narrow conduits that allow them to conserve their slowly acquired carbon and nutrients and survive harsh highland conditions. In contrast, the lowland species have a large stature, large and thick leaves with high nutrient concentrations, and wide conduits that allow them to be competitive and acquisitive under benign lowland conditions (Figure 3.3). The two independent global strategy spectra, i.e. plant size and leaf economics, identified by Díaz et al. (2016) aligned closely together into one conservative-acquisitive spectrum in my study. A reason for this might be that I focused only on trees that reduces the size effects compared to entire plant communities. On the other hand, focusing on a single life form resulted into the emergence of a second strategy spectrum of tissue toughness representing the phylogenetic split between Rhododendrons with tough tissue and the conifers with soft tissues in the highlands (Figure 3.3).

5.3.2 Functional traits that best predict tree species' elevational positions

I also predicted that traits associated with a conservative-acquisitive strategy spectrum would best predict species' positions along an elevational gradient. Indeed, I found that four traits related to that spectrum best predict tree species' positions along the elevational gradient (Figure 3.4; Figure 5.1; Table 3.3). These four traits were negatively associated with elevation suggesting that the highland species have small size (small basal area), low hydraulic efficiency (narrow conduits) and lower light competitiveness (low leaf area per xylem area and specific branch length). Such properties allow highland tree species to be persistent and conservative under harsh highland conditions; whereas the lowland species have an opposite suite of traits that allow them to be competitive and acquisitive under benign lowland conditions. Interestingly, along this extreme environmental gradient, stem and branch traits that integrate multiple plant organs and functions are better predictors of species' elevational distributions than leaf traits.

5.4 Climate change induced species range shifts (*Chapter 4*)

In montane landscapes throughout the world, climate warming is causing many plant species to shift their distribution ranges upslope to cooler climatic conditions (Feeley et al., 2011; Geppert et al., 2020; He et al., 2019; Marshall et al., 2020). Species show substantial variation in the magnitude of these elevational shifts, but the underlying drivers are unclear (Neate-Cegg et al., 2021). In *Chapter 4*, I asked how future predicted global warming will affect species' elevational ranges and distribution areas?

5.4.1 Rates of shift amongst low and high elevation species

In the face of climate change species have to 1) acclimate or adapt to the changed conditions, 2) migrate to track suitable climatic ranges through dispersal and shift their ranges upward, or 3) otherwise go extinct. Tracking suitable climatic ranges through migration could probably be the best long-term survival strategy. Therefore, in this thesis, I studied which areas are rendered unsuitable resulting in local extinction and which areas are predicted to become suitable under future climatic conditions through ecological niche models. Because upslope movements along steep slopes result in rapid decrease in temperature, I hypothesized that highland species that occur on steeper slopes would have to shift upslope at slower rates than low elevation species despite elevation dependent warming. However, I found that highland species show larger predicted elevational shifts than lowland species (Figure 4.2). Such faster predicted range shifts of highland species suggest that along this extreme elevational gradient upslope range shifts are primarily controlled by faster observed and predicted temporal rates of warming i.e. elevation dependent warming (Gao et al., 2018; Luitel et al., 2020; Pepin et al., 2015) and not by decrease in temperature resulting from upslope movements. The average upslope shifts of the maximum elevation limit of the tree species are predicted to be as high as 8 m yr^{-1} (Figure 4.2c inset) which is more than 2 times faster than the currently observed average upward shifts of the upper distribution limit of highland tree species in the Himalayas (3 m yr^{-1}, Gaire et al., 2014; Telwala et al., 2013) and much faster than the global average of 0.6 m yr^{-1} (Parmesan & Yohe, 2003). These results imply that the highland species might not be able track the environmental changes in the future and therefore, it should be considered to establish migration corridors through landscapes that probably are fragmented by conversion to other types of land use, or even assist species to migrate to potentially suitable future highland habitats through direct seeding or planting (cf. Yan & Tang, 2019).

5.4.2 Changes in distribution area amongst low and high elevation species

Because migration to higher elevations results in smaller available surface areas, I hypothesized that all tree species will reduce their distribution area, and that low elevation species will show the largest reductions in distribution area, as they are likely to be forced to shift their ranges to slopes of the lowland plains. In contrast, I found that the majority (71%) of the tree species are predicted to enlarge their distribution area: these are particularly species from the lowlands or highlands whereas species from mid-elevations are predicted to reduce their distribution area (Figure 4.3, Figure 4.4). The prediction that lowland species expand their distribution area is partly explained by the possibility that the warm-adapted Himalayan lowland species extend their upper limits upslope while they maintain their lower limits, despite warming (Figure 4.2, Figure 4.4). However, in the long run, with an ongoing increase in temperature, these lowlands may surpass the thermal maximums of the lowland species leading to the net loss in lowland species richness as a consequence of climate change induced upslope range shifts and lowland extinctions (lowland biotic attrition, Colwell et al., 2008; Feeley & Silman, 2010). Lowland species should, therefore, be monitored for ensuring their long-term viability especially at the trailing edge of their distribution ranges. The prediction that many mid-elevation species (between 1,000 and 2,500 m a.s.l.) reduce their distribution area can be explained by the smaller upslope surface areas available above 1,000 m a.s.l. (see Figure 4.1a), and their lower limits becoming unsuitable for them to survive. The prediction that highland species expand their distribution areas is in line with the findings of other studies in the Himalayas (Anderson et al., 2020; He et al., 2019; He et al., 2020; Yan & Tang, 2019) and in alpine ecosystems in general (Rew et al., 2020). This suggests that warming is likely to make a large area of intermountain valleys and highland plateaus situated around 4,500 m a.s.l. (Elsen & Tingley, 2015; Figure 4.1; Figure 4.2c) suitable for the upslope shifting highland species. This suggests that along the Himalayan elevational gradient, the actual change in distribution area depends on the Himalayan topography and the surface area of each elevational belt (cf. Elsen & Tingley, 2015).

5.4.3 Environmental variables that control species range shifts

Because the Himalayas are predicted to become warmer and wetter (MoFE, 2019; Table S4.1a, e), I hypothesized that species for which species distribution models are driven by responses to temperature and precipitation would show upslope shifts in their optimum elevations resulting in reduction of their distribution areas. Indeed, the species for which their species distribution models are determined by temperature (i.e. mean annual temperature) showed the strongest predicted upslope shifts. But in contrast, they showed the largest expansion in their predicted distribution areas (Figure 4.5). This suggests that for warm-adapted lowland species such increase in temperature may facilitate range expansion in the Himalayas. As predicted climate change also leads to increased precipitation and decrease in aridity creating wetter systems, aridity may also affect the magnitude of upslope shifts and changes in distribution area. The species for which their species distribution models are determined by aridity indeed showed the strongest predicted upslope shifts and significant contraction in their predicted distribution areas (Figure 4.5). Several studies from the Himalayas (Gaire et al., 2014; Telwala et al., 2013) and other mountain ranges (Crimmins et al., 2011; Feeley et al., 2011; Lenoir et al., 2008; Pauli et al., 2012; Zhang et al., 2020) have highlighted such important roles of precipitation–in addition to warming–in controlling species range shifts. This suggests that for the species that prefer cool and dry to moist sites, such increase in temperature and precipitation may lead to range contraction. Interestingly, soil clay content (ClayC) appeared as another important environmental variable (Figure 4.5) suggesting that species' responses to climate change are also strongly modified by soil clay content. As species, particularly high-elevation species, shift upslope, they are likely to spill over to large clayey intermountain valleys and highland plateaus situated around 4,500 m a.s.l. (Elsen & Tingley, 2015; Figure 4.1; Figure 4.2c; Table S4.1m) that are presently not suitable as result of present bioclimatic conditions. Hence, fixed soil properties in combination with changing bioclimatic conditions may strongly constrain and modify species' responses to climate change along the Himalayan elevational gradient. Other studies – but from Andes – also found that responses of tree species and communities to global warming are highly heterogeneous (cf. Duque et al., 2015; Fadrique et al., 2018), and depend not only on the magnitude of temperature change at that specific elevation (Fadrique et al., 2018) but also on local soil conditions that can constrain the immigration and establishment of non-specialists (Duque et al., 2015). This suggests that soil effect is not Himalaya specific, but generic. In addition to soil conditions, exposure and slope may also add up to the heterogeneity in species' response to climate change (not significant in this case, Figure 4.5). Consequently, many individuals may persist in pockets that are micro-climatically suitable that cannot be predicted by my models. Hence, it is unlikely that species will go extinct over large parts of their distribution range. However, the populations may become more fragmented and less viable due to increased chances of inbreeding or severe decline in population size.

5.4.4 Traits as proxies to predict species range shifts and changes in distribution area

Traits could be used as proxies to predict the magnitude of climate change induced distribution shifts. Because acquisitive trait values (in this case wide conductive conduits) allow species to acquire resources faster and attain faster growth under optimal resource conditions (Estrada et al., 2016), and because conduit diameter is strongly negatively related to species optimum elevation in the Himalayas (Chapter 3), I hypothesized that species with acquisitive trait values would exhibit large range shifts and changes in distribution area. In contrast, I found that species with conservative trait values have the largest predicted upslope shifts (Figure 4.6a-c, Table 4.1), whereas conduit diameter was not significantly associated with predicted changes in distribution area (Figure 4.6d , Table 4.1). It should be acknowledged that my species distribution modelling approach (MaxEnt) does not include traits and mechanistic processes, and just models species distribution based on associations with the environment and future projections therein. In the Himalayas, species with acquisitive trait values (wide conduits) dominate lowlands (Chapter 3), probably because wide conduits facilitate water transport and growth, and enhance competitive ability in dense, moist and productive lowland forests (cf. Venturas et al., 2017). Indeed, the majority of these warm-adapted lowland species with acquisitive trait values are predicted to maintain their current lower elevation limits while they are predicted to shift their upper elevation limits upslope (Figure 4.2). Moreover, this suggests that an easily measurable trait, such as conduit diameter, can be used as a proxy for predicting species elevational range shifts in the Himalayas, and possibly in other montane regions.

5.5 Recommendations for future research and methodological improvement

Based on the results of this thesis, I provide first three recommendations for future research and then five recommendations for methodological improvement:

- **Trees in warmer, wetter and CO_2 rich Himalayas**. Nepal is predicted to be warmer and wetter in future (MoFE, 2019; Table S4.1a, e) and indeed temperature and aridity are identified to be key drivers of species range shifts (Figure 4.5). I did not include CO_2 concentration in this analysis. Future research on effects of warmer (e.g. temperature dependent photosynthesis and respiration), wetter (e.g. water use efficiency) and CO_2 richer environment (e.g. CO_2 dependent photosynthesis, allocation and water use) on growth and overall performance of tree species in the Himalayas could provide better understanding of species' responses to predicted future environmental changes. Moreover, my thesis emphasizes to include the interaction between temperature, soil properties and slope to assess climate change effects on montane trees.

- **Tree growth performance vs. leaf, branch and stem traits**. Interestingly, leaf traits (such as potassium concentration and leaf area ratio) had little effect on species' elevational positions, whereas stem and branch traits (such as basal area, conduit diameter, leaf area per xylem area and specific branch length) had large effects (Figure 3.4, Table 3.3). This suggests that for trees along this harsh environmental gradient, traits at higher integration levels (i.e. plant-level and branch-level traits) are more important for plant performance than traits at lower integration level (i.e. leaf traits). Future research on tree growth performance vs. leaf, branch and stem traits could further clarify the relationship between tree growth and tree traits along this extreme gradient.
- **Fate of highland biodiversity in the face of climate change**. It should be acknowledged that species distribution modelling approach (MaxEnt) that I used in this thesis mostly neglects that species could acclimate to new conditions. However, it is likely that species, to a certain extent, acclimate physiologically to increased warming (Slot & Winter, 2017), and partially maintain their current elevational distributions. Still the question remains whether these species will not be outcompeted by warm-adapted species that move upwards. Future research on competition resulting from species that move upwards and new arriving species could be useful to ascertain the fate of highland biodiversity in the face of climate change.
- **Improve spatial resolution of environmental predictors**. For species ecological niche modelling, I used global environmental datasets with a spatial resolution of 1 × 1 km. It is likely that these datasets did not fully capture all the local details in the Himalayas because: i) the environmental conditions may vary over short distances in the Himalayas and ii) the observed data that are at the base of these global interpolations are sparse in the Himalayas (Deblauwe et al., 2016). I recommend to produce national/regional datasets with a higher spatial resolution, through more rigorous field measurements. This will allow to develop more reliable species ecological niche models.
- **Include physiological and phenological traits in species' distribution analysis**. In this thesis, I used soft traits i.e. morphological and anatomical traits that serve as proxies for plant functions (Table 3.1). As morphological, anatomical and physiological traits interact and determine together species' habitat preferences (Belluau & Shipley, 2018; Sterck et al., 2011, 2014), I recommend to include additional traits in the analysis. Important traits could be traits related to freezing induced cavitation, cold damage to

leaves, temperature dependent photosynthesis and respiration, flowering and fruiting time, etc.

- **Process based models.** In this thesis, I used a correlative machine learning species distribution/ecological niche model, MaxEnt, that is neither process-based nor dynamic. MaxEnt models project species distributions, and thus mostly neglect that species could acclimate to new conditions. Improved mechanistic understanding would particularly benefit from model improvements that include incorporating dispersal and migration limitations in MaxEnt or incorporating mechanistic responses to environmental drivers (temperature and CO_2-dependent photosynthesis, freezing induced cavitation and freezing damage) and biotic interactions (e.g. competition with plants, but ideally also plant-pollinator and plant-herbivore interaction) in a dynamic process based model.
- **Include a diversity of life forms to assess climate change impacts.** Species vary considerably in their stature, life span and architectural complexity. Herbs are usually small statured, short-lived and architecturally less complex while trees are large statured, long-lived and architecturally more complex. Small short-lived species may migrate more easily but persist less easily in the face of climate change and vice versa. Often these different plant life forms co-dominate in different habitats. In general, trees and lianas dominate the lowland tropical forests while shrubs and herbs dominate the high elevation alpine scrubs and meadows. Fast-growing lowland species shifting upslope may outcompete highland species at their lower limits. Therefore, these different plant life forms can be expected to respond to climate change differently. However, in this thesis, I funneled down the analysis to tree species only. Future studies should take into account all major plant life forms: trees, shrubs, lianas and herbs from all elevational belts and their biotic interactions to evaluate the overall effects of climate change on plant species distribution and diversity.
- **Experimental tests**. The results of this thesis provides a primary indication on how trees in mountain ranges such as the Himalayas may respond to climate change. Additional information could be obtained through transplantation experiments where seedlings are planted at low, intermediate and high elevations. Through monitoring ecophysiological processes and performance, a better idea can be obtained about the mechanisms driving species responses to novel environments or suboptimal environments. Such experiments could be done for different ecological groups (e.g. acquisitive vs. conservative, different life forms, small vs. wide-ranging species) to get a better idea how ecophysiological processes and performance of these groups will be affected.

5.6 Management recommendations

Although Nepal's contribution to global greenhouse gas emission is negligible (0.027%, MoPE, 2016), it is amongst the countries most severe affected by climate warming (Eckstein et al., 2019). All sectors are experiencing severe adverse effects of climate change; be it natural sectors (such as agriculture, forests and biodiversity, and water resources) or social sectors (such as public health, rural and urban settlements and infrastructure, and tourism, natural and cultural heritage; MoFE, 2018). Adaptation to the adverse effects of climate change is a priority for Nepal. Most recently, Nepal initiated the process of formulation of National Adaptation Plan (NAP) with the goal of reducing vulnerability and building resilience to climate change by integrating adaptation across sectors and levels of government (MoFE, 2018). In this background, based on the results of this thesis, I provide the following management recommendations for the NAP for designing climate adaptation measures for forests and biodiversity.

- **Assisted migration.** The average upslope shifts of the maximum elevation of the tree species are predicted to be more than 2 times larger (8 m yr^{-1}, Figure 4.2c inset) than the observed average upward shifts of the upper distribution limit of highland tree species in the Himalayas (3 m yr^{-1}, Gaire et al., 2014; Telwala et al., 2013). Therefore, to enable species to track climate change, it should be considered to establish migration corridors through the landscapes fragmented by topography or land use, or even assist species to migrate to potentially suitable future highland habitats through direct seeding or planting (cf. Yan & Tang, 2019). Particularly in the highlands, where the distributions may be disjunct because the highland plateaus and valleys are intersected by mountain ranges, and because the valleys have different soil conditions, such as clayey deposits (Table S4.1m) and a higher organic carbon content (Devi & Sherpa, 2019; Table S4.1o), assisted migration might be the only way to enable species to track their preferred climatic niches.
- **Monitoring tree species populations**. The results of this thesis provide a primary indication on how trees in mountain ranges such as the Himalayas may respond to climate change. Simply because there is still too much uncertainty left for all species along this gradient. It is thus recommended to monitor whether species are able to maintain a viable population size especially for the species with the largest predicted contractions in distribution areas (e.g. *Betula alnoides*, *Prunus cerasoides*, *Pyrus pashia* and *Quercus floribunda*, Table S4.1) and the species with the largest predicted upslope shifts (e.g. *Abies densa*, *A. pindrow*, *Acer campbellii* and *Larix griffithii*, Table S4.2).
- **Potential additional uses of the results**. The results of this thesis may also be used in numerous additional ways such as locating currently undocumented species locations, potential locations where species may occur in the future, or potential locations where

the species could be seeded or planted to enable species to track their climatic niches, thus contributing to the species conservation and management.

5.7 General conclusions

In this thesis, I analysed the distribution patterns of 277 plant species along an elevational gradient in the Himalayas in Nepal and showed that the plant species distributions in the Himalayas are best predicted by temperature and its temperature (e.g. temperature extremes) and non-temperature (such as irradiance and PET) covariates followed by soil clay content and slope, but that future distributions will also be affected by changes in precipitation. I showed how multiple trade-offs in plant size, hydraulic efficiency and light competition determine species' positions along this elevational gradient. The Himalayan plant species face an uncertain future, because they are projected to shift upslope at much faster rates in response to the climate warming than the rates currently observed, and the question remains whether they will be able to track the predicted environmental changes. Based on these findings, here, I call for the need of assisted migration, as it might be the only way to save imperilled species that cannot track their preferred climatic niches. Conserving and managing rich biodiversity across the tropical montane landscapes is a challenge and it will become more challenging with the predicted environmental changes. Nevertheless, with improved understandings of the mechanisms that shape species' elevational distributions and the consequences that future climate change may have on species' elevational ranges and distribution areas, we can probably better predict the implications for the montane biodiversity and take informed actions to conserve and improve biodiversity along the slopes of the Himalayas for the benefit of not only the montane communities but also the global community.

References

Acharya, K. P., Vetaas, O. R., & Birks, H. J. B. (2011). Orchid species richness along Himalayan elevational gradients. *Journal of Biogeography*, *38*, 1821–1833. https://doi.org/10.1111/j.1365-2699.2011.02511.x

Adhikary, S. (2012). Seasonal and spatial variation of solar radiation in Nepal Himalayas. *Journal of Hydrology and Meteorology*, *8(1)*, 1–9.

Aguirre-Gutiérrez, J., Carvalheiro, L. G., Polce, C., van Loon, E. E., Raes, N., Reemer, M., & Biesmeijer, J. C. (2013). Fit-for-Purpose: Species Distribution Model Performance Depends on Evaluation Criteria–Dutch Hoverflies as a Case Study. *PLoS ONE*, *8(5)*, e63708. https://doi.org/10.1371/journal.pone.0063708

Amissah, L., Mohren, G. M. J., Bongers, F., Hawthorne, W. D., & Poorter, L. (2014). Rainfall and temperature affect tree species distribution in Ghana. *Journal of Tropical Ecology*, *30(5)*, 435–446. https://doi.org/10.1017/S026646741400025X

Anderson, K., Fawcett, D., Cugulliere, A., Benford, S., Jones, D., & Leng, R. (2020). Vegetation expansion in the subnival Hindu Kush Himalaya. *Global Change Biology*, *26(3)*, 1608–1625. https://doi.org/10.1111/gcb.14919

Anfodillo, T., Petit, G., Sterck, F., Lechthaler, S., & Olson, M. E. (2016). Allometric Trajectories and "Stress": A Quantitative Approach. *Frontiers in Plant Science*, *7*, 1–6. https://doi.org/10.3389/fpls.2016.01681

Angelo, C. L., & Daehler, C. C. (2015). Temperature is the major driver of distribution patterns for C 4 and C 3 BEP grasses along tropical elevation gradients in Hawaiʻi, and comparison with worldwide patterns. *Botany*, *93(1)*, 9–22. https://doi.org/10.1139/cjb-2014-0075

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, *22(1)*, 42–47. https://doi.org/10.1016/j.tree.2006.09.010

Austin, M. (2007). Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling*, *200(1–2)*, 1–19. https://doi.org/10.1016/j.ecolmodel.2006.07.005

Barry, R. G. (1992a). Mountain Climatology and Past and Potential Future Climatic Changes in Mountain Regions: A Review. *Mountain Research and Development*, *12(1)*, 71–86.

Barry, R. G. (1992b). *Mountain Weather and Climate* (2nd ed.). London and New York: Routledge.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15(4)*, 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Belluau, M., & Shipley, B. (2018). Linking hard and soft traits: Physiology, morphology and anatomy interact to determine habitat affinities to soil water availability in herbaceous dicots. *PLoS ONE*, *13(3)*, 1–15. https://doi.org/10.1371/journal.pone.0193130

Bertrand, R., Lenoir, J., Piedallu, C., Dillon, G. R., De Ruffray, P., Vidal, C., … Gégout, J. C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, *479(7374)*, 517–520. https://doi.org/10.1038/nature10548

Bhatta, K. P., Grytnes, J. A., & Vetaas, O. R. (2018). Downhill shift of alpine plant assemblages under contemporary climate and land-use changes. *Ecosphere*, *9(1)*. https://doi.org/10.1002/ecs2.2084

Bhattarai, K. R., & Vetaas, O. R. (2006). Can Rapoport's rule explain tree species richness along the Himalayan elevation gradient, Nepal? *Diversity and Distributions*, *12(4)*, 373–378. https://doi.org/10.11111/j.1366-9516.2006.00244.x

Bhattarai, K. R., Vetaas, O. R., & Grytnes, J. A. (2004). Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, *31*, 389–400.

Bhujel, K. B., Maskey-Byanju, R., & Gautam, A. P. (2017). Wildfire Dynamics in Nepal from 2000-2016. *Nepal Journal of Environmental Science*, *5*, 1–8. https://doi.org/10.3126/njes.v5i0.22709

Bitencourt, C., Rapini, A., Santos Damascena, L., & De Marco Junior, P. (2016). The worrying future of the endemic flora of a tropical mountain range under climate change. *Flora: Morphology, Distribution, Functional Ecology of Plants*, *218*, 1–10. https://doi.org/10.1016/j.flora.2015.11.001

Blundo, C., Malizia, L. R., Blake, J. G., & Brown, A. D. (2012). Tree species distribution in Andean forests: Influence of regional and local factors. *Journal of Tropical Ecology*, *28(1)*, 83–95. https://doi.org/10.1017/S0266467411000617

Boet, O., Arnan, X., & Retana, J. (2020). The role of environmental vs. biotic filtering in the structure of European ant communities: A matter of trait type and spatial scale. *PLoS ONE*, *15(2)*, 1–18. https://doi.org/10.1371/journal.pone.0228625

Boucher-Lalonde, V., Morin, A., & Currie, D. J. (2012). How are tree species distributed in climatic space? A simple and general pattern. *Global Ecology and Biogeography*, *21*, 1157–1166. https://doi.org/10.1111/j.1466-8238.2012.00764.x

Bowes, B. G., & Mauseth, J. D. (2008). *Plant Structure–A Colour Guide* (Second Edi). London, UK: Manson Publishing.

Bradie, J., & Leung, B. (2016). A quantitative synthesis of the importance of variables used in MaxEnt species distribution models. *Journal of Biogeography*, *44*, 1344–1361. https://doi.org/10.1111/jbi.12894

Cavender-Bares, J., Ackerly, D. D., Baum, D. A., & Bazzaz, F. A. (2004). Phylogenetic overdispersion in Floridian oak communities. *American Naturalist*, *163(6)*, 823–843. https://doi.org/10.1086/386375

Cha, K.-S., & Kim, T.-H. (2011). Evaluation of slope stability with topography and slope stability analysis method. *KSCE Journal of Civil Engineering*, *15(2)*, 251–256. https://doi.org/10.1007/s12205-011-0930-5

Chaudhary, R. P., Uprety, Y., & Rimal, S. K. (2016). Deforestation in Nepal: Causes, consequences and responses. In J. F. Shroder & R. Sivanpillai (Eds.), *Biological and Environmental Hazards, Risks, and Disasters* (pp. 335–372). Elsevier Inc. https://doi.org/10.1016/B978-0-12-394847-2.00020-6

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*, 1024–1026. https://doi.org/10.1126/science.1206432

Chen, Lingxiu, Xiang, W., Wu, H., Lei, P., Zhang, S., Ouyang, S., … Fang, X. (2017). Tree growth traits and social status affect the wood density of pioneer species in secondary subtropical forest. *Ecology and Evolution*, *7(14)*, 5366–5377. https://doi.org/10.1002/ece3.3110

Chen, Litong, Niu, K., Wu, Y., Geng, Y., Mi, Z., Flynn, D. F. B., & He, J. S. (2013). UV radiation is the primary factor driving the variation in leaf phenolics across Chinese grasslands. *Ecology and Evolution*, *3(14)*, 4696–4710. https://doi.org/10.1002/ece3.862

Chhetri, P. K., Gaddis, K. D., & Cairns, D. M. (2018). Predicting the Suitable Habitat of Treeline Species in the Nepalese Himalayas Under Climate Change. *Mountain Research and Development*, *38(2)*, 153–163. https://doi.org/10.1659/MRD-JOURNAL-D-17-00071.1

Cianfrani, C., Buri, A., Vittoz, P., Grand, S., Zingg, B., Verrecchia, E., & Guisan, A. (2019). Spatial modelling of soil water holding capacity improves models of plant distributions in mountain landscapes. *Plant Soil*, *438*, 57–70. https://doi.org/https://doi.org/10.1007/s11104-019-04016-x

Clark, D. A., & Clark, D. B. (1992). Life History Diversity of Canopy and Emergent Trees in a Neotropical Rain Forest. *Ecological Monographs*, *62(3)*, 315–344. https://doi.org/10.2307/2937114

Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. *Science*, *322(October)*, 258–261. https://doi.org/10.1126/science.1162547

Colwell, R. K., & Hurtt, G. C. (1994). Nonbiological Gradients in Species Richness and a Spurious Rapoport Effect. *The American Naturalist*, *144(4)*, 570–595.

Colwell, R. K., & Lees, D. C. (2000). The mid-domain effect: Geometric constraints on the geography of species richness. *Trends in Ecology and Evolution*, *15(2)*, 70–76. https://doi.org/10.1016/S0169-5347(99)01767-X

Coomes, D. A., & Allen, R. B. (2007). Effects of size, competition and altitude on tree growth. *Journal of Ecology*, *95*, 1084–1097. https://doi.org/10.1111/j.1365-2745.2007.01280.x

Coste, S., Baraloto, C., Leroy, C., Marcon, É., Renaud, A., Richardson, A. D., … Hérault, B. (2010). Assessing foliar chlorophyll contents with the SPAD-502 chlorophyll meter: a calibration test with thirteen tree species of tropical rainforest in French Guiana. *Annals of Forest Science*, *67(6)*, 607–607. https://doi.org/10.1051/forest/2010020

Cramer, W., Yohe, G. W., Auffhammer, M., Huggel, C., Molau, U., da Silva Dias, M. A. F., … Tibig, L. (2014). Detection and attribution of observed impacts. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, … L. L. White (Eds.), *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 979–1037). Cambridge University Press.

Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T., & Mynsberge, A. R. (2011). Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, *331(6015)*, 324–327. https://doi.org/10.1126/science.1205029

Deblauwe, V., Droissart, V., Bose, R., Sonké, B., Blach-Overgaard, A., Svenning, J. C., … Couvreur, T. L. P. (2016). Remotely sensed temperature and precipitation data improve species distribution modelling in the tropics. *Global Ecology and Biogeography*, *25(4)*, 443–454. https://doi.org/10.1111/geb.12426

Devi, S. B., & Sherpa, S. S. S. S. (2019). Soil carbon and nitrogen stocks along the altitudinal gradient of the Darjeeling Himalayas, India. *Environmental Monitoring and Assessment*, *191(6)*. https://doi.org/10.1007/s10661-019-7470-8

DFRS. (2015). *State of Nepal's Forests*. Kathmandu: Department of Forest Research and Survey.

Díaz, S., Cabido, M., & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, *9(1)*, 113–122. https://doi.org/10.2307/3237229

Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., … Zak, M. R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, *15(3)*, 295–304. https://doi.org/10.1658/1100-9233(2004)015[0295:TPTTDE]2.0.CO;2

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529(7585)*, 167–171. https://doi.org/10.1038/nature16489

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carr, G., … Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36(1)*, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Drollinger, S., Müller, M., Kobl, T., Schwab, N., Böhner, J., Schickhoff, U., & Scholten, T. (2017). Decreasing nutrient concentrations in soils and trees with increasing elevation across a treeline ecotone in Rolwaling Himal, Nepal. *Journal of Mountain Science*, *14(5)*, 843–858. https://doi.org/10.1007/s11629-016-4228-4

Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Vittoz, P., & Guisan, A. (2013). Improving the prediction of plant species distribution and community composition by adding edaphic to topo-climatic variables. *Journal of Vegetation Science*, *24(4)*, 593–606. https://doi.org/10.1111/jvs.12002

Duque, A., Stevenson, P. R., & Feeley, K. J. (2015). Thermophilization of adult and juvenile tree communities in the northern tropical Andes. *Proceedings of the National Academy of Sciences of the United States of America*, *112(34)*, 10744–10749. https://doi.org/10.1073/pnas.1506570112

Eckstein, D., Künzel, V., Schäfer, L., & Winges, M. (2019). *Global Climate Risk Index 2020: Who suffers most from extreme weather events? Weather-related loss events in 2018 and 1999 to 2018*. Bonn, Germany. Retrieved from https://germanwatch.org/sites/germanwatch.org/files/20-2-01e Global Climate Risk Index 2020_14.pdf

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., … Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29(2)*, 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17(1)*, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Elsen, P. R., & Tingley, M. W. (2015). Global mountain topography and the fate of montane species under climate change. *Nature Climate Change*, *5(8)*, 772–776. https://doi.org/10.1038/nclimate2656

Estrada, A., Morales-Castilla, I., Caplat, P., & Early, R. (2016). Usefulness of Species Traits in Predicting Range Shifts. *Trends in Ecology & Evolution*, *31(3)*, 190–203. https://doi.org/10.1016/j.tree.2015.12.014

Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., … Feeley, K. J. (2018). Widespread but heterogeneous responses of Andean forests to climate change. *Nature*, *564(7735)*, 207–212. https://doi.org/10.1038/s41586-018-0715-9

FAO. (2015). *Understanding Mountain Soils: A contribution from mountain areas to the International Year of Soils 2015*. Rome: Food and Agriculture Organization of the United Nations.

Feeley, K. J., & Silman, M. R. (2010). Biotic attrition from tropical forests correcting for truncated temperature niches. *Global Change Biology*, *16(6)*, 1830–1836. https://doi.org/10.1111/j.1365-2486.2009.02085.x

Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., … Saatchi, S. (2011). Upslope migration of Andean trees. *Journal of Biogeography*, *38(4)*, 783–791. https://doi.org/10.1111/j.1365-2699.2010.02444.x

Feng, J., Hu, X., Wang, J., & Wang, Y. (2016). Support for the elevational Rapoport's rule among seed plants in Nepal depends on biogeographical affinities and boundary effects. *Ecology and Evolution*, *6*, 7246–7252. https://doi.org/10.1002/ece3.2473

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37(12)*, 4302–4315. https://doi.org/10.1002/joc.5086

Franceschi, V. R., Krokene, P., Christiansen, E., & Krekling, T. (2005). Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist*, *167(2)*, 353–376. https://doi.org/10.1111/j.1469-8137.2005.01436.x

Fraser-Jenkins, C. R., & Kandel, D. R. (2019). *Ferns and Fern-Allies of Nepal* (Vol. 2). Kathmandu, Nepal: Department of Plant Resources.

Fraser-Jenkins, C. R., Kandel, D. R., & Pariyar, S. (2015). *Ferns and Fern-Allies of Nepal* (Vol. 1). Kathmandu, Nepal: National Herbarium and Plant Laboratories.

Friend, A. D., & Woodward, F. I. (1990). Evolutionary and Ecophysiological Responses of Mountain Plants to the Growing Season Environment. *Advances in Ecological Research*, *20*, 59–124. https://doi.org/10.1016/S0065-2504(08)60053-7

Fyllas, N. M., Bentley, L. P., Shenkin, A., Asner, G. P., Atkin, O. K., Díaz, S., … Malhi, Y. (2017). Solar radiation and functional traits explain the decline of forest primary productivity along a tropical elevation gradient. *Ecology Letters*, *20(6)*, 730–740. https://doi.org/10.1111/ele.12771

Gaire, N. P., Koirala, M., Bhuju, D. R., & Borgaonkar, H. P. (2014). Treeline dynamics with climate change at the central Nepal Himalaya. *Climate of the Past*, *10(4)*, 1277–1290. https://doi.org/10.5194/cp-10-1277-2014

Gale, J. (1972a). Availability of Carbon Dioxide for Photosynthesis at High Altitudes: Theoretical Considerations. *Ecology*, *53(3)*, 494–497. https://doi.org/10.2307/1934239

Gale, J. (1972b). Elevation and Transpiration: Some Theoretical Considerations with Special Reference to Mediterranean-Type Climate. *Journal of Applied Ecology*, *9(3)*, 691–702. https://doi.org/10.2307/2401898

Gao, Y., Chen, F., Lettenmaier, D. P., Xu, J., Xiao, L., & Li, X. (2018). Does elevation-dependent warming hold true above 5000 m elevation? Lessons from the Tibetan Plateau. *Npj Climate and Atmospheric Science*, *1(1)*, 1–7. https://doi.org/10.1038/s41612-018-0030-z

García-Cervigón, A. I., Fajardo, A., Caetano-Sánchez, C., Camarero, J. J., & Olano, J. M. (2020). Xylem anatomy needs to change, so that conductivity can stay the same: xylem adjustments across elevation and latitude in Nothofagus pumilio. *Annals of Botany*, *125*, 1101–1112. https://doi.org/10.1093/aob/mcaa042

Gates, D. M. (1968). Transpiration and leaf temperature. *Annual Review of Plant Physiology*, *19*, 211–238. https://doi.org/10.1146/annurev.pp.19.060168.001235

Geppert, C., Perazza, G., Wilson, R. J., Bertolli, A., Prosser, F., Melchiori, G., & Marini, L. (2020). Consistent population declines but idiosyncratic range shifts in Alpine orchids under global change. *Nature Communications*, *11(1)*, 1–11. https://doi.org/10.1038/s41467-020-19680-2

Giovanelli, J. G. R., de Siqueira, M. F., Haddad, C. F. B., & Alexandrino, J. (2010). Modeling a spatially restricted distribution in the Neotropics: How the size of calibration area affects the performance of five presence-only methods. *Ecological Modelling*, *221(2)*, 215–224. https://doi.org/10.1016/j.ecolmodel.2009.10.009

Godsoe, W., Franklin, J., & Blanchet, F. G. (2017). Effects of biotic interactions on modeled species' distribution can be masked by environmental gradients. *Ecology and Evolution*, *7(2)*, 654–664. https://doi.org/10.1002/ece3.2657

Guisan, A., Theurillat, J.-P., & Kienast, F. (1998). Predicting the potential distribution of plant species in an alpine environment. *Journal of Vegetation Science*, *9*, 65–74. https://doi.org/10.2307/3237224

Hacke, U. G., & Sperry, J. S. (2001). Functional and Ecological Xylem Anatomy. *Perspectives in Plant Ecology, Evolution and Systematics*, *4(2)*, 97–115. https://doi.org/10.1007/978-3-319-15783-2

Hao, T., Elith, J., Lahoz-Monfort, J., & Guillera-Arroita, G. (2020). Testing whether ensemble modelling is advantageous for maximising predictive performance of species distribution models. *Ecography*, *43*, 549–558. https://doi.org/10.1111/ecog.04890

He, X., Burgess, K. S., Yang, X. F., Ahrends, A., Gao, L. M., & Li, D. Z. (2019). Upward elevation and northwest range shifts for alpine Meconopsis species in the Himalaya–Hengduan Mountains region. *Ecology and Evolution*, *9(7)*, 4055–4064. https://doi.org/10.1002/ece3.5034

He, Y., Xiong, Q., Yu, L., Yan, W., & Qu, X. (2020). Impact of climate change on potential distribution patterns of alpine vegetation in the Hengduan Mountains Region, China. *Mountain Research and Development*, *40(3)*, R48–R54. https://doi.org/10.1659/MRD-JOURNAL-D-20-00010.1

Hemp, A. (2006). Continuum or Zonation? Altitudinal Gradients in the Forest Vegetation of Mt. Kilimanjaro. *Plant Ecology*, *184(1)*, 27–42. https://doi.org/10.1007/s

Hengl, T., de Jesus, J. M., Heuvelink, G. B. M., Gonzalez, M. R., Kilibarda, M., Blagotić, A., … Kempen, B. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLoS ONE*, *12(2)*, e0169748. https://doi.org/10.1371/journal.pone.0169748

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2017). dismo: Species Distribution Modeling. R package version 1.1-4. https://cran.r-project.org/web/packages/dismo/index.html. *CRAN*, p. 55. https://doi.org/10.1016/j.jhydrol.2011.07.022.

HMGN/MFSC. (2002). *Nepal Biodiversity Strategy*. Kathmandu: HMG Nepal/Ministry of Forests and Soil Conservation.

Hodgson, J. G., Montserrat-Martí, G., Charles, M., Jones, G., Wilson, P., Shipley, B., … Pla, F. R. (2011). Is leaf dry matter content a better predictor of soil fertility than specific leaf area? *Annals of Botany*, *108*, 1337–1345. https://doi.org/10.1093/aob/mcr225 http://www.efloras.org/. (2019). Retrieved October 15, 2019, from eFloras website: http://www.efloras.org/

Huggett, R. J. (2004). *Fundamentals of Biogeography* (Second Edi). London and New York: Routledge.

IPCC. (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (T. F. Stocker, D. Qin, G.-K. Plattner, M. M. B. Tignor, S. K. Allen, J. Boschung, … P. M. Midgley, Eds.). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

IPCC. (2014). *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, … L. L. White, Eds.). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

Jackson, J. K. (1994). *Manual of Afforestation in Nepal* (Second Edi, Vol. 2). Kathmandu, Nepal: Forest Research and Survey Centre.

Jourdain, N. C., Gupta, A. Sen, Taschetto, A. S., Ummenhofer, C. C., Moise, A. F., & Ashok, K. (2013). The Indo-Australian monsoon and its relationship to ENSO and IOD in reanalysis data and the CMIP3/CMIP5 simulations. *Climate Dynamics*, *41(11–12)*, 3073–3102. https://doi.org/10.1007/s00382-013-1676-1

Kansakar, S. R., Hannah, D. M., Gerrard, J., & Rees, G. (2004). Spatial pattern in the precipitation regime of Nepal. *International Journal of Climatology*, *24*, 1645–1659. https://doi.org/10.1002/joc.1098

Keddy, P. A. (1992). Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, *3*, 157–164. https://doi.org/10.2307/3235676

Körner, C. (2007). The use of "altitude" in ecological research. *Trends in Ecology and Evolution*, *22(11)*, 569–574. https://doi.org/10.1016/j.tree.2007.09.006

Körner, C. (2016). Plant adaptation to cold climates. *F1000Research*, *5*, 1–5. https://doi.org/10.12688/f1000research.9107.1

Körner, C., & Diemer, M. (1987). In situ photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. *Functional Ecology*, *1(3)*, 179–194. https://doi.org/10.2307/2389420

Körner, C., Neumayer, M., Menendez-Riedl, S. P., & Smeets-Scheel, A. (1989). Functional Morphology of Mountain Plants. *Flora*, *182(5–6)*, 353–383. https://doi.org/10.1016/S0367-2530(17)30426-7

Laiolo, P., & Obeso, J. R. (2017). Life-History Responses to the Altitudinal Gradient. In J. Catalan, J. M. Ninot, & M. M. Aniz (Eds.), *High Mountain Conservation in a Changing World*: *Vol. Advances i* (pp. 253–283). Cham: Springer. https://doi.org/10.1007/978-3-319-55982-7

Lee, C.-B., Chun, J.-H., Song, H.-K., & Cho, H.-J. (2013). Altitudinal patterns of plant species richness on the Baekdudaegan Mountains, South Korea: mid-domain effect, area, climate, and Rapoport's rule. *Ecological Research*, *28*, 67–79. https://doi.org/10.1007/s11284-012-1001-1

Lenoir, J., Gégout, J. C., Marquet, P. A., De Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, *320(5884)*, 1768–1771. https://doi.org/10.1126/science.1156831

Lenoir, J., & Svenning, J. C. (2015). Climate-related range shifts–a global multidimensional synthesis and new research directions. *Ecography*, *38(1)*, 15–28. https://doi.org/10.1111/ecog.00967

Lillesø, J.-P. B., Shrestha, T. B., Dhakal, L. P., Nayaju, R. P., & Shrestha, R. (2005). *The map of potential vegetation of Nepal–a forestry/agro-ecological/biodiversity classification system*. Forest & Landscape Denmark.

Linting, M., & van der Kooij, A. (2012). Nonlinear Principal Components Analysis With CATPCA: A Tutorial. *Journal of Personality Assessment*, *94(1)*, 12–25. https://doi.org/10.1080/00223891.2011.627965

Liu, C., White, M., & Newell, G. (2011). Measuring and comparing the accuracy of species distribution models with presence absence data. *Ecography*, *34(2)*, 232–243. https://doi.org/10.1111/j.1600-0587.2010.06354.x

Liu, W., Zheng, L., & Qi, D. (2020). Variation in leaf traits at different altitudes reflects the adaptive strategy of plants to environmental changes. *Ecology and Evolution*, *10(15)*, 8166–8175. https://doi.org/10.1002/ece3.6519

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462(7276)*, 1052–1055. https://doi.org/10.1038/nature08649

Luitel, D. R., Jha, P. K., Siwakoti, M., Shrestha, M. L., & Munniappan, R. (2020). Climatic trends in different bioclimatic zones in the Chitwan Annapurna Landscape, Nepal. *Climate*, *8(136)*, 1–18. https://doi.org/10.3390/cli8110136

MacArthur, R. H. (1972). *Geographical Ecology: Patterns in the Distribution of Species*. New York: Harper & Row.

Macek, P., Klimeš, L., Adamec, L., Doležal, J., Chlumská, Z., De Bello, F., … Řeháková, K. (2012). Plant nutrient content does not simply increase with elevation under the extreme environmental conditions of Ladakh, NW Himalaya. *Arctic, Antarctic, and Alpine Research*, *44(1)*, 62–66. https://doi.org/10.1657/1938-4246-44.1.62

MacKenzie, D. I. (2005). Was it there? Dealing with imperfect detection for species presence/absence data. *Australian & New Zealand Journal of Statistics*, *47(1)*, 65–74.

MacLean, S. A., & Beissinger, S. R. (2017). Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. *Global Change Biology*, *23(10)*, 4094–4105. https://doi.org/10.1111/gcb.13736

Maharjan, S. K., Poorter, L., Holmgren, M., Bongers, F., Wieringa, J. J., & Hawthorne, W. D. (2011). Plant functional traits and the distribution of West African Rain Forest trees along the rainfall gradient. *Biotropica*, *43(5)*, 552–561. https://doi.org/10.1111/j.1744-7429.2010.00747.x

Malhi, Y., Aragao, L. E. O. C., Galbraith, D., Huntingford, C., Fisher, R., Zelazowski, P., … Meir, P. (2009). Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences*, *106(49)*, 20610–20615. https://doi.org/10.1073/pnas.0804619106

Mamantov, M. A., Gibson-Reinemer, D. K., Linck, E. B., & Sheldon, K. S. (2021). Climate-driven range shifts of montane species vary with elevation. *Global Ecology and Biogeography*, *30(4)*, 784–794. https://doi.org/10.1111/geb.13246

Mao, L., Chen, S., Zhang, J., & Zhou, G. (2018). Altitudinal patterns of maximum plant height on the Tibetan Plateau. *Journal of Plant Ecology*, *11(1)*, 85–91. https://doi.org/10.1093/jpe/rtw128

Marshall, L., Perdijk, F., Dendoncker, N., Kunin, W., Roberts, S., & Biesmeijer, J. C. (2020). Bumblebees moving up: shifts in elevation ranges in the Pyrenees over 115 years. *Proceedings of the Royal Society B: Biological Sciences*, *287(1938)*. https://doi.org/10.1098/rspb.2020.2201

Marteinsdóttir, B., & Eriksson, O. (2014). Trait-based filtering from the regional species pool into local grassland communities. *Journal of Plant Ecology*, *7(4)*, 347–355. https://doi.org/10.1093/jpe/rtt032

Merckx, B., Steyaert, M., Vanreusel, A., Vincx, M., & Vanaverbeke, J. (2011). Null models reveal preferential sampling, spatial autocorrelation and overfitting in habitat suitability modelling. *Ecological Modelling*, *222(3)*, 588–597. https://doi.org/10.1016/j.ecolmodel.2010.11.016

Merow, C., Smith, M. J., & Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography*, *36(10)*, 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Miehe, G., Miehe, S., Vogel, J., Co, S., & La, D. (2007). Highest Treeline in the Northern Hemisphere Found in Southern Tibet. *Mountain Research and Development*, *27(2)*, 169–173. https://doi.org/10.1659/mrd.0792

Minder, J. R., Letcher, T. W., & Liu, C. (2018). The character and causes of elevation-dependent warming in high-resolution simulations of Rocky Mountain climate change. *Journal of Climate*, *31(6)*, 2093–2113. https://doi.org/10.1175/JCLI-D-17-0321.1

Ming, T., & Fang, R. (1990). The phylogeny and evolution of genus Rhododendron. *Acta Botanica Yunnanica*, *12(4)*, 353–365.

Mittermeier, R. A., Robles Gil, P., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C. G., … Da Fonsec, G. A. B. (2004). *Hotspots revisited*. Mexico City: CEMEX.

MoFE. (2018). *Nepal's National Adaptation Plan (NAP) Process: Reflecting on lessons learned and the way forward*. Kathmandu, Nepal. Retrieved from http://napglobalnetwork.org/wp-content/uploads/2018/07/napgn-en-2018-nepal-nap-process.pdf

MoFE. (2019). *Climate Change Scenarios for Nepal*. Kathmandu, Nepal.

MoPE. (2016). *Nationally Determined Contributions*. Kathmandu, Nepal. Retrieved from https://www4.unfccc.int/sites/ndcstaging/PublishedDocuments/Nepal First/Nepal First NDC.pdf

Morueta-Holme, N., Engemann, K., Sandoval-Acuña, P., Jonas, J. D., Segnitz, R. M., & Svenning, J. C. (2015). Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences of the United States of America*, *112(41)*, 12741–12745. https://doi.org/10.1073/pnas.1509938112

Mu, W., Yu, F., Li, C., Xie, Y., Tian, J., Liu, J., & Zhao, N. (2015). Effects of rainfall intensity and slope gradient on runoff and soil moisture content on different growing stages of spring maize. *Water*, *7(6)*, 2990–3008. https://doi.org/10.3390/w7062990

Müller, M., Schickhoff, U., Scholten, T., Drollinger, S., Böhner, J., & Chaudhary, R. P. (2016). How do soil properties affect alpine treelines? General principles in a global perspective and novel findings from Rolwaling Himal, Nepal. *Progress in Physical Geography*, *40(1)*, 135–160. https://doi.org/10.1177/0309133315615802

Müller, M., Schwab, N., Schickhoff, U., Böhner, J., & Scholten, T. (2016). Soil temperature and soil moisture patterns in a Himalayan alpine treeline ecotone. *Arctic, Antarctic, and Alpine Research*, *48(3)*, 501–521. https://doi.org/10.1657/AAAR0016-004

Neate-Cegg, M. H. C., Jones, S. E. I., Tobias, J. A., Newmark, W. D., & Şekercioğlu, Ç. H. (2021). Ecological Correlates of Elevational Range Shifts in Tropical Birds. *Frontiers in Ecology and Evolution*, *9*, 1–16. https://doi.org/10.3389/fevo.2021.621749

Neuner, G., Huber, B., Plangger, A., Pohlin, J. M., & Walde, J. (2020). Low temperatures at higher elevations require plants to exhibit increased freezing resistance throughout the summer months. *Environmental and Experimental Botany*, *169(103882)*, 1–9. https://doi.org/10.1016/j.envexpbot.2019.103882

Nielsen, R. L., James, J. J., & Drenovsky, R. E. (2019). Functional traits explain variation in chaparral shrub sensitivity to altered water and nutrient availability. *Frontiers in Plant Science*, *10(April)*. https://doi.org/10.3389/fpls.2019.00505

Nunez, S., Arets, E., Alkemade, R., Verwer, C., & Leemans, R. (2019). Assessing the impacts of climate change on biodiversity: is below 2 °C enough? *Climatic Change*, *154(3–4)*, 351–365. https://doi.org/10.1007/s10584-019-02420-x

Olson, M. E., Soriano, D., Rosell, J. A., Anfodillo, T., Donoghue, M. J., Edwards, E. J., … Méndez-Alonzo, R. (2018). Plant height and hydraulic vulnerability to drought and cold. *PNAS*, *115(29)*, 7551–7556. https://doi.org/10.1073/pnas.1721728115

Onoda, Y., & Anten, N. P. R. (2011). Challenges to understand plant responses to wind. *Plant Signaling & Behavior*, *6(7)*, 1057–1059. https://doi.org/10.4161/psb.6.7.15635

Onoda, Y., Westoby, M., Adler, P. B., Choong, A. M. F., Clissold, F. J., Cornelissen, J. H. C., … Yamashita, N. (2011). Global patterns of leaf mechanical properties. *Ecology Letters*, *14*, 301–312. https://doi.org/10.1111/j.1461-0248.2010.01582.x

Pacifici, M., Visconti, P., Butchart, S. H. M., Watson, J. E. M., Cassola, F. M., & Rondinini, C. (2017). Species' traits influenced their response to recent climate change. *Nature Climate Change*, *7(3)*, 205–208. https://doi.org/10.1038/nclimate3223

Palazzi, E., Mortarini, L., Terzago, S., & von Hardenberg, J. (2019). Elevation-dependent warming in global climate model simulations at high spatial resolution. *Climate Dynamics*, *52(5–6)*, 2685–2702. https://doi.org/10.1007/s00382-018-4287-z

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421(6918)*, 37–42. https://doi.org/10.1038/nature01286

Paudyal, K. P., & Haq, N. (2008). Variation of pomelo (Citrus grandis (L.) Osbeck) in Nepal and participatory selection of strains for further improvement. *Agroforestry Systems*, *72(3)*, 195–204. https://doi.org/10.1007/s10457-007-9088-z

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Benito Alonso, J. L., … Grabherr, G. (2012). Recent Plant Diversity Changes on Europe's Mountain Summits. *Science*, *336(6079)*, 353–355.

Pearson, R. G., Raxworthy, C. J., Nakamura, M., & Peterson, A. T. (2007). Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, *34*, 102–117. https://doi.org/10.1111/j.1365-2699.2006.01594.x

Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., … Yang, D. Q. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, *5(5)*, 424–430. https://doi.org/10.1038/nclimate2563

Pérez-Harguindeguy, N., Díaz, S., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., … Cornelissen, J. H. C. (2013). New Handbook for standardized measurment of plant functional traits worldwide. *Australian Journal of Botany*, *61*, 167–234. https://doi.org/10.1071/BT12225

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M., & Araújo, M. B. (2011). *Ecological niches and geographic distributions*. New Jersey: Princeton University Press. https://doi.org/10.5860/CHOICE.49-6266

Phillips, S. J. (2010). A Brief Tutorial on Maxent. *Lessons in Conservation*, *3*, 108–135. https://doi.org/10.4016/33172.01

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–259.

Phillips, S. J., Dudík, M., & Schapire, R. E. (2004). A maximum entropy approach to species distribution modeling. *Proceedings of the Twenty-First International Conference on Machine Learning*, 655–662. https://doi.org/10.1145/1015330.1015412

Pintor, A. F. V., Schwarzkopf, L., & Krockenberger, A. K. (2015). Rapoport's Rule: Do climatic variability gradients shape range extent? *Ecological Monographs*, *85(4)*, 643–659.

Pittermann, J., & Sperry, J. S. (2006). Analysis of Freeze-Thaw Embolism in Conifers. The Interaction between Cavitation Pressure and Tracheid Size. *Plant Physiology*, *140(January)*, 374–382. https://doi.org/10.1104/pp.105.067900

Pollock, L. J., Morris, W. K., & Vesk, P. A. (2012). The role of functional traits in species distributions revealed through a hierarchical model. *Ecography*, *35*, 716–725. https://doi.org/10.1111/j.1600-0587.2011.07085.x

Poorter, L., & Bongers, F. (2006). Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, *87(7)*, 1733–1743. https://doi.org/10.1890/0012-9658(2006)87[1733:LTAGPO]2.0.CO;2

R Core Team. (2017). *R: A Language and Environment for Statistical Computing (R-3.4.3). Vienna: R Foundation for Statistical Computing. https://www.r-project.org/*. Retrieved from https://www.r-project.org/

Raes, N. (2012). Partial versus full species distribution models. *Natureza a Conservacao*, *10(2)*, 127–138. https://doi.org/10.4322/natcon.2012.020

Raes, N., & Aguirre-Gutiérrez, J. (2018). A Modeling Framework to Estimate and Project Species Distributions in Space and Time. In C. Hoorn, A. Perrigo, & A. Antonelli (Eds.), *Mountains, Climate and Biodiversity* (pp. 309–320). John Wiley & Sons Ltd.

Raes, N., & Ter Steege, H. (2007). A null-model for significance testing of presence-only species distribution models. *Ecography*, *30(5)*, 727–736. https://doi.org/10.1111/j.2007.0906-7590.05041.x

Rajbhandari, K. R., & Rai, S. K. (2019). *A Handbook of The Flowering Plants of Nepal* (Vol. 2). Kathmandu, Nepal: Department of Plant Resources.

Rajbhandari, R., Shrestha, A. B., Nepal, S., & Wahid, S. (2016). Projection of Future Climate over the Koshi River Basin Based on CMIP5 GCMs. *Atmospheric and Climate Sciences*, *06(02)*, 190–204. https://doi.org/10.4236/acs.2016.62017

Rangwala, I., Sinsky, E., & Miller, J. R. (2013). Amplified warming projections for high altitude regions of the northern hemisphere mid-latitudes from CMIP5 models. *Environmental Research Letters*, *8(2)*. https://doi.org/10.1088/1748-9326/8/2/024040

Rasmann, S., Alvarez, N., & Pellissier, L. (2014). The Altitudinal Niche-Breadth Hypothesis in Insect-Plant Interactions. *Annual Plant Reviews*, *47*, 339–360. https://doi.org/10.1002/9781118472507.ch10

Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1992). Leaf Life-Span in Relation to Leaf , Plant , and Stand Characteristics among Diverse Ecosystems. *Ecological Monographs*, *62(3)*, 365–392. https://doi.org/10.2307/2937116

Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., & Walters, M. B. (2003). The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies. *International Journal of Plant Science*, *164(3 Suppl.)*, S143–S164. https://doi.org/10.1086/374368

Ren, Y. Y., Ren, G. Y., Sun, X. B., Shrestha, A. B., You, Q. L., Zhan, Y. J., … Wen, K. M. (2017). Observed changes in surface air temperature and precipitation in the Hindu Kush Himalayan region over the last 100-plus years. *Advances in Climate Change Research*, *8(3)*, 148–156. https://doi.org/10.1016/j.accre.2017.08.001

Rew, L. J., McDougall, K. L., Alexander, J. M., Daehler, C. C., Essl, F., Haider, S., … Rabitsch, W. (2020). Moving up and over: redistribution of plants in alpine, Arctic, and Antarctic ecosystems under global change. *Arctic, Antarctic, and Alpine Research*, *52(1)*, 651–665. https://doi.org/10.1080/15230430.2020.1845919

Sabin, T. P., Krishnan, R., Vellore, R., Priya, P., Borgaonkar, H. P., Singh, B. B., … Ramadoss, M. (2020). Climate change over the Himalayas. In R. Krishnan, J. Sanjay, C. Gnanaseelan, M. Mujumdar, A. Kulkarni, & S. Chakraborty (Eds.), *Assessment of Climate Change over the Indian Region–A Report of the Ministry of Earth Sciences (MoES), Government of India* (pp. 207–222). Springer Singapore. https://doi.org/https://doi.org/10.1007/978-981-15-4327-2_11

Schellenberger Costa, D., Gerschlauer, F., Kiese, R., Fischer, M., Kleyer, M., & Hemp, A. (2018). Plant niche breadths along environmental gradients and their relationship to plant functional traits. *Diversity and Distributions*, *24(12)*, 1869–1882. https://doi.org/10.1111/ddi.12815

Schietti, J., Emilio, T., Rennó, C. D., Drucker, D. P., Costa, F. R. C., Nogueira, A., … Magnusson, W. E. (2014). Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. *Plant Ecology & Diversity*, *7(1–2)*, 241–253.

Schmitt, C. B., Senbeta, F., Woldemariam, T., Rudner, M., & Denich, M. (2013). Importance of regional climates for plant species distribution patterns in moist Afromontane forest. *Journal of Vegetation Science*, *24(3)*, 553–568. https://doi.org/10.1111/j.1654-1103.2012.01477.x

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of Image Analysis. *Nat Methods*, *9(7)*, 671–675. https://doi.org/10.1038/nmeth.2089

Scholz, A., Klepsch, M., Karimi, Z., & Jansen, S. (2013). How to quantify conduits in wood? *Frontiers in Plant Science*, *4(March)*, 1–11. https://doi.org/10.3389/fpls.2013.00056

Shrestha, A. B., Agrawal, N. K., Alfthan, B., Bajracharya, S. R., Maréchal, J., & van Oort, B. (Eds.). (2015). *The Himalayan Climate and Water Atlas–Impact of Climate Change on Water Resources in Five of Asia's Major River Basins*. ICIMOD, GRID-Arendal and CICERO.

Shrestha, K. B., Hofgaard, A., & Vandvik, V. (2015). Recent treeline dynamics are similar between dry and mesic areas of Nepal, central Himalaya. *Journal of Plant Ecology*, *8(4)*, 347–358. https://doi.org/10.1093/jpe/rtu035

Shrestha, K. K., Bhattarai, S., & Bhandari, P. (2018). *Handbook of Flowering Plants of Nepal (Volume1. Gymnosperms and Angiosperms: Cycadaceae–Betulaceae)*. Jodhpur, India: Scientific Publishers.

Shrestha, N., Wang, Z., Su, X., Xu, X., Lyu, L., Liu, Y., … Feng, X. (2018). Global patterns of Rhododendron diversity: The role of evolutionary time and diversification rates. *Global Ecology and Biogeography*, *27*, 913–924. https://doi.org/10.1111/geb.12750

Slot, M., & Winter, K. (2017). Photosynthetic acclimation to warming in tropical forest tree seedlings. *Journal of Experimental Botany*, *68(9)*, 2275–2284. https://doi.org/10.1093/jxb/erx071

Smith, W. K., & Geller, G. N. (1979). Plant Transpiration at High Elevations: Theory, Field Measurements, and Comparisons with Desert Plants. *Oecologia*, *41*, 109–122. https://doi.org/10.1007/BF00344841

Soberón, J., & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, *2*, 1–10.

Sterck, F. J., Van Gelder, H. A., & Poorter, L. (2006). Mechanical branch constraints contribute to life-history variation across tree species in a Bolivian forest. *Journal of Ecology*, *94(6)*, 1192–1200. https://doi.org/10.1111/j.1365-2745.2006.01162.x

Sterck, F., Markesteijn, L., Schieving, F., & Poorter, L. (2011). Functional traits determine trade-offs and niches in a tropical forest community. *Proceedings of the National Academy of Sciences*, *108(51)*, 20627–20632. https://doi.org/10.1073/pnas.1106950108

Sterck, F., Markesteijn, L., Toledo, M., Schieving, F., & Poorter, L. (2014). Sapling performance along resource gradients drives tree species distributions within and across tropical forests. *Ecology*, *95(9)*, 2514–2525. https://doi.org/10.1890/13-2377.1

Stevens, G. C. (1992). The Elevational Gradient in Altitudinal Range: An Extension of Rapoport's Latitudinal Rule to Altitude. *The American Naturalist*, *140(6)*, 893–911.

Subedi, S. C., Bhattarai, K. R., Perez, T. M., & Sah, J. P. (2020). Gymnosperm species richness patterns along the elevational gradient and its comparison with other plant taxonomic groups in the Himalayas. *Frontiers of Biogeography*, *12(1)*, 1–14. https://doi.org/10.21425/F5FBG44232

Suwal, M. K., Shrestha, K. B., Guragain, L., Shakya, R., Shrestha, K., Bhuju, D. R., & Vetaas, O. R. (2016). Land-use change under a warming climate facilitated upslope expansion of Himalayan silver fir (Abies spectabilis (D. Don) Spach). *Plant Ecology*, *217(8)*, 993–1002. https://doi.org/10.1007/s11258-016-0624-7

Telwala, Y., Brook, B. W., Manish, K., & Pandit, M. K. (2013). Climate-Induced Elevational Range Shifts and Increase in Plant Species Richness in a Himalayan Biodiversity Epicentre. *PLoS ONE*, *8(2)*. https://doi.org/10.1371/journal.pone.0057103

Terashima, I., Masuzawa, T., Ohba, H., & Yokoi, Y. (1995). Is photosynthesis suppressed at higher elevations due to low CO2 pressure? *Ecology*, *76(8)*, 2663–2668. https://doi.org/10.2307/2265838

Tingley, M. W., Monahan, W. B., Beissinger, S. R., & Moritz, C. (2009). Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *106(SUPPL. 2)*, 19637–19643. https://doi.org/10.1073/pnas.0901562106

TISC. (2002). *Forest and Vegetation Types of Nepal–TISC Document Series No. 104*. Kathmandu: Tree Improvement and Silviculture Component/Natural Resource Management Sector Assistance Programme/Department of Forest/Ministry of Forests and Soil Conservation/HMG Nepal.

Title, P. O., & Bemmels, J. B. (2018). ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*, *41(2)*, 291–307. https://doi.org/10.1111/ecog.02880

Toledo, M., Peña-Claros, M., Bongers, F., Alarcón, A., Balcázar, J., Chuviña, J., … Poorter, L. (2012). Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *Journal of Ecology*, *100(1)*, 253–263. https://doi.org/10.1111/j.1365-2745.2011.01890.x

Turunen, M., & Latola, K. (2005). UV-B radiation and acclimation in timberline plants. *Environmental Pollution*, *137(3)*, 390–403. https://doi.org/10.1016/j.envpol.2005.01.030

van Proosdij, A. S. J., Sosef, M. S. M., Wieringa, J. J., & Raes, N. (2016). Minimum required number of specimen records to develop accurate species distribution models. *Ecography*, *39(6)*, 542–552. https://doi.org/10.1111/ecog.01509

Venturas, M. D., Sperry, J. S., & Hacke, U. G. (2017). Plant xylem hydraulics: What we understand, current research, and future challenges. *Journal of Integrative Plant Biology*, *59(6)*, 356–389. https://doi.org/10.1111/jipb.12534

Vetaas, O. R., & Grytnes, J. A. (2002). Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography*, *11(4)*, 291–301. https://doi.org/10.1046/j.1466-822X.2002.00297.x

Vincent, A. G., Sundqvist, M. K., Wardle, D. A., & Giesler, R. (2014). Bioavailable Soil Phosphorus Decreases with Increasing Elevation in a Subarctic Tundra Landscape. *PLoS ONE*, *9(3)*, e92942. https://doi.org/10.1371/journal.pone.0092942

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116(5)*, 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x

Walthert, L., & Meier, E. S. (2017). Tree species distribution in temperate forests is more influenced by soil than by climate. *Ecology and Evolution*, *7(22)*, 9473–9484. https://doi.org/10.1002/ece3.3436

Wang, H., Prentice, I. C., Davis, T. W., Keenan, T. F., Wright, I. J., & Peng, C. (2017). Photosynthetic responses to altitude: an explanation based on optimality principles. *New Phytologist*, *213*, 976–982. https://doi.org/10.1111/nph.14332

Wang, J., Wen, X., Zhang, X., Li, S., & Zhang, D.-Y. (2018). Co-regulation of photosynthetic capacity by nitrogen, phosphorus and magnesium in a subtropical Karst forest in China. *Scientific Reports*, *8(1)*, 1–9. https://doi.org/10.1038/s41598-018-25839-1

Wang, Q., Fan, X., & Wang, M. (2014). Recent warming amplification over high elevation regions across the globe. *Climate Dynamics*, *43(1–2)*, 87–101. https://doi.org/10.1007/s00382-013-1889-3

Whittaker, R. H. (1967). Gradient analysis of vegetation. *Biological Reviews of the Cambridge Philosophical Society*, *42(2)*, 207–264.

Wilson, A. M., & Jetz, W. (2016). Remotely Sensed High-Resolution Global Cloud Dynamics for Predicting Ecosystem and Biodiversity Distributions. *PLoS Biology*, *14(3)*, 1–20. https://doi.org/10.1371/journal.pbio.1002415

Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., & Guisan, A. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, *14*, 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., … Svenning, J. C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, *88(1)*, 15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x

Woodward, F. I., & Diament, A. D. (1991). Functional approaches to predicting the ecological effects of global change. *Functional Ecology*, *5(2)*, 202–212. https://doi.org/10.2307/2389258

Yan, Y., & Tang, Z. (2019). Protecting endemic seed plants on the Tibetan Plateau under future climate change: migration matters. *Journal of Plant Ecology*, *12(6)*, 962–971. https://doi.org/10.1093/jpe/rtz032

Yang, D., Wang, A.-Y., Zhang, J.-L., Bradshaw, C. J. A., & Hao, G.-Y. (2020). Variation in Stem Xylem Traits is Related to Differentiation of Upper Limits of Tree Species along an Elevational Gradient. *Forests*, *11*, 1–14.

Yin, X. H., Sterck, F., & Hao, G. Y. (2018). Divergent hydraulic strategies to cope with freezing in co-occurring temperate tree species with special reference to root and stem pressure generation. *New Phytologist*, *219(2)*, 530–541. https://doi.org/10.1111/nph.15170

Zhang, K., Sun, L., & Tao, J. (2020). Impact of climate change on the distribution of Euscaphis japonica (Staphyleaceae) trees. *Forests*, *11(525)*, 1–13. https://doi.org/10.1016/j.ecoinf.2021.101244

Zhang, L., Chen, Y., Hao, G., Ma, K., Bongers, F., & Sterck, F. J. (2020). Conifer and broadleaved trees differ in branch allometry but maintain similar functional balances. *Tree Physiology*, *40*, 511–519. https://doi.org/10.1093/treephys/tpz139

Zhang, L., Copini, P., Weemstra, M., & Sterck, F. (2016). Functional ratios among leaf, xylem and phloem areas in branches change with shade tolerance, but not with local light conditions, across temperate tree species. *New Phytologist*, *209*, 1566–1575. https://doi.org/10.1111/nph.13731

Zizka, A., & Antonelli, A. (2015). speciesgeocodeR: An R package for linking species occurrences, user-defined regions and phylogenetic trees for biogeography, ecology and evolution. *BioRxiv–The Preprint Server for Biology*, *(November)*, https://doi.org/10.1101/032755. https://doi.org/10.1101/032755

Zu, K., Wang, Z., Zhu, X., Lenoir, J., Shrestha, N., Lyu, T., … Zhou, J. (2021). Upward shift and elevational range contractions of subtropical mountain plants in response to climate change. *Science of the Total Environment*, *783*, 146896. https://doi.org/10.1016/j.scitotenv.2021.146896

Summary

The Himalayas are amongst the global hotspots of biodiversity. Climate warming is forcing species to shift upslope at an alarming rate in the Himalayas, posing a serious threat to its biodiversity. To ensure present-day conservation and to accurately predict how montane plant species are likely to respond to future climate change, it is urgently needed to understand how environmental conditions and species properties (i.e. functional traits) shape species' distributions along an elevational gradient (i.e. species' elevational distributions). In this thesis, I analysed the elevational distribution patterns of 277 plant species along an elevational gradient in the Himalayas in Nepal, and showed which environmental factors best predict species' elevational distributions and whether highland species occupy wider elevational ranges than lowland species; how functional traits shape species' elevational positions and lead to species partitioning of the elevational gradient; and how future global warming will affect species' elevational ranges and distribution areas.

In *Chapter 2*, I asked which environmental factors best predict species' elevational distributions and whether highland species occupy wider elevational ranges than lowland species because species living at harsher, more stressful and variable highland conditions would have wider physiological tolerances to environmental conditions and therefore occupy wider elevational ranges. For the 277 selected Himalayan plant species, I modelled their environmental niches using MaxEnt, by combining species occurrence data with 19 climatic, topographic and edaphic factors. I found that mean annual temperature, followed by soil clay content and slope are the key environmental factors that best predict species' elevational distributions in the Himalayas. Apart from obvious changes in temperature and its temperature (e.g. temperature extremes) and non-temperature (such as irradiance and PET) covariates, both soil conditions and topography thus also play a major role in shaping species distributions in the Himalayas. Mid-elevation species (2,000-3,000 m a.s.l.) had relatively wider elevational ranges than lowland and highland species. This suggests that mid-elevation species might be less affected by climate change since their wider elevational ranges may partially buffer against climate change induced range shifts.

In *Chapter 3*, I asked how functional traits shape species' elevational positions and lead to species partitioning of the elevational gradient. For a subset of 31 tree species that occupied different positions along the elevational gradient, I measured 39 traits related to carbon, water and nutrient use. I found that the highland species have a small size, small and thick leaves with low nutrient concentrations, and narrow conduits that allow them to conserve their slowly acquired carbon and nutrients and survive harsh highland conditions. In contrast, the lowland species have a large size, large and thick leaves with high nutrient concentrations, and wide conduits that allow them to be competitive and

acquisitive under benign lowland conditions. I also found that stem traits (i.e. basal area) and branch traits (i.e. conduit diameter, leaf area per xylem area and specific branch length) that integrate multiple plant organs and functions are the best predictors of species' elevational distributions. Stem and branch traits are therefore more important for species elevational distribution than commonly measured leaf traits.

In *Chapter 4*, I asked how future global warming will affect species' elevational ranges and distribution areas. For 137 tree species, I used the MaxEnt models obtained in Chapter 2 to project their spatial distributions using 'near current' (1985) and future (2050) predicted environmental conditions. Highland species show larger predicted elevational shifts than lowland species, probably because of higher rates of warming predicted for high elevations. The upslope shifts that species have to realize to track their climatic niche is predicted to be, on average, more than 2 times faster (8 m yr^{-1}) than currently observed shifts in the Himalayas (3 m yr^{-1}). This implies that species may not be able to track future environmental change. The majority (71%) of the tree species are predicted to enlarge their distribution area: these are particularly species from the lowlands that may expand their upper limit, or species from the highlands that may have access to new potentially suitable highland intermountain valleys and plateaus, whereas species from mid-elevations are predicted to contract their distribution area because less area is available upslope. Hence, the actual change in distribution area depends on the peculiarities of the Himalayan topography and the area available in each elevational belt. I found that the predicted elevational shift in response to climate change varies strongly across species and depends not only on the magnitude of temperature and precipitation change at that specific elevation, but also on local soil conditions. I also found that species with conservative trait values have the largest predicted upslope shifts suggesting that an easily measurable trait, such as conduit diameter, can be used as a proxy for predicting species elevational range shifts in the Himalayas, and possibly in other montane regions.

I conclude that the plant species distribution in the Himalayas are best predicted by temperature and its temperature (e.g. temperature extremes) and non-temperature (such as irradiance and PET) covariates followed by soil clay content and slope, but that future distributions will also be affected by changes in precipitation. Multiple trade-offs in plant size, hydraulic efficiency and light competition determine species' positions along this elevational gradient. The Himalayan plant species face an uncertain future, because they are projected to shift upslope at much faster rates in response to the climate warming than currently observed rates of shift. Based on these findings, here, I call for the establishment of migration corridors, for assisted migration such as direct seeding or planting in new potentially suitable future habitats, and for urgent and informed actions to conserve and improve biodiversity along the slopes of the Himalayas for the benefit of not only the montane communities but also the global community.

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Short biography

Surya Kumar Maharjan was born in a farming family in a beautiful village called Thecho, Lalitpur, Nepal in 1982. As a kid, he grew up playing in the farm and the forest. He completed his primary and secondary level education from Bashishtha Secondary School, Chapagaun, Lalitpur, and higher secondary level education from United Academy, Kumaripati, Lalitpur.

After completing higher secondary level education, he joined Tribhuvan University (TU), Institute of Forestry (IoF)–Pokhara Campus, Pokhara, Nepal for his BSc Forestry. In his BSc thesis, he studied the factors triggering landslides and carried out landslide hazard zonation of the four villages of the Upper Andhi Khola Watershed, Syangja, Nepal. BSc Merit Scholarship from IoF funded his BSc Forestry. After obtaining his BSc Forestry in 2006, he started his career with an internship in WWF, Nepal. In 2007, he joined MSc European Forestry–Erasmus Mundus Joint Master Degree Programme and obtained a joint degree on Forest and Nature Conservation from Wageningen University and Research (WUR), The Netherlands, and Agriculture and Forestry from University of Joensuu (now University of Eastern Finland), Finland. In his MSc thesis, he studied the role of functional traits in shaping the distribution of West African rainforest plant species. Erasmus Mundus Joint Masters Scholarship from European Union funded his MSc European Forestry. He has always been a hardworking student and obtained excellent academic results – distinction (cum laude) at every level from higher secondary level education through MSc degree.

After obtaining MSc degree in 2009, he worked for a few years with local communities and local governments in his home country for sustainable management of forests and their resources, and adaptation to climate change. During these years, he had privilege to be part of many reputed national and international organizations, projects and programs, and to travel to various remote areas of Nepal.

In 2016, he started his PhD at WUR. Sandwich PhD Scholarship from WUR funded his PhD. Research grants from Stichting het Kronendak, The Rufford Foundation and KNAW Fonds Ecologie funded his PhD fieldwork. During his PhD, he had privilege to work together with numerous amazing people, and collaborate with many reputed institutions. This PhD thesis entitled "Plant species distribution along an elevational gradient in the Himalayas, Nepal: on drivers, mechanisms and the effects of climate change" that you are now holding in your hands is the result of those productive collaborations and hard work. However, his academic and research journey does not end here. Surya has decided to stay in academia and research, and has recently joined TU, IoF in a capacity of Assistant Professor.

PE&RC training and education statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (4.5 ECTS)

- Climatic effects on plant species distribution along the Himalayan altitudinal gradient, Nepal

Writing of project proposal (7.3 ECTS)

- Climate change and its effect on plant species distribution and diversity in Nepal; WUR
- Climate change and its effect on plant species distribution and diversity; NUFFIC
- Climatic effects on plant species distribution and diversity along the Himalayan altitudinal gradient, Nepal; The Rufford Foundation
- Climatic effects on tree and plant species distribution along the Himalayan altitudinal gradient, Nepal; Stichting het Kronendak
- Climatic effects on tree and plant species distribution along the Himalayan altitudinal gradient, Nepal; KNAW

Post-graduate courses (4.5 ECTS)

- Introduction to ecological niche modelling; Centre for Research in Geo-Space Science (CICGE) (2016)
- Linear models; PE&RC & SENSE (2016)
- Generalized linear models; PE&RC & SENSE (2016)
- Resilience of living systems from fundamental concepts to interdisciplinary applications; WGS (2018)

Laboratory training and working visits (1.5 ECTS)

- Branch sample preparation, sample cross-sectioning using sliding microtome, permanent slide preparation, and tissue recognition; National Herbarium and Plant Laboratories, Godawari, Nepal (2018)
- Photographing cross-section of branch sample using microscope; Department of Plant Resource, Thapathali, Kathmandu, Nepal (2018)
- New forest inventory technology field-map; research team from Czech University of Life Sciences; Institute of Forestry, Pokhara, Nepal (2018)

Invited review of (unpublished) journal manuscript (2 ECTS)

- Oecologia: intraspecific variation in traits and tree growth along an elevational gradient in a subtropical forest (2019)
- Annals of Forest Science: leaf functional traits as predictors of cloud forest tree seedling survival along an elevation gradient (2019)

Competence strengthening / skills courses (1.45 ECTS)

- Ethical approaches to forest management; University of Joensuu, Finland (2008)
- Reviewing a scientific paper; WUR Library and PE&RC (2016)
- Essentials of scientific writing and presenting; Wageningen in'to Languages (2016)
- Research data management part 1,2,3; Wageningen University and Research Library (2018)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)

- PE&RC First years weekend (2016)
- Wageningen PhD symposium diversity in science (2016)
- PE&RC Last year; online (2020)
- PE&RC Afternoon event; online (2020)

Discussion groups / local seminars or scientific meetings (3.2 ECTS)

- Plant-Soil Interactions discussion group meeting (2016)
- Modelling and Statistics Network (MSN) discussion group meeting (2016)
- PhD Progress sharing seminar at Institute of Forestry; Pokhara, Nepal (2017)
- Ecological Theory and Application discussion group meeting (2018)
- Bi-weekly FEM journal club (2018)
- MSc Thesis defence seminar at Institute of Forestry; Pokhara, Nepal (2019)
- BSc Thesis proposal defence seminar at Institute of Forestry; Hetauda, Nepal (2021)
- MSc Thesis proposal defence seminar at Institute of Forestry; Hetauda, Nepal (2021)

International symposia, workshops and conferences (4.7 ECTS)

- Association for Tropical Biology and Conservation (ATBC) Asia Pacific Chapter Conference; oral presentation (2019)
- Tropical ecology and conservation: advances in technology; TropiCon20 (2020)
- Virtual meeting of the Association for Tropical Biology and Conservation; oral presentation (2021)

Lecturing / supervision of practicals / tutorials (11.7 ECTS)

- Forest ecology and forest management; WUR, Netherlands (2018)
- Forest Ecology; Pokhara, Nepal (2019)
- Forest Ecology and Management; Pokhara, Nepal (2019)
- Local volume table preparation and tree biomass modelling; Pokhara, Nepal (2021)

Supervision of MSc student (9 ECTS)

- Traits and species distribution along the altitudinal gradient of the Himalayas, Nepal
- Acclimation of tree functional traits to altitude
- Effects of climate change on tree species distributions along the Himalayan altitudinal gradient in Nepal

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