

## Taxonomic and functional plant diversity patterns along an elevational gradient through treeline ecotone in Kashmir

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**Abstract:** Species distribution and community assembly patterns along elevation gradients have been studied world over but not much information in this regard is available about the Indian Himalayan region, including the Kashmir Himalaya. It is in this context that we studied elevational (2200–3800 m) patterns in plant species richness, and functional and taxonomic group diversity with particular reference to treeline ecotone (3200–3700 m). Present study revealed that the patterns of species richness were not consistent across taxonomic or functional groups of plants. Four patterns of species richness in relation to elevation were observed: low-elevation plateau with a mid-peak in bryophytes and lichens, mid-peak pattern in pteridophytes and inverted hump-shaped pattern in monocots. During the present investigation, rapid changes in species composition and physiognomy were recorded in the treeline ecotone over small elevational increases. Number of tree species in this zone declined rapidly from four species at an elevation of 3200 m to one at 3700 m. While from 2200 m to 3200 m the vegetation was predominated by fir (*Abies pindrow*) forming a closed canopy forest, but beyond 3200 m its density decreased rapidly with concomitant increase in the density of birch (*Betula utilis*). Ultimately birch was the dominant treeline species and grew in association with *Rhododendron campanulatum* up to 3700 m, beyond which treeless alpine meadow existed. The present study is first of its kind carried out in Kashmir Himalaya and would hence serve an important baseline for similar such studies that would pave way for better understanding and conservation of plant communities in such mountainous regions.

**Key words:** Birch, elevation pattern, fir, species richness, treeline, timberline.

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### Introduction

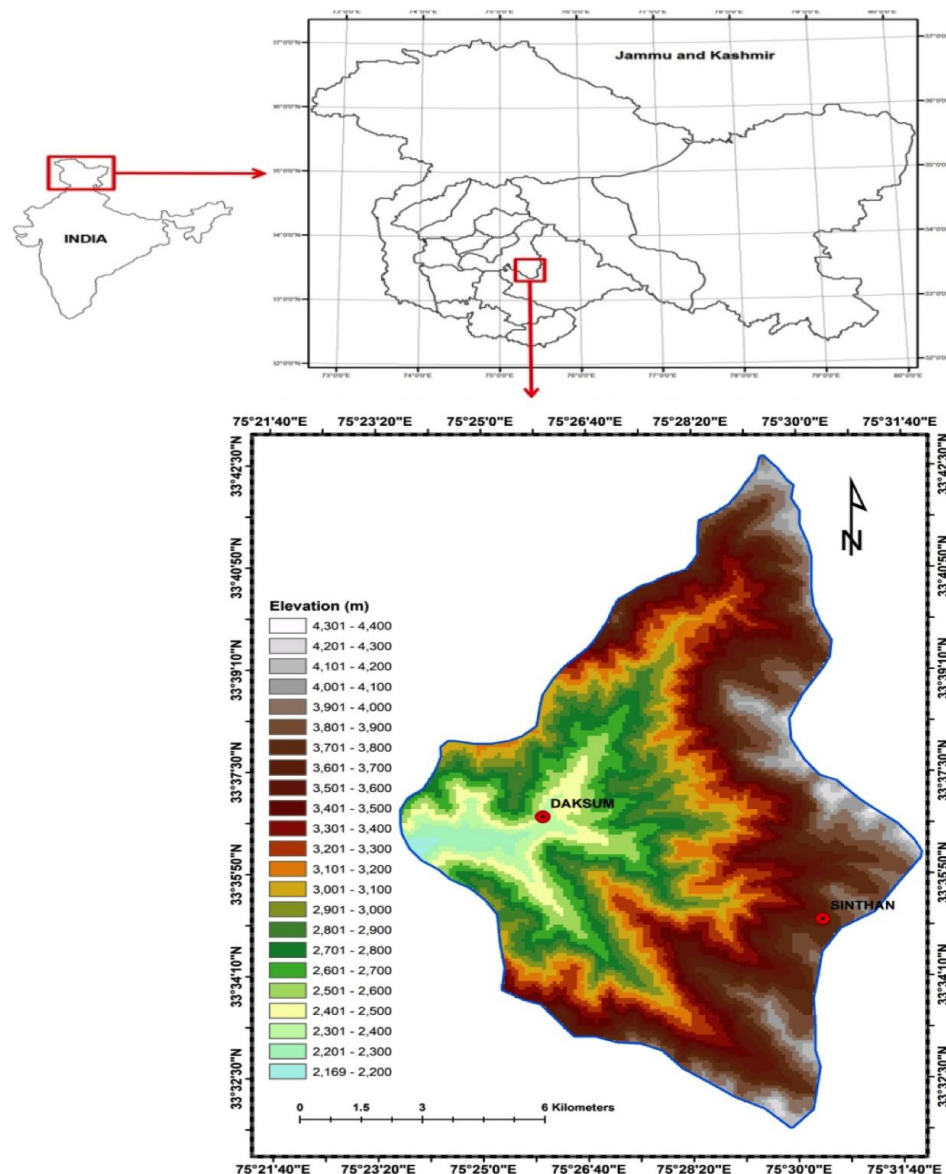
Vegetation in mountainous areas varies in physiognomy, species richness and diversity along elevational gradients (Kluge *et al.* 2017; Manish *et al.* 2017; Peters *et al.* 2016). A number of studies in different parts of the world have revealed that species diversity shows monotonic, unimodal or multimodal patterns in relation to elevation (Rahbek 2005). Mid-gradient peaks of species richness (Mid Domain Effect) have also been reported (Colwell & Lees 2000; Colwell *et al.* 2004; Grytnes & Vetaas 2002; Grytnes 2003). Understanding the underlying mechanisms that

govern such elevational patterns in species diversity not only constitutes a central theme of macroecology, but also has practical implications in discerning the response of species to climate change, particularly in mountainous areas (Saikia *et al.* 2017; Yadav *et al.* 2017). The recent meta-analyses of the studies have enhanced our understanding of the effect of climatic and spatial factors on elevational species richness species and community assembly (Kessler *et al.* 2011; McCain 2007; McCain 2010; Romdal & Grytnes 2007).

Most of the studies that have examined the patterns of species diversity along elevational

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**Fig. 1.** Location map of the study area and study site.

gradients have used species richness as a surrogate for diversity, thereby assuming taxonomic, functional and phylogenetic equivalence among different species (Swenson *et al.* 2012). Patterns of taxonomic biodiversity along elevational gradients are also used as proxies for variation in environmental characteristics (Körner 2007) such as, climate (Schwörer *et al.* 2014; Tuhkanen 1993), temperature and length of growing season (Holtmeier 2009; Hustich 1979; Schickhoff 2005), local climate, topography, site history, and ecology of plant species, current biotic and anthropogenic influences (Holtmeier 2009). Another limitation of studies dealing with elevational pattern in species

diversity is the excessive focus only on one or the other plant group assuming that diversity patterns are uniform across different groups of organisms. However, such an approach limits our understanding of the response of different organisms or taxa to complex gradient of elevation wherein other factors such as temperature, precipitation and other local ecological factors co-vary (Grytnes *et al.* 2006; He *et al.* 2018).

It is also becoming increasingly apparent that taxonomic approach does not adequately capture variation in functional and phylogenetic dimensions of diversity which often respond to environmental gradients differently than does the taxonomic

dimension (Chun *et al.* 2017). Disentangling the underlying processes that govern taxonomic, functional and phylogenetic patterns is of pivotal importance (Chun *et al.* 2017) because of their conservation implications particularly in the context of Himalayas which are warming 2–5 times more than global average. It also needs to be emphasized that changes in species diversity are not uniform along the entire elevational gradient; instead changes are more rapid in the treeline ecotone which extends from the forest limit or the upper limit of the continuous closed forest canopy to the treeless alpine zone above (Dutta *et al.* 2014; Körner 2012; Tranquillini 1979; Wielgolaski *et al.* 2017; Wieser & Tausz 2007).

Thus, the present study was carried out in the Kashmir Himalaya to document taxonomic and functional diversity of all major plant groups, including angiosperms, gymnosperms, ferns, bryophytes and lichens along an elevational gradient. The present study is significant since it simultaneously studied pattern of taxonomic and functional diversity in different groups of plants unlike most previous studies that have studied only taxonomic diversity mostly of one or the other plant group. Furthermore, the present study is first of its kind in the Kashmir Himalaya and hence would add to the body of knowledge about the elevational patterns of species richness in different parts of Himalaya which is necessary to have an overarching understanding of species diversity patterns along elevational gradients particularly in the context of climate change and other anthropogenic stressors.

## Materials and methods

### *Study area*

Present study was carried out in the Daksum and Sinthan Top area of the Kashmir Himalaya (Fig. 1). Daksum lies within the geographical coordinates of 33°36'43"N 75°26'6"E and is located at an altitude of 2,200 m above the sea level at a distance of 40 km from the main district headquarter of Anantnag and about 85 km from Srinagar. Sinthan Top (3800 m) lies within the geographical coordinates of 33°34'N and 75°30'E and a road (NH1B highway) traverses through this top that connects Kashmir valley with Kishtwar which lies in Jammu province of the State. Daksum-Sinthan Top area is about 130 km south of Srinagar, 73 km from Anantnag and 48 km from Kokernag. Climate of the study area is akin to

general climate of Kashmir Valley. Average annual temperature is 12.8 °C. Precipitation here averages 1035 mm. It is largely non-monsoonal and most of the precipitation falls in March averaging 161 mm.

### *Vegetation sampling*

For vegetation sampling, the altitudinal gradient of 2200 to 3800 m in the study area was divided into seventeen (17) altitudinal bands of 100 m each. Three plots of 50 × 50 m area were established in each of these altitudinal bands. In each plot ten (10 × 10) quadrats for trees, 20 (5 × 5 m) for shrubs and 40 (1 × 1 m) for herbs were laid randomly for vegetation sampling. Thus, in each elevational band, 30 quadrats were laid for documenting the diversity of trees, 60 quadrats for shrubs and 120 quadrats for herbs. Across the entire elevational gradient, in all 510 quadrats were sampled for recording tree species richness, 1020 quadrats for recording species richness of shrubs and 2040 quadrats for recording species richness of herbs.

### *Taxonomic diversity*

It was quantified on the basis of collection, identification and inventorization of species belonging to angiosperms, gymnosperms, bryophytes, ferns, lichens from each of the elevational bands employing quadrat method.

### *Functional diversity*

Following functional traits of spermatophytes were studied during the present study:

Growth form: Trees (>2 cm dbh, height 5–15 m), shrubs (height <2 m) and herbs (height <0.5 m).

Life span: Annual/Perennial

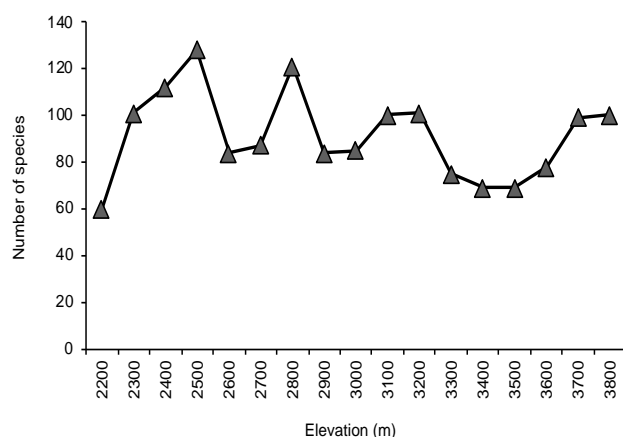
Stem tissue: Herbs/shrubs/trees

For bryophytes and lichens following growth forms were recognized:

Bryophytes: Liverworts (leafy) and mosses

Lichens: Thallus growth form (foliose, fruticose, crustose, leprose, etc.)

Species accumulation curves for trees, shrubs and herbs and rarefaction curves for trees and shrubs were computed using EstimateS (Colwell 2013). Species accumulation curves, sometimes called collectors curves, plot the cumulative number of species recorded as a function of sampling effort, such as number of samples laid (Colwell & Coddington 1994). They were used to indicate the adequacy of sampling effort in different elevational



**Fig. 2.** Overall species richness along the elevational gradient in Kashmir Himalaya.

**Table 1.** Composition of plant species in the study area.

Plant group	No. of species	Genera	Families
Dicots	175	131	44
Monocots	19	16	10
Gymnosperms	4	4	2
Pteridophytes	33	16	9
Bryophytes	39	33	22
Lichens	155	68	30
Total	425	268	117

bands. Since number of individuals of trees and shrubs sampled in different elevational bands was different, a direct comparison of species richness would have been meaningless (Grytnes & Beaman 2006). Thus, rarefaction method was used to compare samples that have different numbers of specimens sampled by randomly drawing an equal number of specimens from the samples and counting the number of species drawn from each sample (Gotelli & Colwell 2001; Magurran 2004).

### Statistical analyses

Relationship between different dependent and independent variables was assessed employing various regression and other statistical models. We selected the regression model based on  $r^2$ .

## Results

### Species richness and composition

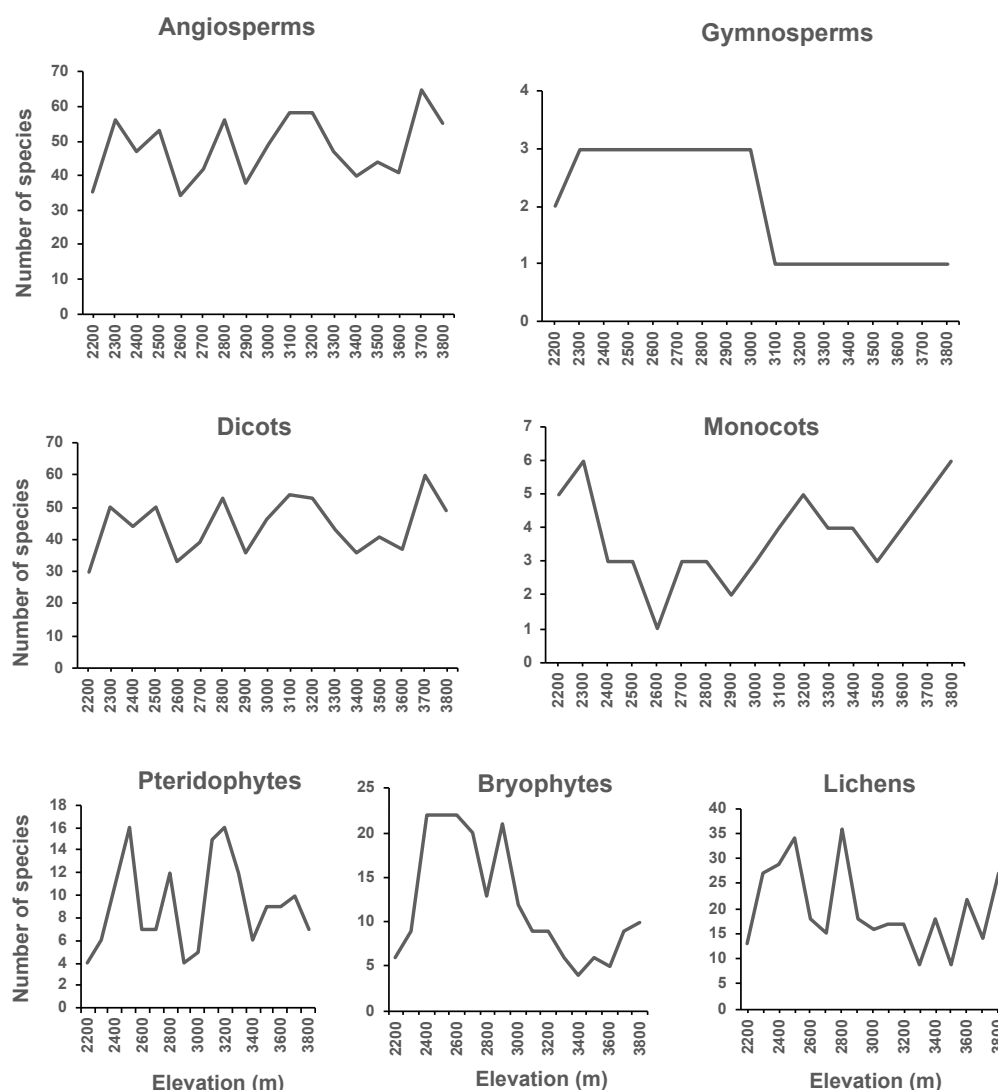
Floristic surveys in the study area of Daksum-Sinthan Top in the Kashmir Himalaya resulted in

collection and identification of 425 plant species belonging to 268 genera and 117 families (Table 1). Amongst these, the flowering plants were predominant, with dicots sharing 175 species in 131 genera and 44 families, and monocots only 19 species in 16 genera of 10 families. Gymnosperms were represented by 4 species belonging to 4 genera and 2 families. Besides, 33 species of pteridophytes in 16 genera and 9 families, 39 species of bryophytes in 33 genera and 22 families and 155 species of lichens in 68 genera and 30 families were also recorded from the area.

### Elevational trend in species richness

The total species richness ranged from a lowest of 60 species at an altitude of 2200 m amsl to a highest of 128 species recorded in the elevational band of 2500 m amsl. Overall pattern exhibits a mid-elevation peak in species richness followed by decline with increase in altitude (Fig. 2) but with a moderate increase in alpine zone. The number of angiosperm species was highest in the elevational band of 3700 m with lowest in the 2200 m band (Table 2). Highest (60 spp) and lowest (30 spp) number of dicot species was recorded in 3700 m and 2200 m elevational bands, respectively. Monocots were not well represented in the study area and the number of monocot species in different elevational bands ranged from 1 to 6 species. Number of gymnosperm species was invariably higher in lower altitudes with highest being 3 species recorded upto 3000 m beyond which only one gymnosperm species was recorded in each of the elevational bands. Number of pteridophytes across the elevational gradient ranged from 4 to 16 while that of bryophytes it varied from 4 to 22 species. Number of lichen species ranged from a minimum of 9 species recorded in 3300 and 3500 m elevational band to a maximum of 36 species recorded at an elevation of 2800 m. Angiosperm species number was highest in 17 bands while in 5 bands lichens had the highest number of species. Bryophytes and pteridophytes followed them in species richness per band.

Elevational patterns of various taxonomic and functional plant groups are presented in Figs. 3–7. Angiosperms including dicots and pteridophytes show a wavy pattern distribution along increasing altitude with several peaks and troughs. Monocots showed a characteristic pattern of mid-elevational decline and subsequent increase in higher elevations while bryophytes kept on decreasing with increasing altitude. Lichen richness peaked in



**Fig. 3.** Elevational pattern in species richness of different plant groups.

mid elevations and declined in higher elevations with modest increase in alpine zone (Fig. 3). In all, four patterns of species richness in relation to elevation were observed during the present study: low-elevation plateau with a mid-peak in bryophytes, mid-peak pattern in pteridophytes and lichens, and inverted hump-shaped pattern in monocots.

Functional groups of spermatophytes viz, trees, shrubs and herbs also showed specific elevational patterns in species richness (Figs. 4–7). Trees showed a characteristic mid-elevational peak, but overall curve was wavy, with several rises and falls. Shrubs, on the contrary, showed highest richness at 2300 m and thereafter declined sharply up to 2700 m, where after it leveled off. Herbs, on the other hand presented a wavy pattern with many peaks and

troughs but overall curve showed no tendency for species decline within the study elevational range. Patterns of species richness studied in terms of life span of species (Fig. 5) revealed that annuals and perennials show more or less similar patterns of increase and decrease with increasing elevation. The overall trend was similar to that of herbs. Growth forms of bryophytes characterized in terms of liverworts and mosses more or less showed mid-elevation peaks and decline in higher elevations (Fig. 6). While mid-elevation peaks in species richness of lichens was observed in crustose, foliose and fruticose functional types (Fig. 7), leprose functional type showed highly irregular pattern in species richness in relation to elevation. Species richness peak occurred at 3700–3800 m for angiosperms as a whole, dicots and monocots and all herbs, at 3200 m

**Table 2.** Number of species of different plant groups in different elevational bands.

Plant group	Elevational band																
	2200	2300	2400	2500	2600	2700	2800	2900	3000	3100	3200	3300	3400	3500	3600	3700	3800
Angiosperms	35	56	47	53	34	42	56	38	49	58	58	47	40	44	41	65	55
Dicots	30	50	44	50	33	39	53	36	46	54	53	43	36	41	37	60	49
Monocots	5	6	3	3	1	3	3	2	3	4	5	4	4	3	4	5	6
Gymnosperms	2	3	3	3	3	3	3	3	3	1	1	1	1	1	1	1	1
Pteridophytes	4	6	11	16	7	7	12	4	5	15	16	12	6	9	9	10	7
Bryophytes	6	9	22	22	22	20	13	21	12	9	9	6	4	6	5	9	10
Lichens	13	27	29	34	18	15	36	18	16	17	17	9	18	9	22	14	27
Total species richness	95	157	159	181	118	129	176	122	134	158	159	122	109	113	119	164	155

**Table 3.** Taxonomic conspectus of species in the treeline ecotone. Values in parentheses are the percentage of species recorded in the entire elevation transect.

Plant group	No. of species	No. of genera	No. of families
Angiosperms	111(57.2%)	92	37
Dicots	102 (58.3%)	85	32
Monocots	9 (47.3%)	7	5
Gymnosperms	2 (50%)	2	2
Pteridophytes	21 (63.4%)	12	8
Bryophytes	16 (41.0%)	14	10
Lichens	75 (48.3%)	37	24
Total	225 (52.9%)	157	81

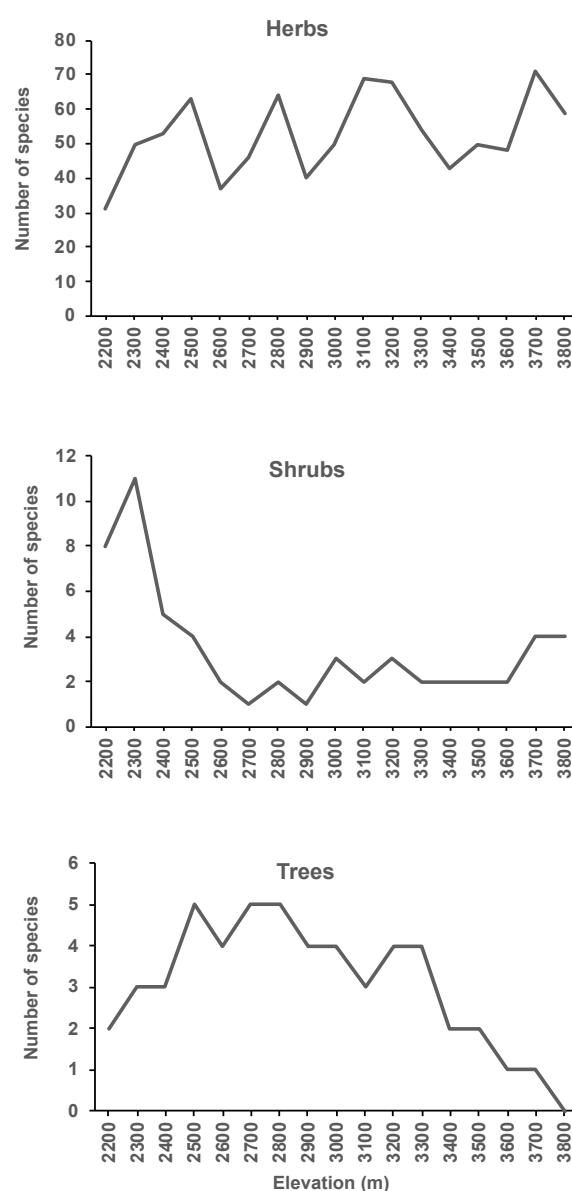
**Table 4.** Number of species belonging to different growth forms in the treeline ecotone.

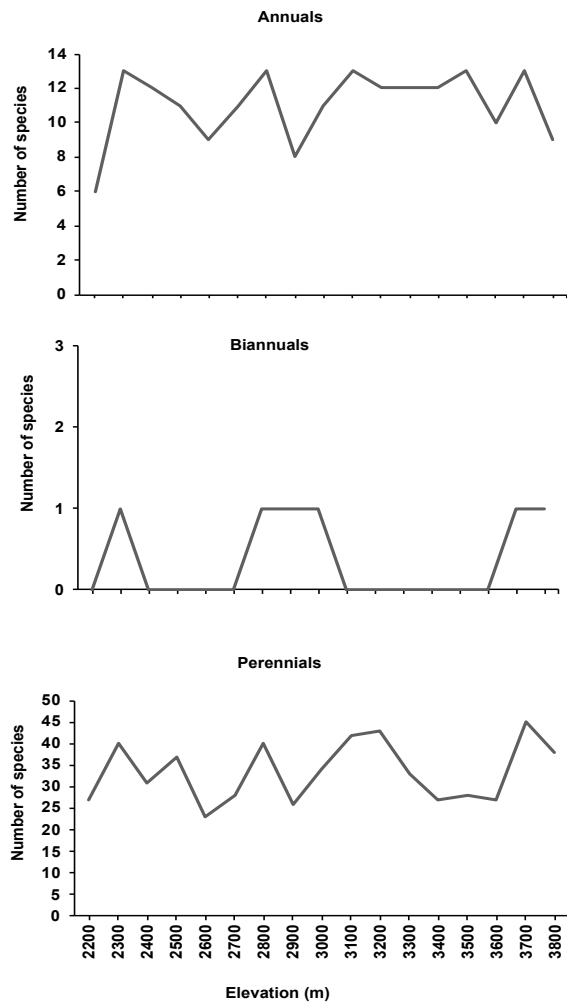
Growth form	No. of species
Herbs	121
Shrubs	9
Trees	4
Total	134

for pteridophytes, at 2800 m for lichens, at 2500–2800 m for trees and 2400 m for bryophytes.

#### *Species richness in treeline ecotone*

The treeline ecotone of study area stretches from the timberline limit (3200 m asl) to the treeless alpine zone (> 3700 m asl). The treeline ecotone is species rich comprising 225 species belonging to 157 genera and 81 families (Table 3). Trends in species richness along elevational gradient in the treeline ecotone (Fig. 8) reveal that the overall species richness is in the lowest elevation of treeline ecotone (3200 m) and thereafter it declines rapidly

**Fig. 4.** Elevational pattern in growth forms of spermatophytes.

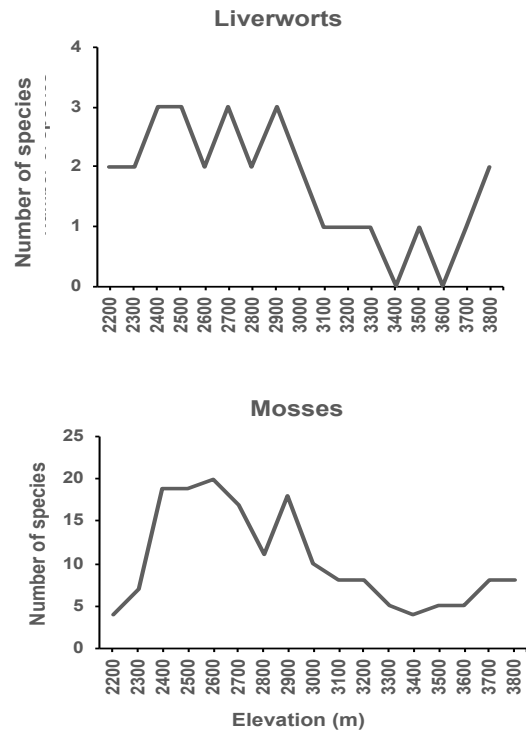


**Fig. 5.** Elevational pattern in species with different life spans in spermatophytes.

and shows modest increase beyond 3600 m and more or less similar pattern in evident in respect of angiosperms and gymnosperms and lichens. Other groups of plants, such as monocots, gymnosperms, pteridophytes and bryophytes do not show any significant variation in relation to elevation in the treeline ecotone.

Relatively, treeline ecotone (ranging from 3200 to 3700 m and including six bands) is richer than the lower part of the elevation gradient (ranging from 2200 to 3200 m and including twelve 100 m elevation bands). About 33% of the elevational transect that represented the treeline ecotone had about 53% of total species recorded in the transect (225 of 425 species). It contained almost 63% of pteridophytes, about half of lichens, but was relatively low in bryophytes.

Functional diversity of vascular plants characterized in terms of growth forms (Table 4)



**Fig. 6.** Elevational pattern in growth forms of bryophytes.

reveals that herbs predominate with 121 species (90%). Elevational pattern of herbs was more or less similar to overall species richness pattern with high species richness at 3200 m and some decline between 3000 to 3600 m and then again in increase in the elevation zone of 3700 m. Shrubs, though less in number, also show a more or less similar elevational pattern. Trees, on the other hand, showed relatively high species richness at 3200 m, thereafter declined with no tree species recorded beyond 3700 m (Fig. 8).

Perusal of data in Fig. 9 reveals that *Abies pindrow* is the dominant tree species upto 3400 m. In fact, it is the timberline species in the study area. However, *Betula utilis* which appears at an altitude of 3300 m increases in numbers relative to *Abies pindrow* and ultimately becomes the dominant tree species at 3600 m but decreases in abundance at 3700 m (Fig. 9).

## Discussion

The present study demonstrates that the elevational patterns of species richness are not consistent across taxonomic or functional groups of plants. Four patterns of species richness in relation

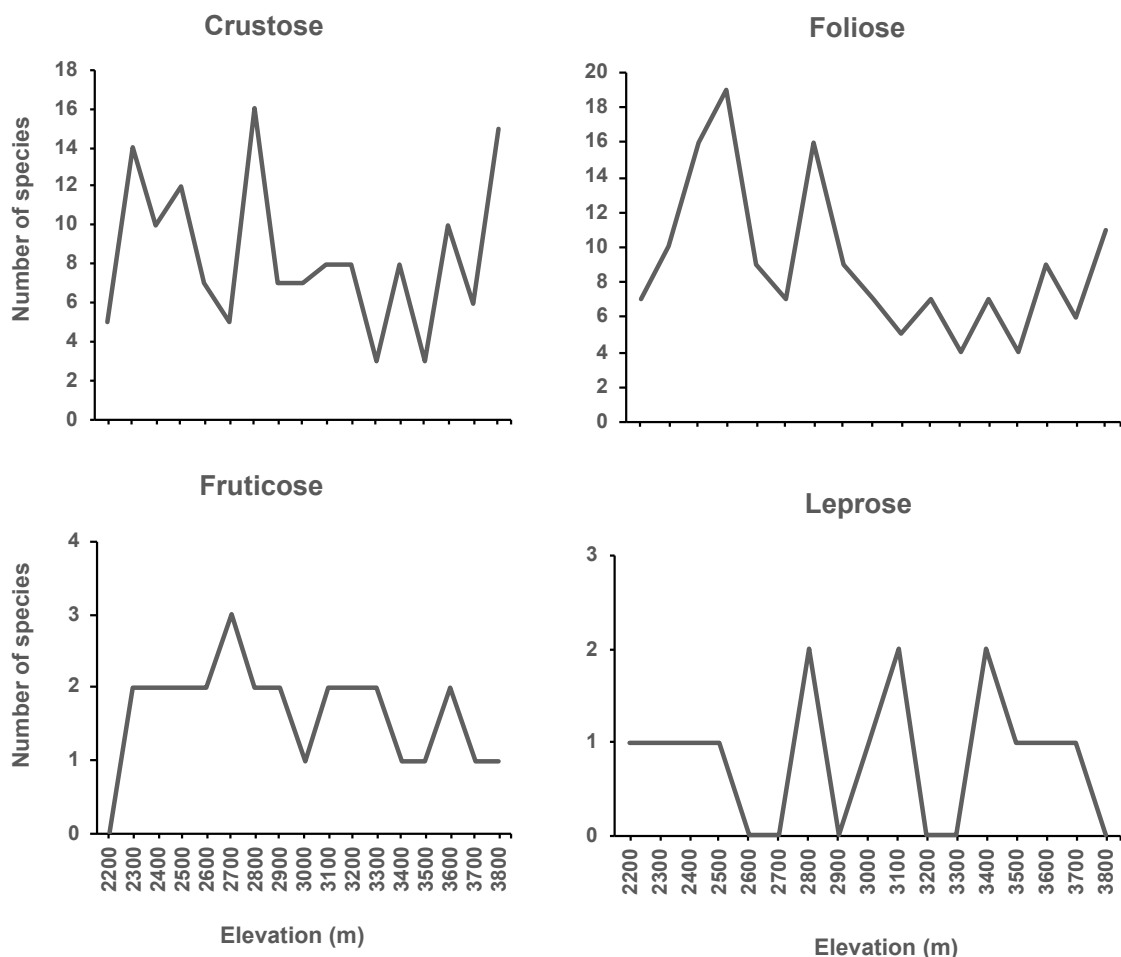


Fig. 7. Elevational pattern in growth forms of lichens.



Fig. 8. Elevation pattern in species richness of trees, shrubs and herbs.

to elevation were observed: low plateau pattern in gymnosperms, low-elevation plateau with a mid-peak in bryophytes, mid-peak pattern in pteridophytes and lichens, and inverted hump-shaped pattern in monocots (Figs. 10–11). Unlike

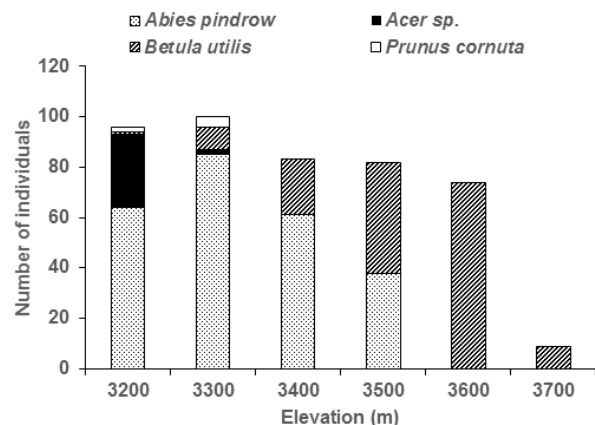
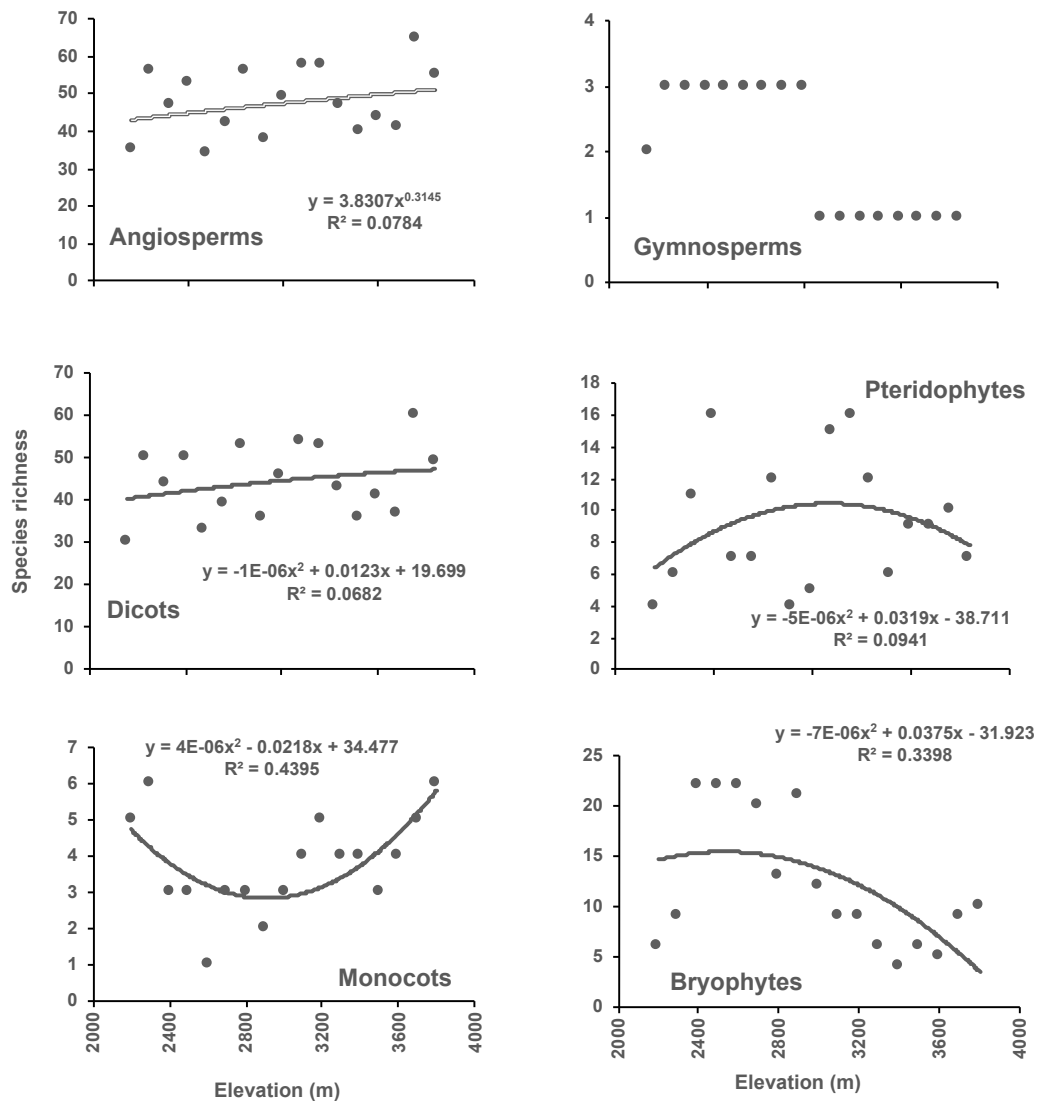


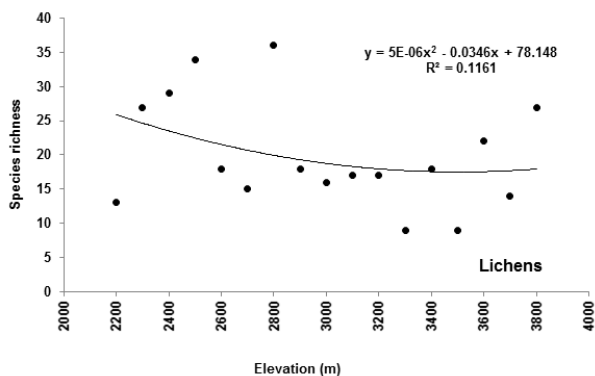
Fig. 9. Density of important tree species in the treeline ecotone.

differing elevational patterns observed in different plant groups in the present study, a hump-shaped pattern in species richness along the elevational gradient is commonly reported (Behera & Kushwaha 2007; Carpenter 2005; Sánchez-González & López-





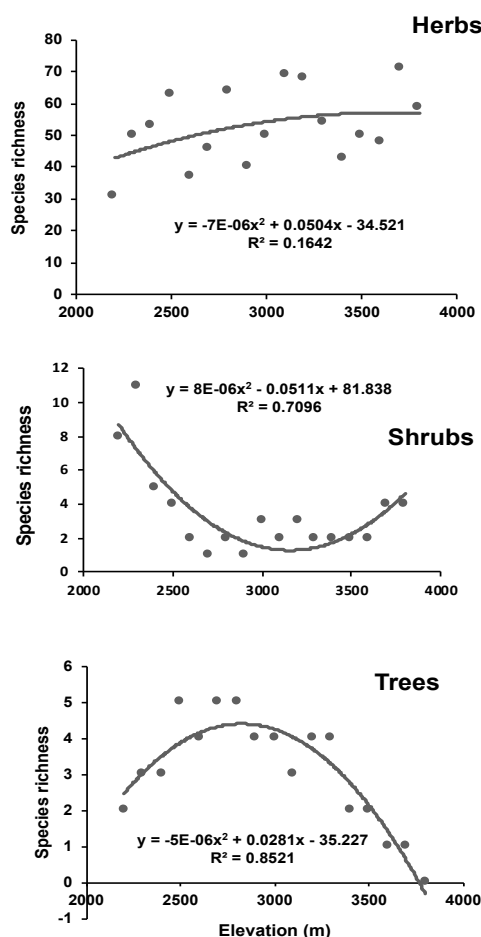
**Fig. 10.** Relationship between species richness of different plant groups and elevation.



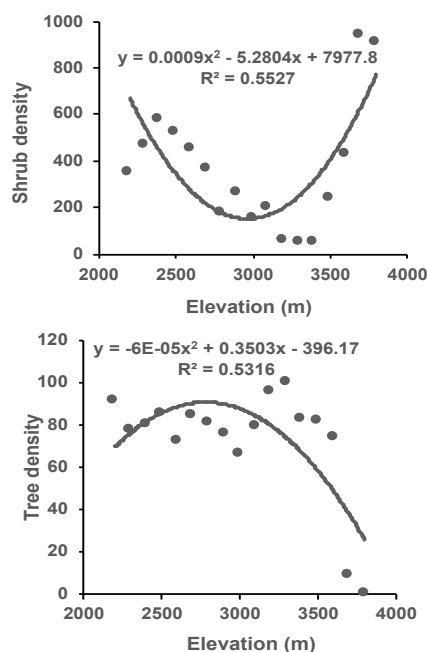
**Fig. 11.** Relationship between species richness of lichens and elevation.

Mata 2005; Tripathi *et al.* 2004) and for a wide range of taxa in the Himalaya, such as flowering plants

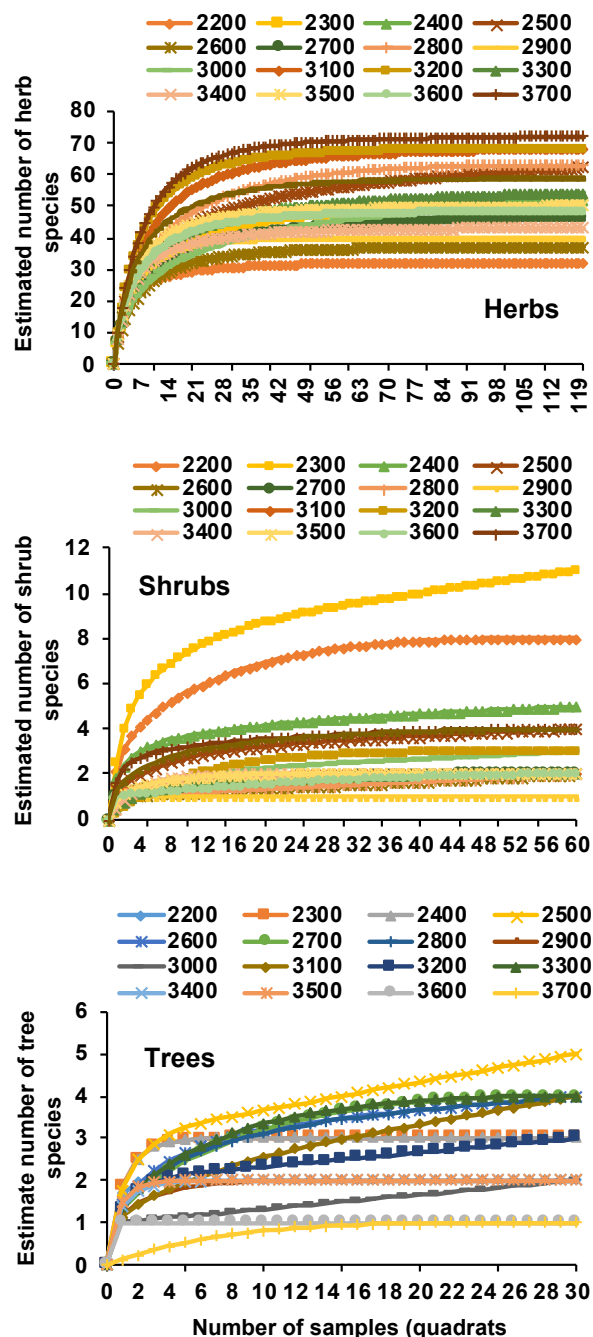
(Bhattarai & Vetaas 2003, 2006; Grytnes & Vetaas 2002), seed plants (Kluge *et al.* 2017), endemic and non-endemic angiosperms (Manish *et al.* 2017), woody plants (Oommen & Shanker 2005), understorey plant species (Carpenter 2005), liverworts and mosses (Grau *et al.* 2007), orchids (Acharya *et al.* 2011), lichens (Baniya *et al.* 2010). Important determinants of mid-elevation peaks in species richness are temperature, humidity, soil characteristics (Carpenter 2005; Kessler 2001; Sánchez-González & López-Mata 2005) and mid-domain (Colwell & Hurtt 1994; Colwell *et al.* 2004; Grytnes & Vetaas 2002). Surprisingly, angiosperms and dicots did not reflect any pattern in species richness in relation to elevations in the present study though inverted hump-shaped pattern was observed in monocots. Since dicots were predominant in the



**Fig. 12.** Relationship between species richness of different plant functional groups and elevation.



**Fig. 13.** Relationship between tree and shrub density and elevation.



**Fig. 14.** Species accumulation curves for trees, shrubs and herbs in different elevational bands.

study area, the pattern in angiosperms was more due to dicots instead of monocots. It is Herb species richness did not show any particular relation with elevation which is consistent with the results of Willinghöfer *et al.* (2011). It may be because herbs have shorter generation times than trees and are morphologically more flexible in their adaptations that allows them to grow across the entire elevational gradient.

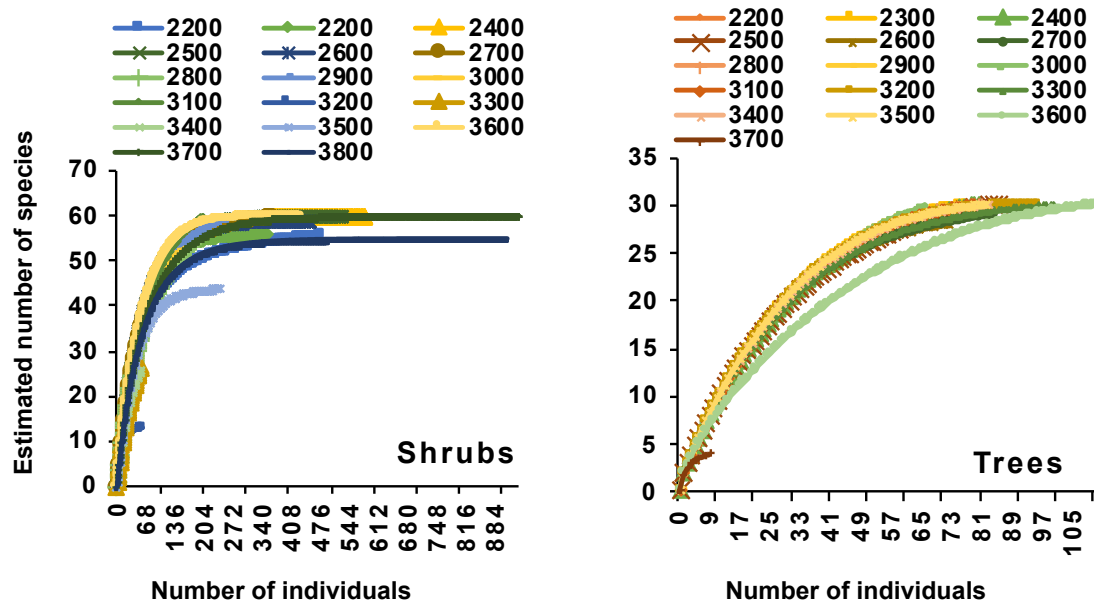


Fig. 15. Rarefaction curves based on individuals sampled for trees and shrubs in different elevational bands.

The present study thus brings out that elevational patterns are taxon-specific and often reported mid-elevational peaks (Rahbek 2005) do not necessarily reflect the over pattern of biodiversity along the elevational gradients. It has been, in fact, argued that multi-taxa elevational patterns in species diversity could be a new approach to develop more general models to explain elevational patterns in species diversity (Peters *et al.* 2016). Such taxon-specific patterns reflect the ecology of the taxonomic groups, their requirements and their response and relationship with the factors of temperature, precipitation, day length that covary with altitude (McCain 2009, 2010) and such observations draw support from similar findings of Grytnes *et al.* (2006) and Zhang *et al.* (2016).

During the present investigation, it became apparent that growth forms, such as trees, shrubs and herbs showed different elevational patterns (Figs. 12–13). A low-elevation plateau with a mid-peak was seen in trees, shrubs presented an inverted hump shaped pattern and herbs did not exhibit any elevation pattern. Willinghöfer *et al.* (2012) and Ohlemüller & Wilson (2000) also did not notice any particular trend in herbs in relation to elevation. However, other studies carried out on elevational patterns in herbs have reported a U-shaped pattern in Borneo (200–850 m) (Poulsen & Pendry 1995), a monotonic decline between 770 and 1520 m in central Africa (Poulsen *et al.* 2005), a hump-shaped pattern from sea level to 4094 m in

Borneo (Grytnes & Beaman 2006), and a roughly monotonic increase between 1200 and 2700 m in Ethiopia (Desalegn & Beierkuhnlein 2010). Such differences could be attributed to differences in the ecological conditions in these study areas and also to the different elevational spans covered in these studies.

The alpine treeline ecotone, extending between the upper limit of closed forest (timberline) and the highest individuals of tree species showing an upright growth form (treeline), showed changes in species composition, physiognomy, density of trees and shrubs with small increments in altitude. Similar changes have been recorded by Batllori *et al.* (2009) and Orbán *et al.* (2017). In particular, *Abies pindrow*, the timberline species in the study area, decreases in density presumably because trees are reported to be sensitive to climatic variation (Theurillat & Guisan 2001). Infact, a common thermal threshold has been advanced as an explanation for limits to forest and tree growth in higher elevations (Körner & Paulsen 2004). Not only do the variations in physical environment in the treeline ecotone help explain the rapid changes in species composition, but it is quite possible that increased light availability due to sparse cover of forest trees in the ecotone may be enabling many species to grow in the alpine vegetation as has been reported by Grytnes (2000). However, it also needs to be emphasized that plant community composition at a small spatial scale is also

controlled by several factors, such as microtopography, temperature, snow, wind, soil nutrients, moisture availability, pH and other biotic factors (Batllori *et al.* 2009). It is very likely that all these factors may be operative in the study area and in concert may be determining the plant community structure in the treeline ecotone.

It also needs to be emphasized that sampling robustness is essential for accurate portrayal of species richness patterns and hence it is of pivotal importance to determine whether or not sampling effort was enough (Gotelli & Colwell 2001).

The common sampling bias arises as a consequence of less and/or uneven sampling effort across the elevational gradient which can be overcome through use of sample and individual based rarefaction (Gotelli & Colwell 2001). In the present study, the sample-based species accumulation curves (Fig. 14) and individual-based rarefaction curves computed for trees and shrubs (Fig. 15) which make direct comparisons amongst communities on the basis of number of individuals in the smallest sample clearly reveal adequacy of sampling and hence conclusions drawn about elevational patterns during the present study could be considered as robust.

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### References

- Acharya, K. P., O. R. Vetaas & H. J. B. Birks. 2011. Orchid species richness along Himalayan elevational gradients. *Journal of Biogeography* **38**: 1821–1833.
- Baniya, C. B., T. Solhoy, Y. Gauslaa & M. W. Palmer. 2010. The elevation gradient of lichen species richness in Nepal. *The Lichenologist* **42**: 83–96.
- Batllori, E., J. J. Camarero, J. M. Ninot, E. Gutiérrez, E. 2009. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. *Global Ecology and Biogeography* **18**: 460–472.
- Behera, M. D. & S. Kushwaha. 2007. An analysis of altitudinal behaviour of tree species in Subansiri district, Eastern Himalaya. *Biodiversity and Conservation* **16**: 1851–1865.
- Bhattarai, K. R. & O. R. Vetaas. 2003. Variation in plant species richness of different life forms along a subtropical elevation gradient in the Himalayas, East Nepal. *Global Ecology and Biogeography* **12**: 327–340.
- Bhattarai, K. R. & O. R. Vetaas. 2006. Can Rapoport's rule explain tree species richness along the Himalayan elevation gradient, Nepal? *Diversity and Distributions* **12**: 373–378.
- Carpenter, C. 2005. The environmental control of plant species density on a Himalayan elevation gradient. *Journal of Biogeography* **32**: 999–1018.
- Chun, Jung-Hwa & Chang-Bae Lee. 2017. Disentangling the local-scale drivers of taxonomic, phylogenetic and functional diversity in woody plant assemblages along elevation gradients in South Korea. *PloS One* **12**: e0185763.
- Colwell, R. K. 2013. EstimateS: statistical estimation of species richness and shared species from samples. Version 9.—User's Guide and application at <http://purl.oclc.org/estimates>.
- Colwell, R. K. & D. C. Lees. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* **15**: 70–76.
- Colwell, R. K. & G. C. Hurtt. 1994. Non biological gradients in species richness and a spurious Rapoport effect. *The American Naturalist* **144**: 570–595.
- Colwell, R. K. & J. A. Coddington. 1994. Estimating the extent of terrestrial biodiversity through extrapolation. *Philosophical Transactions of Royal Society of London* **345**: 101–118.
- Colwell, R. K., C. X. Mao & J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* **85**: 2717–2727.
- Desalegn, W. & C. Beierkuhnlein. 2010. Plant species and growth form richness along altitudinal gradients in the southwest Ethiopian highlands. *Journal of Vegetation Science* **21**: 617–626.
- Dutta, P. K., B. K. Dutta, A. K. Das & R. C. Sundriyal. 2014. Alpine timberline research gap in Himalaya: a literature review. *Indian Forester* **140**: 419–427.
- Gotelli, N. J. & R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**: 379–391.
- Grau, O., J. A. Grytnes & H. J. B. Birks. 2007. A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *Journal of Biogeography* **34**: 1907–1915.
- Grytnes, J. A. 2000. Fine-scale vascular plant species richness in different alpine vegetation types: Relation-

- ships with biomass and cover. *Journal of Vegetation Science* **11**: 87–92.
- Grytnes, J. A. 2003. Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography* **26**: 291–300.
- Grytnes, J. A. & J. H. Beaman. 2006. Elevational species richness patterns for vascular plants on Mount Kinabalu, Borneo. *Journal of Biogeography* **33**: 1838–1849.
- Grytnes, J. A. & O. R. Vetaas. 2002. Species richness and altitude: A comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *The American Naturalist* **159**: 294–304.
- Grytnes, J. A., E. Heegaard & P. G. Ihlen. 2006. Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in Western Norway. *Acta Oecologica* **29**: 241–246.
- He, X., K. Luo, C. Brown & L. Lin. 2018. A taxonomic, functional, and phylogenetic perspective on the community assembly of passerine birds along an elevational gradient in southwest China. *Ecology and Evolution* **8**: 2712–2720.
- Holtmeier, F. K. 2009. *Mountain Timberlines: Ecology, Patchiness, & Dynamics*. Springer, Netherlands.
- Hustich, I. 1979. Ecological concepts and biographical zonation in the north: the need for a generally accepted terminology. *Ecography* **2**: 208–217.
- Kessler, M. 2001. Patterns of diversity and range size of selected plant groups along and elevational transect in the Bolivian Andes. *Biodiversity and Conservation* **10**: 1897–1921.
- Kessler, M., J. Kluge, A. Hemp & R. Ohlemüller. 2011. A global comparative analysis of elevational species richness patterns of ferns. *Global Ecology and Biogeography* **20**: 868–880.
- Kluge, J., S. Worm, S. Lange, D. Long, J. Bohner, R. Yangzom & G. Miehe. 2017. Elevational seed plant richness patterns in Bhutan, Eastern Himalaya. *Journal of Biogeography* **44**: 1711–1722.
- Körner, C. 2007. The use of altitude in ecological research. *Trends in Ecology and Evolution* **22**: 569–574.
- Körner, C. 2012. *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*. Springer, Basel.
- Körner C. & J. Paulsen. 2004. A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* **31**: 713–732.
- Magurran, A. E. 2004. *Measuring Biological Diversity*. Blackwell Science, Oxford.
- Manish, K., M. K. Pandit, Y. Telwala, D. C. Nautiyal, L. P. Koh & S. Tiwari. 2017. Elevational plant species richness patterns and their drivers across non-endemics, endemics and growth forms in the Eastern Himalaya. *Journal of Plant Research* **130**: 829–844.
- McCain, C. M. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography* **16**: 1–13.
- McCain, C. M. 2009. Global analysis of bird elevational diversity. *Global Ecology and Biogeography* **18**: 346–360.
- McCain, C. M. 2010. Global analysis of reptile elevational diversity. *Global Ecology and Biogeography* **19**: 541–553.
- Ohlemüller, R. & J. B. Wilson. 2000. Vascular plant species richness along latitudinal and altitudinal gradients: a contribution from New Zealand temperate rainforests. *Ecology Letters* **3**: 262–266.
- Oommen, M. A. & K. Shanker. 2005. Elevation species richness patterns emerge from multiple local mechanisms in Himalayan woody plants. *Ecology* **86**: 3039–3047.
- Orbán, I., H. H. Birks, I. Vincze, W. Finsinger, L. Pal, E. Marinova, G. Jakab, M. Braun, K. Hubay, T. Biro & E. K. Magyari. 2018. Treeline and timberline dynamics on the northern and southern slopes of the Retezat Mountains (Romania) during the late glacial and the Holocene. *Quaternary International* **447**: 59–78.
- Peters, M. K., A. Hemp, T. Appelhans, C. Behler, A. Classen, F. Detsch, A. Ensslin, S. W. Ferger, S. B. Frederiksen, F. Gebert & M. Hass. 2016. Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nature Communications* **7**: 13736.
- Poulsen, A. D. & C. A. Pendry. 1995. Inventories of ground herbs at three different altitudes on Bukit Belalong, Brunei, Borneo. *Biodiversity and Conservation* **4**: 745–757.
- Poulsen, A. D., D. Hafashimana, G. Eilu, I. B. Liengola, C. E.N. Ewango & T.B. Hart. 2005. Composition and species richness of forest plants along the Albertine Rift, Africa. *ca. Biologische Skrifter* **55**: 129–143.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species richness patterns. *Ecology Letters* **8**: 224–239.
- Romdal, T. S. & J. A. Grytnes. 2007. An indirect area effect on elevational species richness patterns. *Ecography* **30**: 440–448.
- Saikia, P., J. Deka, S. Bharali, A. Kumar, O. P. Tripathi, L. B. Singha, S. Dayanandan & M. L. Khan. 2017. Plant diversity patterns and conservation status of eastern Himalayan forests in Arunachal Pradesh, Northeast India. *Forest Ecosystems* **4**: 28. DOI 10.1186/s40663-0117-8.
- Sánchez-González, A. & L. Lopez-Mata. 2005. Plant species richness and diversity along an altitudinal gradient in the Sierra Nevada, Mexico. *Diversity and Distribution* **11**: 567–575.

- Schickhoff, U. 2005. The upper timberline in the Himalayas, Hindu Kush and Karakorum: a review of geographical and ecological aspects. *In*: G. Broll & B. Keplin (eds.) *Mountain Ecosystems*. Springer, Berlin, Heidelberg.
- Schwörer, C., P. D. Henne & W. Tinner. 2014. A model-data comparison of Holocene timberline changes in the Swiss Alps reveals past and future drivers of mountain forest dynamics. *Global Change Biology* **20**: 1512–1526.
- Swenson, N. G., D. L. Erickson, X. Mi, N. A. Bourg, J. Forero-Montaña, X. Ge, R. Howe et al. 2012. Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. *Ecology* **93**: 112–125.
- Theurillat, J. P. & A. Guisan. 2001. Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change* **50**: 77–109.
- Tranquillini, W. 1979. *Physiological Ecology of the Alpine Timberline: Tree Existence at High Altitudes with Special References to the European Alps*. Springer Verlag, Berlin.
- Tripathi, O. P., H. N. Pandey & R. S. Tripathi. 2004. Distribution, community characteristics and tree population structure of subtropical pine forest of Meghalaya, northeast India. *International Journal of Ecology and Environmental Sciences* **29**: 207–214.
- Tuhkanen, S. 1993. Treeline in relation to climate, with special reference to oceanic areas. pp. 115–134. *In*: J. N. Alden, J. L. Mastrantonio & S. Ødum (eds.) *Forest Development in Cold Climates*. NATO ASI Series (Series A: Life Sciences), Springer, Boston, MA.
- Wielgolaski, F. E., A. Hofgaard & F. K. Holtmeier. 2017. Sensitivity to environmental change of the treeline ecotone and its associated biodiversity in European mountains. *Climate Research* **73**: 151–166.
- Wieser, G., & M. Tausz. 2007. Current concepts for treeline limitation at the upper timberline. pp. 1–18. *In*: G. Wieser & M. Tausz (eds.) *Trees at their Upper Limit: Treeline Limitation at the Alpine Timberline*. Springer, Netherlands.
- Willinghöfer, S., D. Cicuzza & M. Kessler. 2012. Elevational diversity of terrestrial rainforest herbs: when the whole is less than the sum of its parts. *Plant Ecology* **213**: 407–418.
- Yadav, A. K., Y. K. Sharma, B. Dubey, J. Singh, V. Singh, M. R. Bhutiyani, R. R. Yadav & K. G. Misra. 2017. Altitudinal treeline dynamics of Himalayan pine in Western Himalaya, India. *Quaternary International* **444**: 44–52.
- Zhang, W., D. Huang, R. Wang, J. Liu & N. Du. 2016. Altitudinal patterns of species diversity and phylogenetic diversity across temperate mountain forests of Northern China. *PloS One* **11**: e0159995.

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