

RESEARCH ARTICLE

Functional traits shape tree species distribution in the Himalayas

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Abstract

1. 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?
2. 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.
3. 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.
4. *Synthesis.* Multiple trade-offs in plant size, hydraulics and light competitiveness shape species distribution along the elevational gradient. Along this extreme

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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

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 specialisation 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 specialisation, 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 CO₂ 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 CO₂ 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, 1992) 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 life span, 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 tree species occurring from a warm and wet lowlands with tropical climate to a colder and drier highlands with subalpine climate in the Nepalese Himalayas (HMGN/MFSC, 2002; Lillesø et al., 2005, see Section 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 tree line). 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 hypothesised that plant traits associated with resource conservation versus rapid resource acquisition can best predict species positions along an elevational gradient.

2 | MATERIALS AND METHODS

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 S1). Within a horizontal span of ca. 110 km, elevation varies from c. 90 m at Nijgadh in Bara district in the south to c. 3,850 m (tree line) at Lauribinayak in Rasuwa district in the north. Along this gradient, temperature decreases approximately linearly, and precipitation peaks around 1,000 m and then decreases rapidly (Figure S2). Potential evapotranspiration follows the temperature trend, wind speed shows increasing trend, while topography becomes steeper and soil becomes shallower (Figure S2). Vegetation follows changes in temperature and precipitation patterns and changes from wet (1738 mm/year) and warm (24.1°C) tropical forests to intermediate temperate forests to drier (1,132 mm/year) 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 1; Table S1). 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 S1), thus guaranteeing a wide phylogenetic coverage. As some of the mid- and high-elevation deciduous species were already losing their leaves at the time of fieldwork, we could not include them in this study.

2.2 | Sampling design

To adequately describe species' trait values and account for elevational 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 & 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.

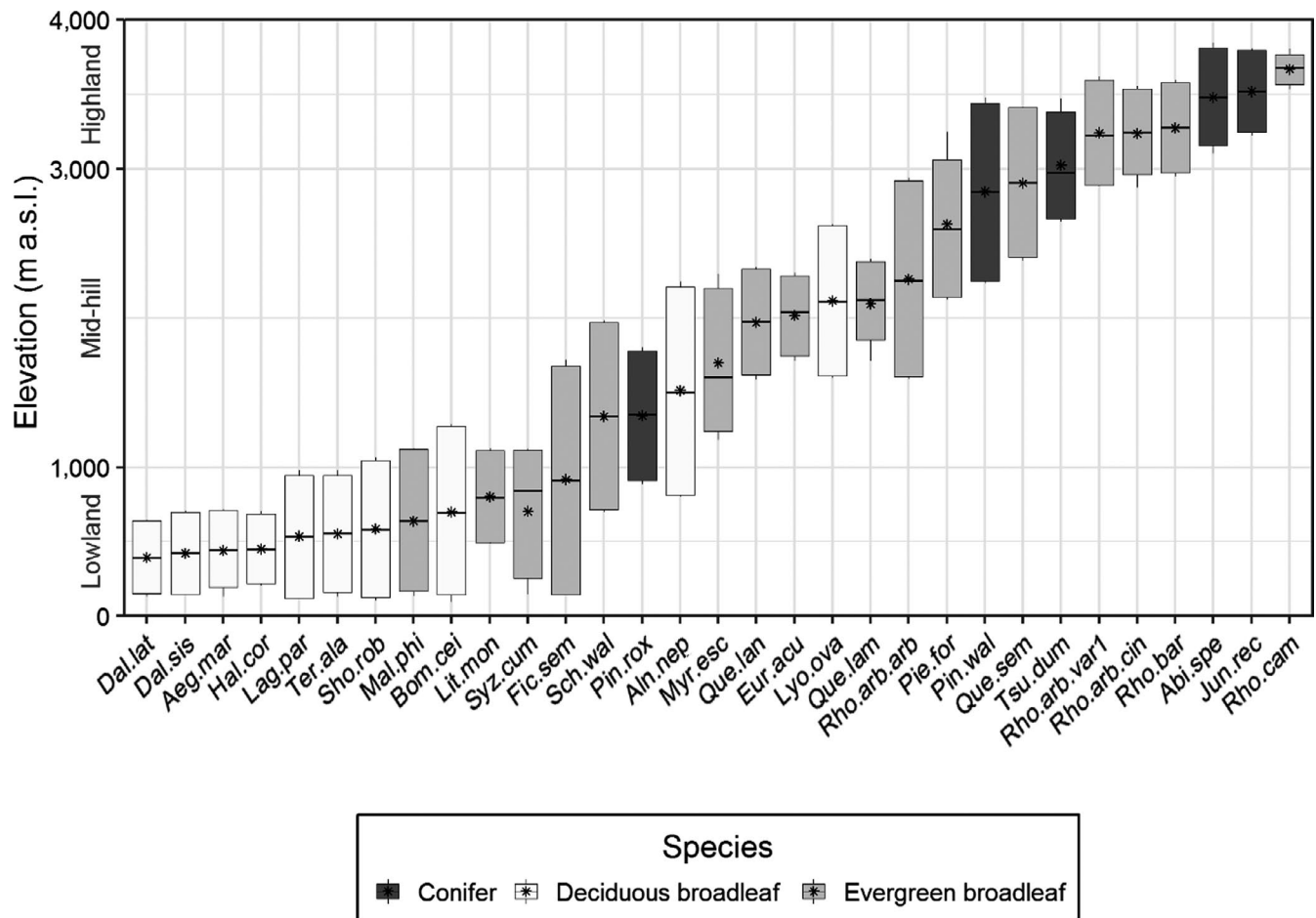


FIGURE 1 Positions of 31 Himalayan tree species along the elevational gradient (lowland: <1,000 m a.s.l.; mid-hill: 1,000–3,000 m a.s.l.; and highland: >3,000 m a.s.l.) based on the field data. Boxplots indicate species' elevational positions and elevation ranges (box—inter-quartile range, a horizontal 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 S1

2.3 | Trait measurements

We selected 39 traits (Table 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 nutrients availability). Traits were measured following standardised 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.

2.3.1 | 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 was determined based on personal experience and literature (<http://www.efloras.org/>, 2019; Jackson, 1994).

2.3.2 | 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 standardised 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

TABLE 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 \times 6 trees). Traits are grouped by organisational 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

					Percentile		
Trait name	Abbreviation	Unit	Function	Median	5th	95th	CV
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	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	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	LI	54.9	21.5	144.7	0.7
Leaf number per branch length	LNBL	count/cm	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	LI	0.5	0.3	0.7	0.3
Leaf area ratio	LAR	cm ² /g	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	2,563.8	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	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	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				

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 standardised 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.

2.3.3 | 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 ($\mu\text{g}/\text{cm}^2$) = $(117.1 \times \text{SPAD}) / (148.84 - \text{SPAD})$ (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.

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 standardised 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) 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 S1) 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 Maharjan et al. (submitted).

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 2) with a strong correlation with elevation (see Table 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 | RESULTS

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 1). Tree species ranged in median height from 5 to 17 m; in basal area from 87 to 661 cm²; and in conduit density from 19 to

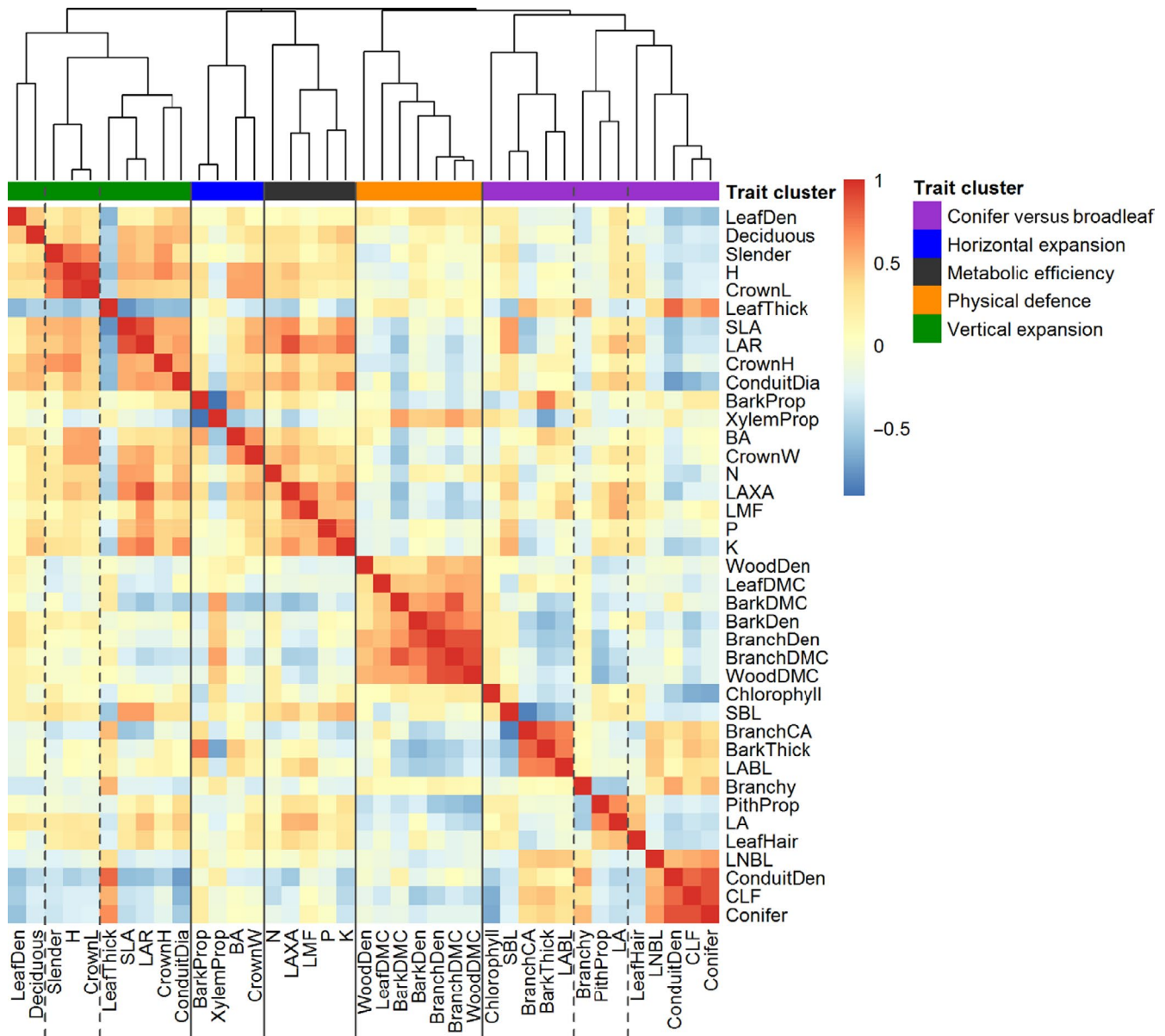


FIGURE 2 Covariance of plant functional traits ($n = 31$ species) analysed by cluster analysis (hierarchical clustering) combined with a heatmap of covariation among the 39 traits. Trait correlations are indicated using colours, warm shades indicate positive correlation and cool shades indicate negative 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 versus 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

TABLE 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 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	<u>-0.81</u>	<u>-0.74</u>	-0.39	
CatPCA axis 2	0.11	0.13	<u>0.80</u>	
Vertical expansion				
Height	-0.49	-0.51	<u>-0.81</u>	
Crown base height	<u>-0.59</u>	<u>-0.57</u>	-0.28	
Crown length	-0.34	-0.50	<u>-0.79</u>	
Height diameter ratio (Slenderness)	-0.19	-0.17	<u>-0.61</u>	
Deciduous	<u>-0.63</u>	<u>-0.67</u>	-0.17	
Leaf are ratio	<u>-0.75</u>	<u>-0.74</u>	-0.30	8.50
Conduit diameter	<u>-0.79</u>	<u>-0.73</u>	-0.34	4.42
Specific leaf area	<u>-0.68</u>	<u>-0.67</u>	0.36	
Leaf thickness	<u>0.64</u>	<u>0.79</u>	-0.52	
Leaf density	-0.44	-0.35	0.06	
Conifer versus broadleaf				
Coniferous	0.37	0.36	0.05	
Branching architecture	0.34	0.22	-0.003	
Bark thickness	-0.05	0.01	<u>-0.77</u>	
Specific branch length	-0.49	-0.51	<u>0.63</u>	1.83
Branch cross-sectional area	0.25	0.32	<u>-0.81</u>	
Leaf area per branch length	-0.16	-0.15	<u>-0.80</u>	
Leaf number per branch length	0.26	0.17	-0.01	
Pith proportion	-0.19	-0.02	0.24	
Conduit density	<u>0.66</u>	<u>0.66</u>	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	<u>0.67</u>	
Leaf hairs	-0.15	-0.11	0.28	
Metabolic efficiency				
Leaf area per xylem area	<u>-0.76</u>	<u>-0.72</u>	-0.50	5.25
Leaf mass fraction	-0.46	-0.42	<u>-0.70</u>	
Leaf N concentration	-0.42	-0.47	<u>0.82</u>	
Leaf P concentration	-0.46	-0.46	0.37	
Leaf K concentration	<u>-0.59</u>	<u>-0.60</u>	<u>-0.71</u>	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	<u>0.73</u>	
Branch dry matter content	0.35	0.25	<u>0.59</u>	4.82
Wood dry matter content	0.08	-0.01	<u>0.75</u>	
Bark dry matter content	0.55	0.51	-0.40	6.88
Leaf dry matter content	0.03	0.12	-0.54	

(Continue)

TABLE 2 (Continued)

Strategy axis and trait	Correlation with elevation		PIC	VIF
	Pearson's <i>r</i>	Spearman's <i>r</i>		
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	

2,564 conduits/mm². Likewise, tree species ranged in SLA from 41 to 143 cm²/g 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 2).

3.2 | Plant strategies among Himalayan tree 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 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 life span. The purple cluster represents the split between **conifer- 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 visualised in the CatPCA (Figure 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). 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 versus 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). 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 life span 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.

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

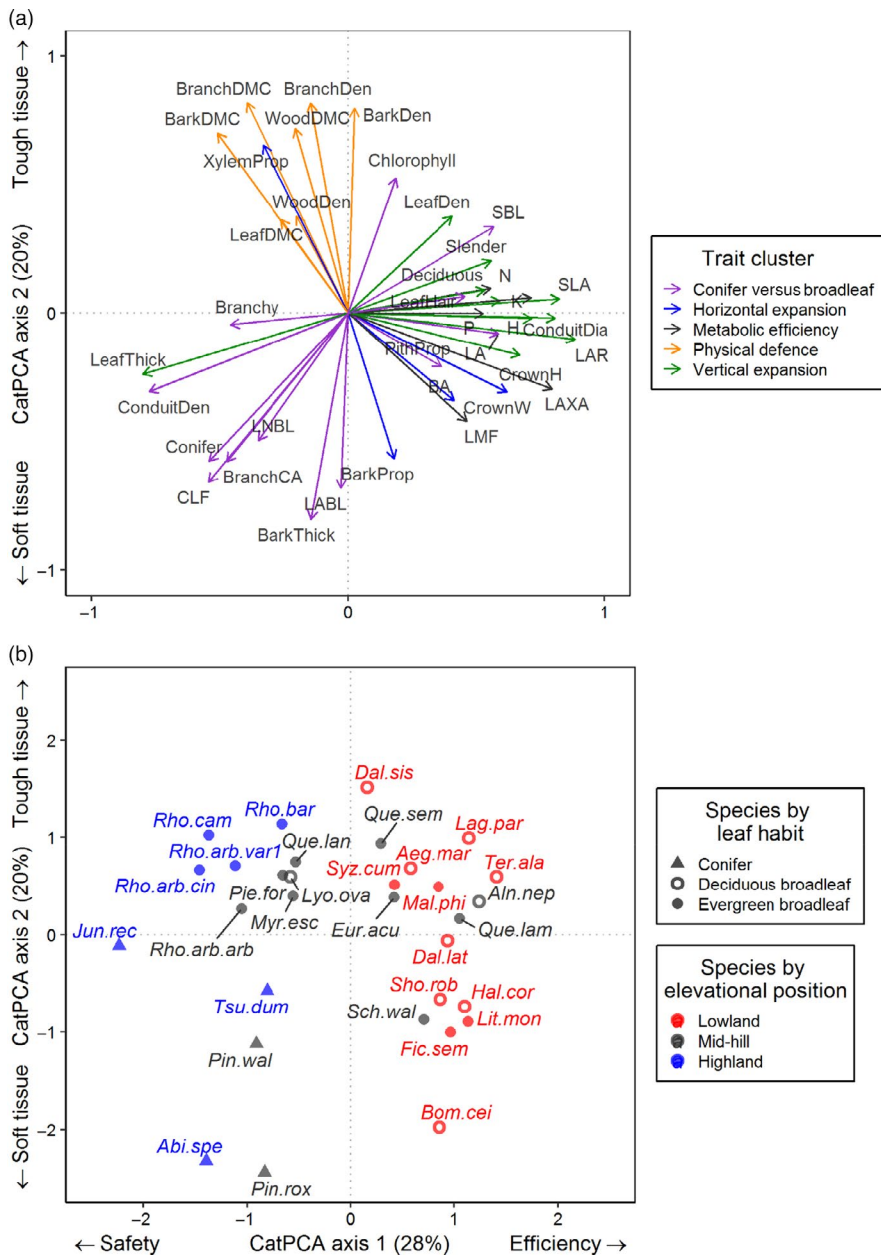


FIGURE 3 Covariance of plant functional traits ($n = 31$ species) analysed by categorical principal component analysis (CatPCA). (a) Trait loadings along the first two CatPCA axes. Arrows are coloured according to trait clusters identified by the cluster analysis (Figure 2). For trait abbreviations, see Table 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 S1. CatPCA axis 1 explains 28% of trait variation and CatPCA axis 2 20%

obtained from parametric (Pearson) and nonparametric (Spearman) correlation analyses (Table 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 21 of 39 traits/strategy axes (54%) 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 2; Figure 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 2; Figure 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). 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 2; Figure 4).

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

FIGURE 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 $p < 0.05$

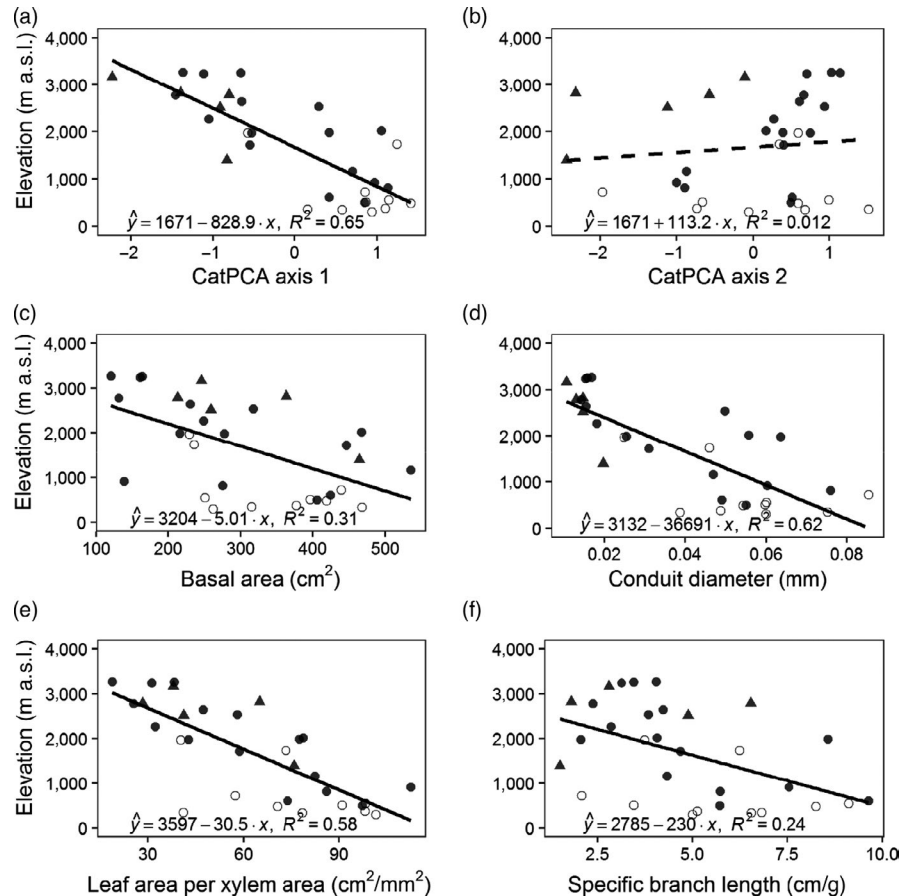


TABLE 3 The selected models (models with $\Delta\text{AICc} < 2$) predicting the effects of traits on species' position along the elevational gradient. All models are significant at $p < 0.001$. Regression coefficients in bold are significant at $p < 0.05$, those in bold and italic are significant at $p < 0.01$, and those in bold and underlined are significant at $p < 0.001$. Number of model parameters (df), Log-likelihood ($\log\text{Lik}$) values, AIC with small sample bias adjustment (AICc), AICc difference from the best model (ΔAICc), model weight (Weight) and adjusted coefficients of determination ($\text{adj.}R^2$) for the selected models and average regression coefficients (Avg), an importance value for individual predictors (Imp) are shown. For trait abbreviations, see Table 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	<u>-0.45</u>	<u>-0.46</u>	<u>-0.45</u>	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		
$\log\text{Lik}$	-16.63	-15.93		
AICc	48.77	50.73		
ΔAICc	0.00	1.96		
weight	0.12	0.05		
$\text{adj.}R^2$	0.80	0.80		

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). 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). The analysis showed that the whole-tree traits (basal area) and the branch traits (conduit diameter, LAXA and SBL) are more 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 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.

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.

4.1 | Key plant strategies among Himalayan tree species

We hypothesised 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) 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 tree 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).

4.2 | Trait-elevation relationships

We hypothesised 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.

4.2.1 | 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 2). Small size (e.g. tree height and basal area) is often observed at highlands (Table 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 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 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 elevations (Table 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 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.

4.2.2 | 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 organisation 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.

4.2.3 | Successful clades at high elevations; Gymnosperms versus Rhododendrons

The second strategy axis, which reflects a trade-off between soft and tough tissues, was independent from elevation. At high elevations (Figure 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.

4.2.4 | 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) and curiously, many species have a high wood density (>800 kg/m³, 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 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*, *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.

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; Figure 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 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 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 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 CO₂ 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 CO₂ uptake. Instead, the larger efficiency in leaf display and branch expansion (specific branch length) at lower elevations (Figure 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, 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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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

S.K.M., F.J.S. and L.P. conceived of the research idea; S.K.M., B.P.D., and M.M. compiled and processed data; S.K.M., with contributions from F.J.S. and L.P., performed statistical analyses; S.K.M. wrote the first draft and F.J.S. and L.P. extensively discussed the results and commented on the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13759>.

DATA AVAILABILITY STATEMENT

Species trait data used in this study are available at Data Archiving and Networked Services (DANS, www.dans.knaw.nl): <https://doi.org/10.17026/dans-25t-ey9t> (Maharjan et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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