

Research Article

Variation in vascular epiphytic assemblage along altitudinal zone in Temperate forest ecosystem

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ABSTRACT

The focus of ongoing research in forest ecosystems is highly biased towards vascular epiphytes that grow non-parasitically on host trees and contribute substantially in shaping biodiversity. In this communication, an effort has been made to understand the vascular epiphytic assemblage and richness along the altitudinal gradients in temperate forests of Darjeeling Himalaya. Additionally, influence of environmental variables was also analyzed. Orchidaceae was the dominant family followed by Polypodiaceae and Ericaceae in terms of species abundance. The epiphytic richness and diversity were greater towards lower altitudinal tier compared to the higher. The epiphytic diversity was positively correlated with host tree CBH (circumference at breast height) and bark texture, while bark pH showed a negative correlation. The outcome of this study establishes a baseline of epiphytic characteristics with respect to elevational range and environmental variables in temperate Himalaya. However, a detailed study on population dynamics, habitat evaluation and geographic aspects with further development on monitoring and conservation effort is of utmost necessity.

Key words: Diversity, orchidaceae, host tree, CBH, environmental variables, conservation

INTRODUCTION

Temperate vegetation comprises dense forests covering an area of about 5.3 million sq km that accounts for approximately 16% of total forest area globally (Hansen *et al.*, 2010). These forests extend from lower to higher elevations harbouring rich ecosystems (Kumari *et al.*, 2017). Temperate forest is characterised by warm summer and cold winters (Yam *et al.*, 2016) and contributes substantially to climate change, carbon storage and species dynamicity (Gairola *et al.*, 2013; Rawat *et al.*, 2020). Although temperate forest has a significant role in species diversity, knowledge about the distribution and ecological importance of vascular epiphytes in this forest system is insufficient (Dawson, 1988; Dickinson *et al.*, 1993; Munoz *et al.*, 2003). Some earlier work reports the diversity of vascular epiphytes rarely outside the tropical region (Benzing, 1995; Gentry & Dodson 1987; Barthlott *et al.*, 2001; Zotz & Hietz, 2001). Over the years, extensive research has been done to estimate the epiphytic diversity patterns (Kromer *et al.*, 2005; Guzman-Jacob *et al.*, 2020; Marcusso *et al.*, 2022). Subsequently, study on several ecological functions of epiphytes in relation to biomass and nutrient partitioning has also been performed (Pocs, 1980; Nadkarni, 1984; Hofstede *et al.*, 1993). However, quantitative data in terms of epiphytic composition and structure in temperate forests including their relationship between environmental variables, host trees or phorophytes are generally inadequate (Wolf, 1994; Hietz & Hietz-Seifert, 1995; Hofstede *et al.*, 2001).

Epiphytic vascular plants are defined as non-parasitic and account for up to 10% of all vascular plants worldwide (Zotz, 2021; Taylor *et al.*, 2022). Vascular epiphytes are one of the most conspicuous life forms that attach themselves to and grow on the host trees or phorophytes (Taylor *et al.*, 2022). Occasionally, epiphytes may grow on rocks or soil considering low competition from terrestrial plants (Dawson, 1988; Zotz, 2005; Zotz, 2016). Similarly, numerous terrestrial plants may also grow occasionally on host substrates as accidental epiphytes (Zotz, 2005). Vascular epiphytes contribute significantly to forest ecologies such as water and nutrient inputs, also numerous taxa depend on them since they provide habitat and resources (Gotsch *et al.*, 2016; Angelini & Silliman, 2014; Mendez-Castro *et al.*, 2018). Additionally, they are well known for their contribution to primary productivity, biomass, litterfall and species diversity (Gentry & Dodson, 1987; Benzing, 1995; Barthlott *et al.*, 2001; Munoz *et al.*, 2003). They can also contribute considerably to other plant biomass (Zotz, 2016).

Moreover, epiphytes also serve as ecological indicators as they are sensitive to environmental changes (Benzing, 1990) while estimating the effect of deforestation and invasion of secondary vegetation and plantations (Hietz *et al.*, 2006). The variations in species diversity are influenced by several ecological gradients (Chawla *et al.*, 2008). Environmental factors including temperature and wind speed, relative humidity and rainfall are a few important factors that have contributed to the immense wealth of epiphytic species richness and

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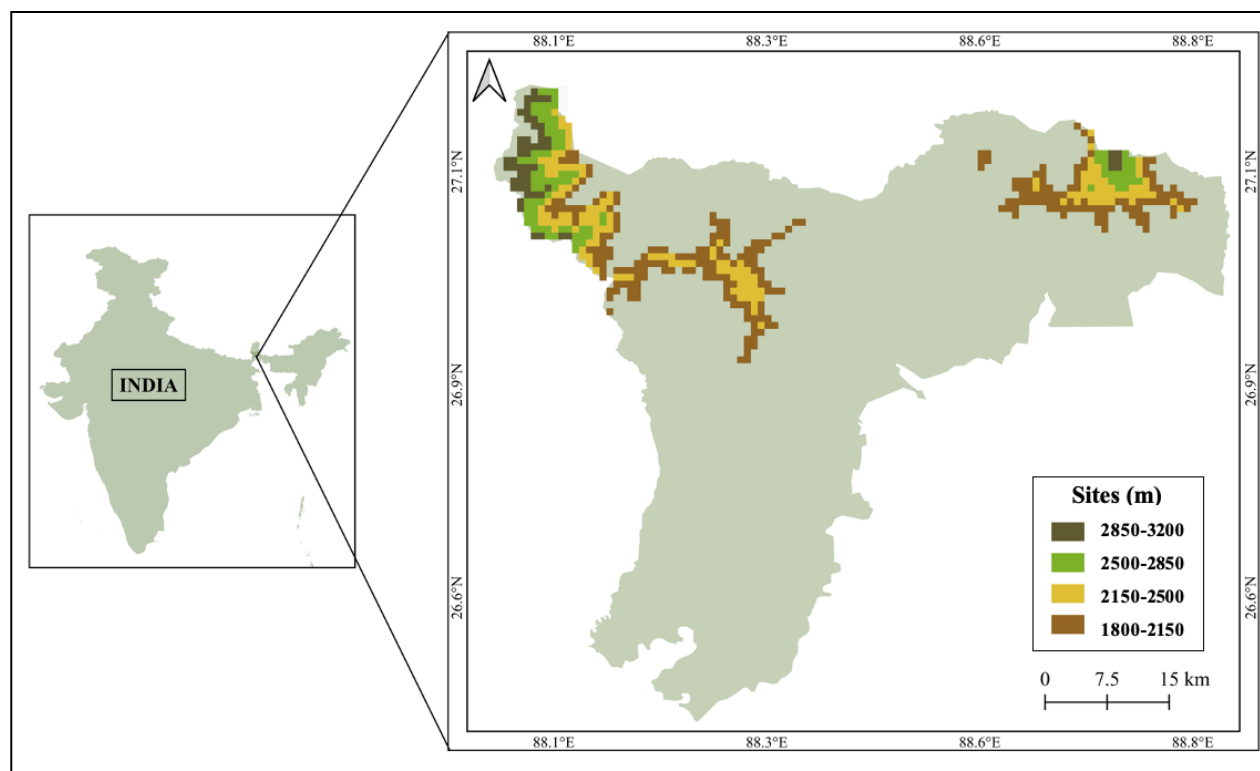


Figure 1. Study area showing different altitudinal sites

diversity (Yam *et al.*, 2010; Sanger & Kirkpatrick, 2017). Similarly, the altitudinal gradient plays a key role in shaping the spatial patterns of species diversity (Ding *et al.*, 2016; Barbosa *et al.*, 2020; Ortiz *et al.*, 2019) as the geographic and climatic conditions change sharply along the altitude (Kharkwal *et al.*, 2005; Saiz *et al.*, 2021). However, information on species richness and diversity patterns along an altitudinal gradient is not sufficient (Bhattarai & Vetaas, 2003). Additionally, complex canopy structures, branches and trunks of large old trees provide habitat for other organisms and aid in enriching the plant diversity (Azuma *et al.*, 2022). The host tree having larger and thicker trunks and branches provide sufficient surface area for the establishment of epiphytic species (Sillett & Pelt, 2007). In general, canopy habitat of epiphytes and vines has a drier and warmer climate than the understory (Bryan, 2011). Thus, host tree microclimatic variables show an impact on the diversity and abundance of epiphytes in different forests (Zotz *et al.*, 1999; Laube & Zotz, 2006). Besides, forest microclimatic condition has a significant role in determining the success or failure of epiphytic plant reintroduction (Yam *et al.*, 2010; Gehrig-Downie *et al.*, 2011). As per Zotz (2005), the vascular epiphytic diversity in temperate regions is widespread mostly in oceanic climates with relatively high humidity and depends on local microclimatic humidity to meet their water requirements (Zotz & Hietz, 2001; Zotz *et al.*, 2001; Parra *et al.*, 2009).

Here, with the comprehensiveness of the data, an attempt is made to investigate overall vascular epiphytic diversity and distributional patterns in the temperate forest ecosystem. Analysis of the epiphytic species richness and abundance along an altitudinal gradient with a focus on the basic aspects including host-tree specificity and climatic variables are also done.

MATERIAL AND METHODS

Study area

The Darjeeling Himalaya forms an integral part of Himalaya Hotspot for Conservation established by IUCN extending between 27°13'10" to 26°27'05" N latitude and 88°53' to 87°30" E longitude covering an altitudinal range between 130 to 3636m asl (Figure 1). A variety of vegetation types has been marked in the study area of which the major types are tropical (up to 500 m), sub-tropical (500 – 1200m), sub-temperate (1200 – 1850m), temperate (1850 – 3200m) and sub-alpine (above 3200m) (Bhujel, 1996). Temperate vegetation occupies most regions of the Darjeeling Himalaya extending from 1850m to 3200m asl. The Temperate vegetation was initially categorized into non-coniferous and upper coniferous (Hooker, 1896). Later it was divided into three sub-types viz. Temperate deciduous forest, Evergreen oak forest and Cold temperate forest (Grierson & Long, 1983).

Anticipating differences in vascular epiphytic diversity along comparable altitudinal gradients, the study area was demarcated into four sites. Site I cover the altitudinal range of 1800 – 2150m. The area receives an average annual rainfall of around 236.07mm and a mean annual temperature of approximately 16.1° C. The average relative humidity remains at 67.25%. Site II (2150 – 2500m) receives an average annual rainfall of around 213.74mm with average annual temperature of 14.2°C. Similarly, site III (2500 – 2850m) and site IV (2850 – 3200m) receives an average annual precipitation of around 177.99mm and 152.17mm respectively. The mean annual percentage of humidity in all sites (II, III and IV) remains 64.43% while the mean annual temperature is about 12.0°C and 10.1°C in sites III and IV respectively.

Field sampling

Several field investigations were made in different sites in temperate regions to document the vascular epiphytes using stratified random sampling. Dominant phorophytes or host trees in all four study sites were noted for vascular epiphytic distribution. As the complex tree architecture was encountered during field surveys the host trees were segregated into two zones i) Trunk zone covering the area below the first branching till the base and ii) Inner crown zone covering the remaining area above the first branching (Johansson, 1974). The CBH of host trees with a diameter >15 cm were measured to understand the girth class distribution at each elevation. Additionally, bark texture of phorophytes was classified following (Altenhovel, 2013) and pH of the bark of host tree was determined as per (Mezaka *et al.*, 2008). The identification of the recorded epiphytic taxa and the host trees was made following suitable literature (Hara, 1966, 1971; Ohashi, 1972; Grierson & Long, 1983, 1984, 1987, 1991, 1999, 2001; Pearce & Cribb, 2002; Frazer-Jenkins, 2008; Kholia, 2010). The correct nomenclature with accepted author citation was maintained following Plants of the World Online (POWO, 2022). The threat status of the recorded taxa was presumed following online data source Threat Search (BGCI, 2022). Properly mounted and labelled herbarium exsiccates were deposited at the Calcutta University Herbarium (CUH) for future study. The elevation and location of each study site were determined using Global Positioning System, Garmin eTrex H.

Data Analyses

Diversity indices for the vascular epiphytes were estimated using PAST version 4.03 (Hammer *et al.*, 2001). Shannon index $H' = - \sum [(ni/N) \ln(ni/N)]$ (Shannon &

Weaver 1963); Richness index $D = S/\sqrt{N}$ (Menhinick, 1964); Evenness index $J = H'/\ln S$ (Pielou, 1966); and Index of dominance $CD = \sum (ni/N)^2$ (Simpson, 1949). Correlation graph, Rarefaction curve and Venn diagram were constructed in R version 4.1.1 (R Core Team, 2013). The bioclimatic variables were obtained from WorldClim 2.0 (Fick & Hijmans, 2017). Canonical corresponding analysis (CCA) was performed using PAST version 4.03 while the map was produced using QGIS version 3.20 (QGIS, 2022).

RESULTS

Epiphytic species richness

Across the study sites, a total of 111 species of vascular epiphytes belonging to 51 genera and 24 families were recorded from the temperate vegetation. A total of 1163 individuals were enumerated from four different elevational zones. Of the total species documented, Orchids were the most diverse and dominant representing 40% (44 spp.) followed by other angiosperm 34% (34 spp.) while 30% (33 spp.) were ferns. The most abundant families were Orchidaceae followed by Polypodiaceae with 19 species and Ericaceae with 7 species while the least diverse families were Acanthaceae, Cucurbitaceae and Zingiberaceae each with single species (Figure 2). Of the 24 families recorded from all study sites, the dicot represented 50% whereas the monocot and pteridophytic groups together accounted 25% each. Amongst the diverse orchid taxa, the frequently occurring species were *Bulbophyllum*, *Coelogyne* and *Dendrobium* whereas the other dominating angiosperm comprises species of *Aeschynanthus*, *Hoya* and *Agapetes* while *Selliguea*, *Lepisorus* and *Haplopteris* were dominant epiphytic ferns.

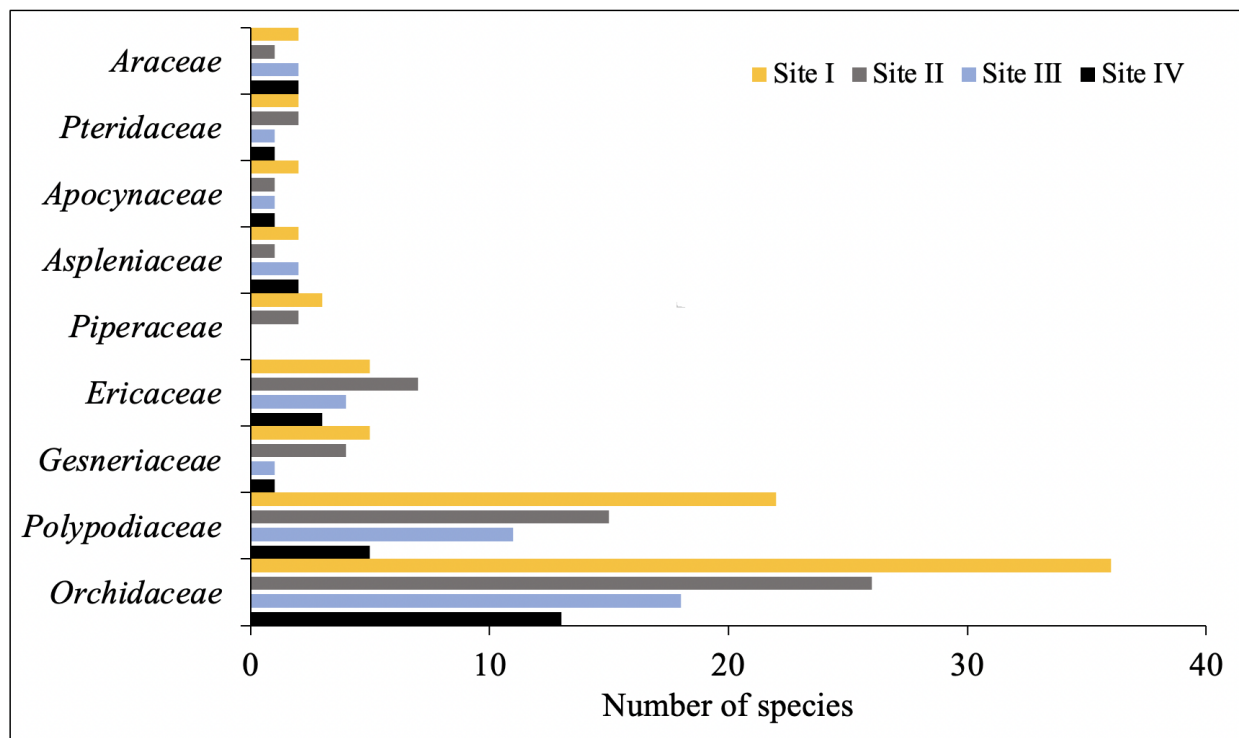


Figure 2. Dominant families with number of epiphytic species

The angiospermic herbs represented 90% of the total taxa, while the climbers and shrubs were 10% and 1% respectively. The study revealed that all the epiphytic angiosperms were found to be perennial, and they are facultative that grew either on the host tree trunk or as terrestrial, except species of *Aeschynanthus* which seems truly epiphytic and the epiphytic ferns that were also observed to be epilithic or terrestrial. The phenological data of the flowering taxa showed that 37% of species flowered during spring and summer while 30% and 27% of species preferred to bloom in monsoon and autumn seasons respectively. Furthermore, only about 6% of the taxa flowered during winter.

The epiphytic diversity indices were estimated across four elevational sites. A low Shannon diversity index of epiphytic community was obtained in site IV ($H' = 3.312$) whereas the highest score was obtained for site I ($H' = 4.399$) followed by site II ($H' = 4.142$). The concentration of species dominance (Simpson's index) was calculated highest as 0.986 in site I compared to sites II, III and IV which were 0.982, 0.972 and 0.959 respectively. The results show that species richness in site I and site II was almost similar. Additionally, Menhinick's index (D) was calculated between the study sites. The values varied from 4.055 in site I to 3.988, 3.373 and 2.764 in sites II, III and IV respectively. The score of Pielou's evenness index was estimated to be 0.87, 0.88, 0.86 and 0.85 in four sites respectively.

Distribution pattern along the altitudinal gradient

The results showed that the vascular epiphytic species richness decreases with an increase in altitude (Table 1).

The lower elevation i.e., site I harboured the highest vascular epiphytic abundance (526 individuals) followed by site II (317 individuals), site III (186 individuals) and site IV (134 individuals) (Figure 3b). Around 39% taxa were recorded from site I with 93 species belonging to 44 genera under 22 families while 71 species under 37 genera within 18 families from site II represented 29%. From site III 19% of the taxa with 46 species under 26 genera and 14 families have been accounted (Figure 3a). Similarly, change in number of species is observed in site IV with 32 species under 22 genera and 13 families representing 13%.

Species diversity in sites I and II shows the highest similarity which is 37% whereas the epiphytic communities in sites I and IV showed least similarity (Figure 4). Vascular epiphytes like *Aeschynanthus*, *Agapetes*, *Hoya*, *Lepisorus*, *Selliguea*, *Bulbophyllum*, *Coelogyne*, *Dendrobium* were most frequently occurring species in both site I and site II. Similarly, *Didymocarpus*, *Peperomia*, *Vaccinium*, *Pleione*, *Gastrochilus* were found mostly in site III and site IV. However, *Aeschynanthus parviflorus*, *Haplopteris sikkimensis*, *Bulbophyllum affine*, *Otochilus albus*, *O. fuscus* were found most diverse in lower elevations (1800-2500m). Similarly, *Haplopteris taeniophylla*, *Lepisorus loriiformis*, *Selliguea lehmannii*, *Bulbophyllum rolfei*, *Dendrobium porphyrochilum*, *Otochilus lancilabius* were found to be distributed at higher altitudes (above 2500m) whereas some species like *Peperomia tetraphylla*, *Vaccinium retusum*, *Selliguea griffithiana*, *Coelogyne corymbosa*, *C. cristata*, *Polygonatum brevistylum* showed wide ecological amplitude and were

Table 1. Summarized data of the vegetation types along elevational range

| Elevation range (m) | Mean Annual Precipitation (mm) | Mean Annual Temperature (°C) | Mean Annual Relative Humidity (%) | Epiphyte species | Epiphyte individuals | Host tree species | Mean Basal area (m ² ±SE) |
|---------------------|--------------------------------|------------------------------|-----------------------------------|------------------|----------------------|-------------------|--------------------------------------|
| 1800 – 2150 | 236.0 | 16.1 | 67.25 | 93 | 526 | 35 | 4.53±0.85 |
| 2100 – 2500 | 213.7 | 14.2 | 64.43 | 71 | 317 | 30 | 3.25±0.80 |
| 2500 – 2850 | 177.9 | 12.0 | 64.43 | 46 | 186 | 14 | 1.57±0.69 |
| 2850 – 3200 | 152.1 | 10.1 | 64.42 | 32 | 134 | 12 | 1.65±0.82 |

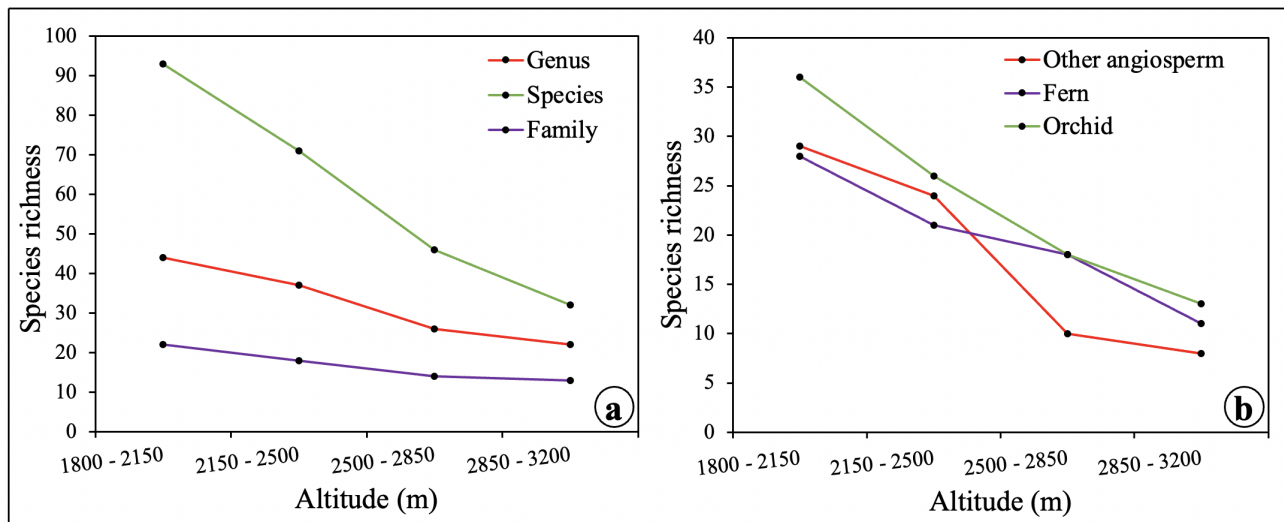


Figure 3. Distribution of taxa along altitudinal gradient

documented from all the study sites. The family Orchidaceae and Polypodiaceae dominated the sites whereas the member of Apocynaceae, Gesneriaceae and Araceae decreased with increasing altitude.

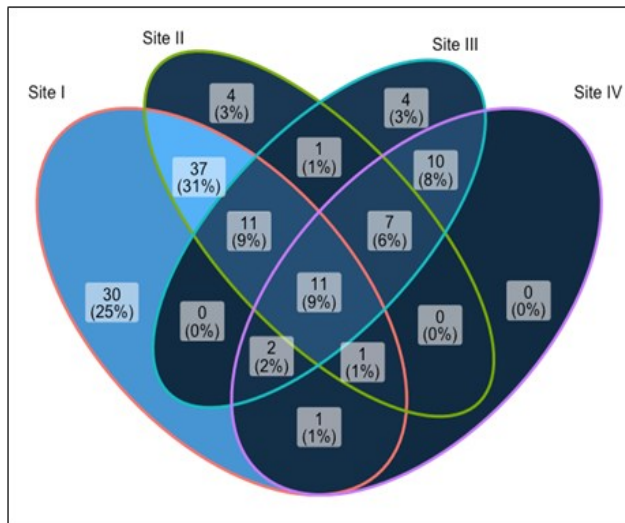


Figure 4. Venn diagram showing number of vascular epiphytes shared between study sites

Overall, the species richness among different study sites was comparable even though differences in sampling effort. The Rarefaction curves (Figure 5) indicate that the expected vascular epiphytes in site I were variably higher than those in site II, III and IV. Of all sites, Site IV hosted consistently less epiphytes and was not significantly different from that of site III.

Distribution within the host tree

Epiphytic diversity and composition are known to be greatly influenced by host tree traits (Wang *et al.*, 2016; Timsina *et al.*, 2016). A total number of 40 host tree species under 27 genera belonging to 19 families were observed in all the study sites. Tree species like *Acer campbellii*, *Alnus nepalensis*, *Castanopsis hystris*, *Engelhardia spicata*, *Exbucklandia populnea*, *Lithocarpus fenestratus*, *Machilus edulis*, *Quercus glauca*, *Machilus odoratissima* were dominant in site I. Similarly, the forest of site II harboured dense multi-layered canopy with dominant tree species like *Betula alnoides*, *Castanopsis tribuloides*, *Cinnamomum impressinervium*, *Elaeocarpus lanceifolius*, *Ilex kingiana*, *Photinia integrifolia*, *Quercus griffithii*, *Q. lanata*, *Symplocos lucida*. Some of the major canopy cover from site III includes *Daphniphyllum himalense*, *Ilex dipyrrena*, *Litsea elongata*, *Lyonia ovalifolia*, *Rhododendron arboreum* var. *cinnamomeum*, *Sorbus rhamnoides*, *Symplocos lucida*. Tree species like *Abies densa*, *Magnolia campbellii*, *Quercus lamellosa*, *Rhododendron falconeri*, *Tsuga dumosa* dominates the site IV. Fagaceae and Lauraceae were frequently occurring and diverse host tree family in both site I and site II whereas families like Symplocaceae and Ericaceae was dominant in site III and site IV. Our study showed that some host tree traits including CBH, pH, Bark texture, canopy size are few important factor that influenced the vascular epiphytic diversity. Since the host trees have been divided into two growth zones, maximum number of vascular epiphytes (90%) was found in trunk zone whereas least number of species was found to be grown on crown zone (10%). Similarly, host tree with rough bark sheltered maximum number of taxa whereas only few

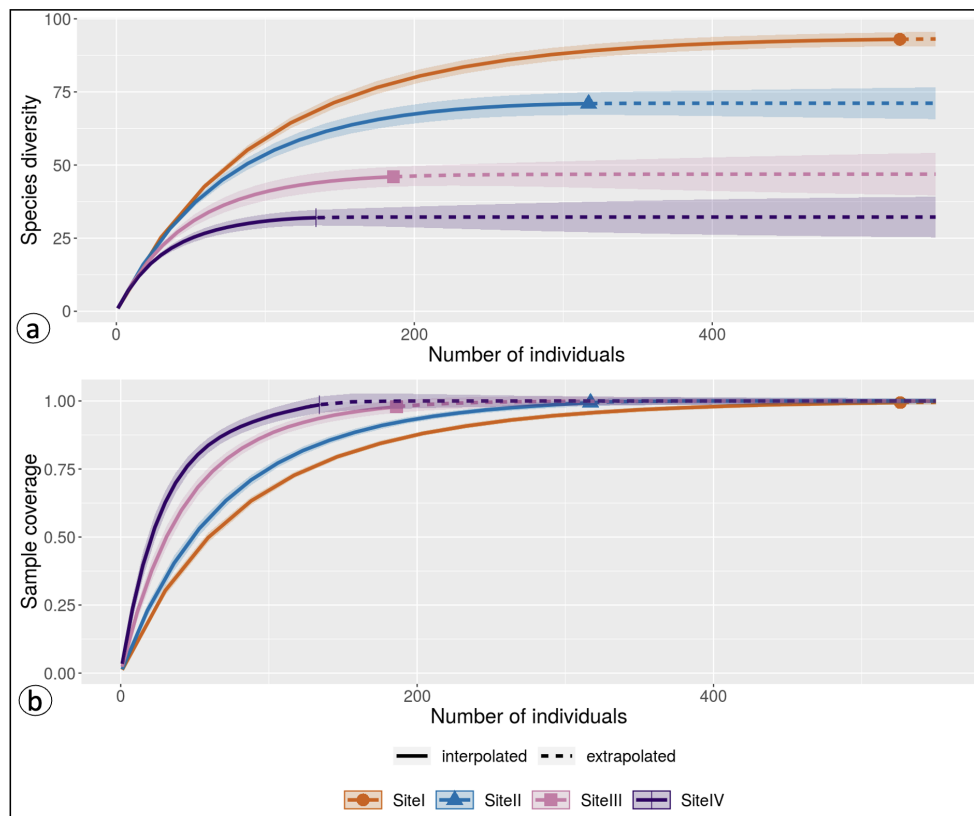


Figure 5. a) Individual based interpolation and extrapolation (rarefaction) curves b) Sample completeness curve with corresponding 95% confidence intervals

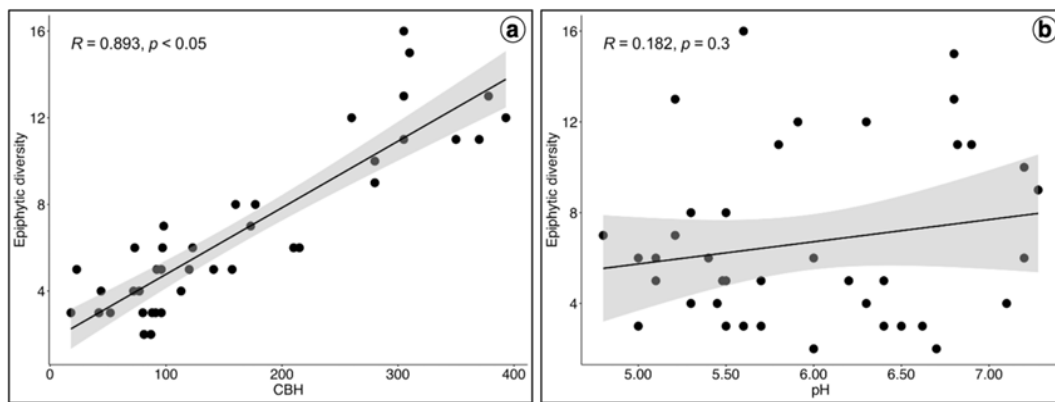


Figure 6. Correlation of epiphytic diversity with host tree (a) CBH (b) Bark pH

species were harboured by trees having smooth bark. In addition to this, greater number of vascular epiphytes was harboured by some host trees with maximum branching viz. *Pinus roxburghii*, *Lithocarpus pachyphyllus*, *Elaeocarpus lanceifolius*, *Castanopsis tribuloides*, *Magnolia doltsopa* while other trees including *Rhododendron arboretum*, *R. falconeri*, *Eriobotrya dubia*, *Ilex hookeri* with thin branching sheltered comparatively lesser species. The study recorded that the host tree CBH ranged from 18cm to 410cm with species like *Acer campbellii* showing narrow girth while species like *Lithocarpus fenestratus*, *Quercus lamellosa*, *Pinus roxburghii*, *Castanopsis hystrix* with CBH above 300cm. Based on CBH measurements, host trees were segregated into five girth class, out of which 12 tree species were found within the range of 10 – 80cm, 13 species within 80 – 160cm, 7 within 240 – 320cm and 4 species each within 160 – 240cm and 320 – 400 cm respectively. pH of the bark varied among different host trees. The lowest pH value was estimated for *Symplocos dryophila* (4.80) whereas *Machilus edulis* showed highest pH value (7.28). When all epiphytic individuals with different host tree CBH and pH values were plotted, epiphytic diversity and CBH were significant and positively correlated ($p < 0.05$) (Figure 6a), whereas the correlation of host tree bark pH with epiphytic diversity shows p-value

greater than the significance level 0.05 implying that they are not much significant to epiphytic diversity (Figure 6b).

Environmental variables as determinants of epiphytic richness and abundance

Environment variables including mean annual temperature, precipitation and relative humidity have greatly influenced the epiphytic richness and abundance in the study area. Result of the Canonical Correspondence Analysis (CCA) shows the association between the vascular epiphytes with different environmental variables including Mean Annual Relative Humidity (MAH), Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP). The first canonical axis explained 77.75% and the second 22.25% of the total variation in the data set (Figure 7). The eigenvalues of these axes accounted for 0.46 and 0.13 respectively. The environmental variables (MAT and MAP) were mostly correlated with CCA axis 1. Similarly, MAH was mostly correlated with CCA axis 2. The CCA ordination shows the distribution of the species in sampling sites and their direct relation to environmental variables is also determined for each site. The mean annual temperature and mean annual precipitation are closely related and showed a strong effect on species distribution.

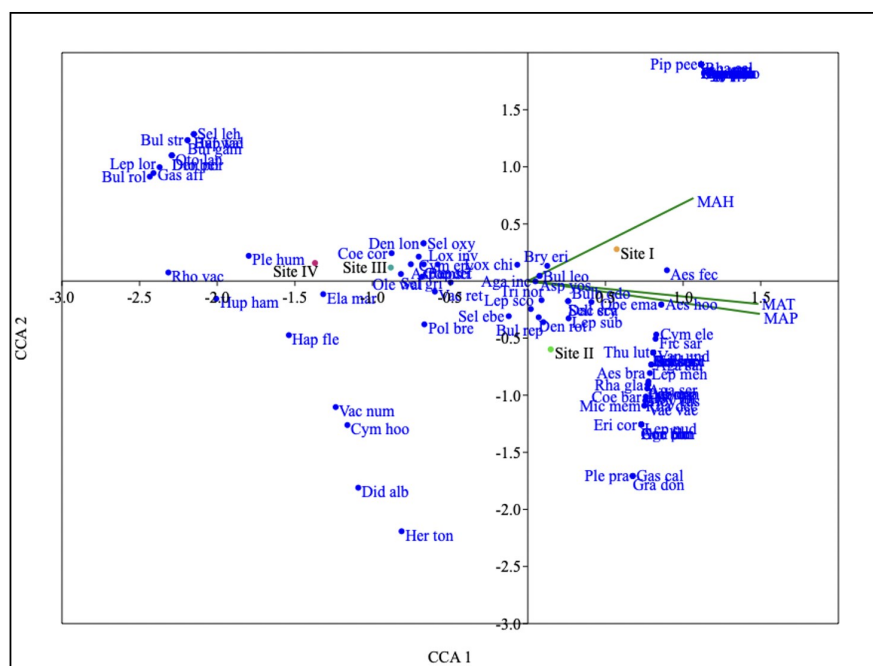


Figure 7. Canonical correspondence analysis (CCA) plot showing the influence of environmental variables

The species *Aeschynanthus hookeri* (CCA species score: 0.85), *A. bracteatus* (0.78), *Agapetes saligna* (0.79), *Bulbophyllum odoratissimum* (0.40), *Coelogyne barbata* (0.76), *Oberonia emarginata* (0.85), *Eria coronaria* (0.73), *Pleione praecox* (0.67), *Gastrochilus calceolaris* (0.67), *Hoya fusca* (0.75), *H. linearis* (0.76), *Lepisorus sublinearis* (0.26), *Microsorium membranaceum* (0.75) showed high frequency at sites having low temperature and precipitation. Similarly, *Bulbophyllum gamblei* (-2.19), *B. striatum* (-2.19), *B. rolfei* (-2.43), *Dendrobium porphyrochilum* (-2.29), *Gastrochilus affinis* (-2.37), *Lepisorus loriformis* (-2.41), *Otochilus lancilabius* (-2.29), *Pleione humilis* (-1.79), *Rhododendron vaccinioides* (-2.31), *Selliguea lehmannii* (-2.15), showed negative relation with temperature and precipitation due to their habitat with low temperature and precipitation. Species like *Aeschynanthus parasiticus*, *Agrostophyllum planicaule*, *Hoya serpens*, *Huperzia pulcherrima*, *Leucostegia truncata*, *Lysionotus serratus*, *Liparis viridiflora*, *Neohymenopogon parasiticus*, *Piper peepuloides*, *Rhaphidophora calophylla* (CCA species score of all species: 1.11) showed maximum abundance towards the direction of high humidity. Some species showed strong negative correlation with humidity such as *Cymbidium hookerianum* (-1.16), *Herpetospermum tonglense* (-0.81), *H. hamiltonii* (-2.00), *Haplopteris flexuosa* (-1.53), *Vaccinium nummularia* (-1.23) because they were dominantly present at sites of low humidity.

Implications for conservation

In the present study, the species were evaluated for their threat category and majority of the taxa were found to be not threatened (54%) and least concern (29%). However, a significant number of taxa were vulnerable (8%) and endangered (5%). Subsequently, species such as *Bulbophyllum leopardinum*, *Pleione humilis* and *Rhaphidophora decursiva* are critically endangered while species namely *Cymbidium hookerianum*, *Dendrobium longicornu*, *D. porphyrochilum*, *Huperzia hamiltonii* and *Liparis resupinata* were found to be endangered (Figure 8).

Species such as *Bulbophyllum helenae*, *Coelogyne punctulata*, *Cymbidium erythraeum*, *D. nobile*, *Elaphoglossum marginatum*, *Haplopteris flexuosa*, *H. pulcherrima*, *P. praecox* have been known to be vulnerable while *Peperomia tetraphylla* was recorded as rare.

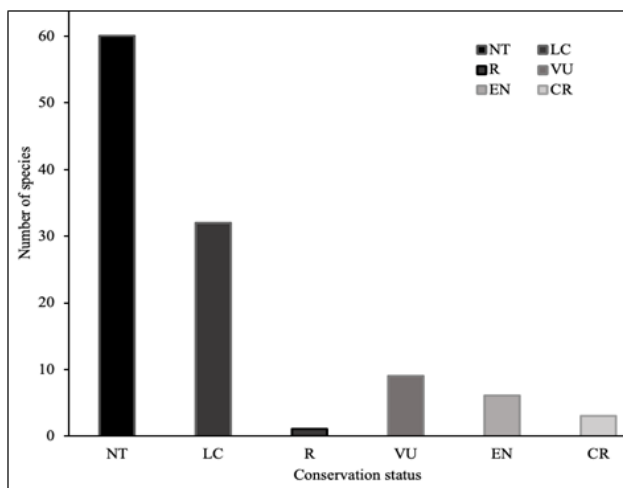


Figure 8. Threat status of epiphytic taxa

Our results clearly revealed that many species are under threat. It is of great significance to study the variation and association of different species in order to understand community assembly at different scales. Several species in this study are critically endangered, endangered and vulnerable which may be due to habitat loss, over exploitation, climate change and pollution in the study sites (Anil *et al.*, 2014). As per Schwenk *et al.*, (2009), it is a crucial matter to understand the relationship between organisms and their environment addressing the problem of environmental change and its consequences for biodiversity conservation. In this context, directing strategies towards the conservation of species is challenging. However, an investigation such as present study would provide further knowledge of given taxa as it establishes a baseline of characteristics such as species richness and composition, association with host tree and distribution patterns with respect to different environmental variables. It is of utmost necessary to carry out an evaluation of RET species using different approaches such as species populations, habitat evaluation and geographic aspects to access more detailed results. Additionally, development of new conservation programs are of utmost need as well as monitoring those that are already established is necessary in order to secure the future stability of the species.

DISCUSSION

Elevational gradient of temperate forest area and some environmental variables emerges as a key driver of vascular epiphytic diversity. This study highlights and compares the epiphytic species richness and abundance along elevational gradients, which often attribute the high epiphytes at lower elevations i.e. from 1800-2500m asl. Previous research on the influence of altitudinal gradients on epiphytic community composition incorporated a considerable gradient (Hietz, 1999; Kreft *et al.*, 2004; Kromer *et al.*, 2005; Cardelus *et al.*, 2006). It is known that vascular epiphytic pattern varies within different altitudes (Munoz & Kuper, 2001; Wolf & Alejandro, 2003; Kuper *et al.*, 2004; Cardelus *et al.*, 2006; Ding *et al.*, 2016; Rodriguez & Zotz, 2021). Indeed, our results also revealed that vascular epiphytes species richness and abundance varied from lower to higher altitudes. Conspicuously, the epiphyte diversity declined with an increase in altitude but differed from other findings i.e., hump-shaped distribution of epiphytes (Hietz, 1999; Wolf & Alejandro, 2003; Kuper *et al.*, 2004). The vertical decline of vascular epiphytes as we move towards higher elevation may be due to stunted forest vegetation near treeline (Kromer *et al.*, 2005), a very low temperature (Rosa-Manzano *et al.*, 2019; Schroter & Obenhuber, 2022), decreased soil fertility (Halbritter, 2018), or could be the result of uneven topography, increase in steep and less top soil depth in high altitude (Timsina *et al.*, 2021).

However, altitude is not only the main factor for present variation in distribution pattern of vascular epiphytes but there are some other significant environmental variables including temperature, rainfall, humidity, etc. that may influence the species diversity. As mentioned in earlier studies, environmental variables is one of the important factors that have an effect on the immense wealth of epiphytes species richness (Timsina *et al.*, 2021; Taylor *et al.*, 2022) and they increase significantly with increasing annual precipitation. Across four

study sites, annual mean precipitation and temperature decrease with elevation resulting in sites I and II with warmer and wetter areas compared to sites III and IV. Thus, finding highest epiphytic species richness and abundance in sites I and II is a well-known fact that epiphyte flourishes well in warmer and wetter areas than the colder and drier areas. In addition to this, epiphytic plant responds to variation in humidity more than other life forms as they lack access to soil (Gentry & Dodson, 1987). Although relative humidity showed little difference across our study sites, relative humidity plays a key role in epiphytic adaptation (Aragon *et al.*, 2015; Sanger & Kirkpatrick, 2017; Williams *et al.*, 2020).

Furthermore, the association of phorophytes with vascular epiphytes including orchids and ferns depends on different host tree traits such as DBH, bark rugosity, pH, etc (Timsina *et al.*, 2016; Adhikari *et al.*, 2016). We found significant associations between epiphytic diversity and some host tree traits. The CBH was the most important parameter for vascular epiphytic diversity. The positive correlation between vascular epiphytes diversity and host tree CBH supports the general belief that bigger and older trees are of importance for epiphytes (Manning *et al.*, 2006; Flores-Palacios *et al.*, 2008). Vascular epiphytes preferred larger host trunks with rougher bark texture as the larger host tree exhibits a large trunk and branch surface area for epiphytic seeds and spores to colonize (Migenis & Ackerman, 1993; Callaway *et al.*, 2002; Zotz & Schultz, 2008; Adhikari *et al.*, 2021). Results of the present study are consistent with the previous research (Wang *et al.*, 2016), in which epiphytic species richness and abundance were decreased from trunk zone to inner crown zone of the host trees indicating the decreasing trend but differed from the study reported by Steege & Cornelissen (1989) and Kromer *et al.*, (2007) as they found maximum epiphytic assemblage on canopy branches. Although our study suggests the influence of environmental variables and host tree traits on vascular epiphyte diversity, quantitative information is still scarce and much process-oriented research in study area is needed to better understand this diverse and rich group of plants.

CONCLUSION

The study reflects a high diversity of vascular epiphytes and variation in species richness, abundance and species composition along different elevational gradient. The influences of environmental parameters in different altitudinal zones tend the vascular epiphytes to be established well in warm and humid conditions. Furthermore, species composition is strongly influenced by host tree traits. This indicates the association between vascular epiphytes and host tree traits vary spatially. Thus, host-epiphyte associations should be studied at a greater scale in order to obtain a precise result. The occurrence of rich diversity including several RET species in the study has contributed to the conservation value and threat status of different taxa in the temperate forests of Darjeeling Himalaya. The habitat conservation of such a rich diversity is of paramount importance. Hence, awareness programmes, future monitoring and collaborative research in broader aspects will help to regulate the species population to a great extent.

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