



# Vascular epiphytic community along elevational zone in sub-tropical forest ecosystem

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**ABSTRACT:** Vascular epiphytes contribute substantially to floral diversity, species richness, productivity, nutrient storage and complex arboreal communities in forest ecosystems. However, they have received insufficient attention due to accessibility limitations. In this communication, we analysed the vascular epiphytic species richness and composition in sub-tropical forests (from 400 to 1300 m) of Darjeeling eastern Himalaya. The study area was classified into three elevations (low, mid and high). We studied the correlation between vascular epiphytic richness and host tree traits such as circumference at breast height (CBH), bark texture and bark pH. Additionally, we applied Canonical Correspondence Analysis (CCA) to explain epiphyte diversity with respect to climatic variables (mean annual temperature, mean annual precipitation and mean annual relative humidity). In total, 942 individuals of vascular epiphytes belonging to 71 species under 46 genera and 21 families were recorded. Orchidaceae was by far the most species-rich family followed by the fern family Polypodiaceae. The results showed the species richness in mid elevations was comparatively lower than in the low and high elevations. Our study suggests that climatic variables and host tree traits such as CBH and bark texture were closely associated with epiphytic richness and diversity. These findings could be seminal in understanding the distribution pattern of vascular epiphytes and community composition with their relation to host tree traits. Nevertheless, effective and strategic conservation of vascular epiphytes must be considered in Darjeeling Himalaya.

**KEY WORDS:** Distribution pattern, climatic variables, Darjeeling, elevational gradients, India, sub-tropical forests, host tree.

## INTRODUCTION

Epiphytes are one of the most important components of tropical and subtropical forests (Benzing, 2004; Zotz, 2013; Song *et al.*, 2016; Gomez, 2017; Rosa-Manzano, 2019) which account for approximately 10% of all vascular plant species worldwide (Zotz, 2013). Although epiphytes are concentrated in tropical and sub-tropical rainforests, they are also found in temperate forests (Diaz *et al.*, 2010; Rohani *et al.*, 2017). Vascular epiphytes attach themselves to and grow on the host plant without extracting any nutrients, they contribute to local and regional floral diversity and perform several ecological functions (Benzing, 2000; Zotz and Hietz, 2001; Angelini and Silliman, 2014; Mendez-Castro *et al.*, 2018). Epiphytes serve as good ecological indicators due to their extensive sensitivity to changes in the environment (Benzing, 1990). Furthermore, the effect of deforestation and the invasion of secondary vegetation or plantations could be assessed by vascular epiphytes (Hietz *et al.*, 2006).

Many biotic and abiotic factors determine the abundance and diversity of vascular epiphytes, such as climate, water availability, host tree size, bark features and tree architecture (Koster *et al.*, 2011; Ding *et al.*, 2016). Epiphytes are significantly influenced by indirect effects such as enhanced nutrients from decomposing leaves (Boelter *et al.*, 2014). Host tree identity could be one of the significant biotic factors influencing the community assembly of epiphytes (Einzmann *et al.*, 2015). Host tree microclimate plays a key role in

determining the epiphytic diversity in different forest ecosystems which eventually affects the germination and survival of epiphytes (Zotz *et al.*, 1999; Laube and Zotz, 2006; Furtado and Menini, 2016). The ability of epiphytes is often described as desiccation tolerance due to their survival canopy climates (Hietz and Briones, 1998; Zotz *et al.*, 1999; Bader *et al.*, 2009). Furthermore, altitude is one of the important factors determining species diversity patterns (Brown, 2001; Ortiz *et al.*, 2019; Das *et al.*, 2020). At a regional scale, high species richness along the elevational gradient has been positively related to water availability (i.e., precipitation) (Kromer *et al.*, 2005; Kessler *et al.*, 2011). Epiphytes are dependent on local microclimatic humidity to meet their water requirements (Wolf, 1994; Benzing, 1998; Zotz and Hietz, 2001; Parra *et al.*, 2009). As a response to a discontinuous water supply, selection pressures have enabled epiphytes to exploit different parts of the canopy (Taylor, 2016). Concurrently, epiphytes are expected to show a high degree of specialisation in relation to forest types due to their strong coupling with the atmosphere and structural dependence. This makes vascular epiphytes an important study subject to understand how forest structure and environmental variables maintain diversity (Rosa-Manzano, 2019).

Although vascular epiphytes are key components of forest ecosystems, studies on their diversity and composition with reference to host trees and environmental variables are scanty in sub-tropical forests of Darjeeling eastern Himalaya. There are critical lacunas

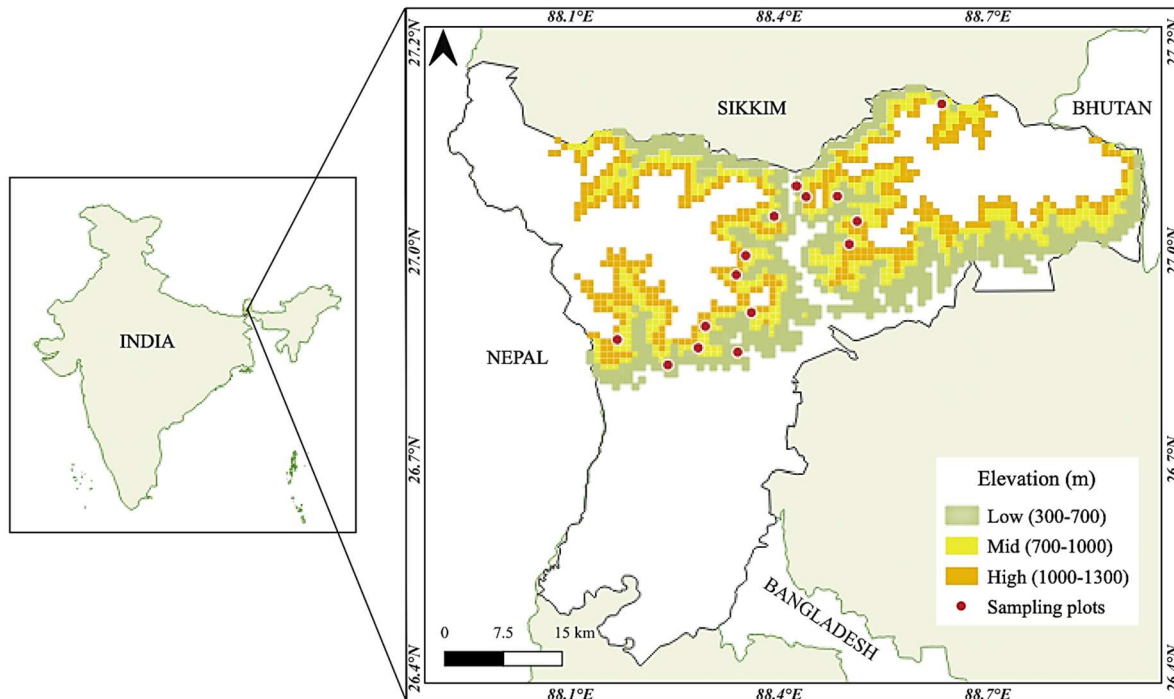


Fig. 1. Study area showing low, mid and high elevations.

in knowledge from this area. Therefore, efforts have been made to quantify the vascular epiphytic diversity across elevational ranges in the sub-tropical ecosystem. We aimed to understand the factors responsible for vascular epiphytic composition. The premeditated objectives of our study include 1) understanding the diversity and distribution of vascular epiphytes along elevational gradients, and 2) determining the correlation between epiphytic species richness with host tree traits and climatic variables.

## MATERIALS AND METHODS

### Study area

Extending across Bhutan, north-eastern India and a major portion of Nepal to northwest China, the eastern Himalaya region covers a total area of 524190 sq. km and is home to immense biological resources. As per WorldAtlas (2022), a total of 10,000 species of plants have been sheltered by the eastern Himalayas, out of which 71 genera with 3,160 different species were reported to be endemic. Lying in the foothills of eastern Himalaya, the Darjeeling Himalaya is well known for its rich biodiversity and lies in the northernmost zone of the Indian state of West Bengal. The area is bordered by Sikkim, Nepal, Bhutan and Bangladesh in the north, west, east and southeast respectively. Geographically, the area extends between 27°13'10"N to 26°27'05"N latitude and 88°53' E to 87°30' E longitude covering an elevational range from 130 to 3636 m asl. Based on climate and

elevations, Bhujel (1996) modified the classification of vegetational type into tropical (plains to 500 m), sub-tropical (500–1200 m), sub-temperate (1200–1850 m), temperate (1850–3200 m) and sub-alpine (above 3200 m). Due to the altitudinal variation that ranges from tropical plain to sub-alpine, different micro-climatic zones in Darjeeling Himalaya offer a suitable environment for the growth and development of diverse plant species resulting in rich vegetation (Das, 2004). Due to complex topography and elevational variation, the climate in this region varies greatly with small micro-climatic zones along different elevational ranges. The area receives a maximum temperature of 24°C in the month of August and a minimum of 2°C in January with annual precipitation of about 2400 mm. Most places in the region receive maximum rainfall from June to October (Mandal and Sarkar, 2021). July and August are usually the hottest months while the coldest is January (Cajee, 2018). The relative humidity remains highest from June to September (95%–100%).

The sub-tropical forests were demarcated into three elevations (Fig. 1). Low elevation (400–700 m) is characterized as a semi-evergreen mixed forest that extends from 400 to 700 m with consistently high temperatures and moist conditions. The forest harbours a dense multi-layered canopy with dominant tree species, such as *Callicarpa vestita*, *Chukrasia tabularis*, *Lagerstroemia parviflora*, *Mallotus repandus*, *Saurauia grandiflora*, *Schima wallichii*, *Shorea robusta*, *Tetrameles nudiflora* and *Terminalia myriocarpa*.



Mid elevation (700–1000 m) comprised of mixed deciduous forest which is typical in Darjeeling sub-Himalayan region. This region receives moderate rainfall and has a consistently high temperature. The dominant host trees present in this region include *Bridelia retusa*, *Diploknema butyracea*, *Senna siamea*, *Sterculia villosa*, *Terminalia bellirica* and *Wrightia sikkimensis*.

High elevation (1000–1300 m) consists of sub-tropical broad-leaved forest that covers the mid-elevation range. This area remains fragmented due to human interference. The major canopy species in the forest include *Castanopsis indica*, *Engelhardia spicata*, *Schima wallichii* and *Syzygium cumini*.

### Epiphyte sampling and data collection

Field surveys were conducted from 2021 to 2022 in different elevational zones. During field survey, around 15 plots, each 10 x 10 m were adopted. Within each plot, ten dominant host trees were selected and altogether 150 host trees were sampled in this study. Epiphytic species were sampled based on the number of individuals present in each host tree (Wolf *et al.*, 2009). The host trees with a circumference at breast height (CBH) having a diameter > 15 cm were sampled. Due to the complex tree architecture encountered during field surveys, we divided the host trees into two zones i) area below the first branching till the base and ii) inner crown zone covering the remaining area above the first branching. Furthermore, vascular epiphytes were classified into holoeiphytes (no contact to the ground), facultative (can grow both on host tree and ground), accidental (for plants that occasionally grow as epiphytes), and hemieiphytes (for those plants that germinate in tree crown but latter establish a connection with the ground) (Klein *et al.*, 2022). The specimens at medium tree height were collected using hooks while the larger canopies were explored with the assistance of a local tree climber. Additionally, bark texture of host trees was observed during field surveys and classified following Altenhovel (2013). The bark pH of host tree was determined following the methodology by Mezaka *et al.*, (2008). For proper identification of the taxa, relevant literature was followed (Hara, 1966, 1971; Ohashi, 1972; Grierson and Long, 1983, 1984, 1987, 1991, 1999, 2001; Pearce and Cribb, 2002; Fraser-Jenkins, 2008; Kholia, 2010; Fraser-Jenkins *et al.*, 2017, 2018, 2021). Correct nomenclature with authority was maintained as per Plants of the World Online (POWO, 2022). The conservation status of the recorded taxa was obtained following the online data source ThreatSearch (BGCI, 2022). Llyod Botanical Garden Herbarium and Calcutta University Herbarium (CUH) were also consulted for the identification of the species. Properly mounted and labelled herbarium exsiccates were deposited for future study. The elevation and location of plots in each elevation were determined using Garmin eTrex H hand held receiver.

### Data Analysis

Paleontological Statistics (PAST) version 4.03 educational software package (Hammer *et al.*, 2001) was utilized in calculating various assessed biodiversity indices. Formulas for different analysed biodiversity indices based on adopted equations are Shannon's index  $H' = -\sum(n_i/N)^2 \ln(n_i/N)$  (Shannon and Weiner, 1963), Pielou's index  $J = H' / \ln S$  (Pielou, 1966), Menhinick's index  $D = S/\sqrt{N}$  (Menhinick, 1964) and Simpson's index  $D' = \sum(n_i/N)^2$  (Simpson, 1949). Sorensen's index of similarity  $C_s = 2a/b+c$  was used to estimate species similarity in different elevations (Sorensen, 1948). The number of epiphytic individuals was correlated with the recorded CBH and bark pH of 150 host trees to observe the association of host tree traits to epiphytic species richness. The inter and extrapolated curve was computed in R version 4.1.1 using iNEXT function to investigate the differences in the number of sampling plots affecting sample completeness, the proportion of the species pool found in each elevational zone was calculated by means of interpolation and extrapolation analyses (Chao *et al.*, 2014). This analysis evaluated the sample completeness based on sample coverage at a 95% confidence interval. The interpolation or observed species richness of vascular epiphytes was produced by merging the observed abundance and species richness of plots per elevation. Extrapolated or expected species richness for each elevation was based on the highest number of individuals. Furthermore, to understand the influence of climatic variables on vascular epiphyte distribution, we performed the Canonical Correspondence Analysis (CCA) in PAST version 4.03. For predictor variables, we used mean annual temperature (MAT), mean annual precipitation (MAP) and mean annual relative humidity (MRH). The climatic data of different elevational zone was obtained from the WorldClim database version 2.0 at ~1 km<sup>2</sup> (30 arc second) resolution (Fick and Hijmans, 2017). The study area map was prepared in QGIS Madeira version 3.20 (QGIS, 2022).

## RESULTS

We recorded a total of 942 individuals of vascular epiphytes belonging to 46 genera and 71 species under 21 families (Table 1). Orchidaceae was the most species-rich family with 28 species representing 39% followed by Polypodiaceae with 9 species representing 13% (Fig. 2). Araceae, Apocynaceae and Piperaceae were distributed with 5, 4, and 3 species, respectively. Slightly fewer species were found within families like Acanthaceae, Aspleniaceae, Commelinaceae, Gesneriaceae, Lycopodiaceae, and Urticaceae with only two species under each, while the least abundant families were Dioscoreaceae, Hypodematiaceae, Lamiaceae, Moraceae, Nephrolepidaceae, Pteridaceae, Ranunculaceae, Rubiaceae, Vitaceae, and Zingiberaceae each with single

**Table 1.** Summarized data of the vegetation types in different elevations.

Elevation range (m)	Epiphyte species	Epiphyte individuals	Mean Annual Precipitation (mm)	Mean Annual Temperature (°C)	Mean Relative Humidity (%)	H'	D	D'	J
400 – 700	46	365	277.5	23.5	72.19	3.46	1.94	0.96	0.96
700 – 1000	34	231	298.2	21.7	70.39	3.05	1.71	0.94	0.94
1000 – 1300	41	346	276.2	18.8	69.78	3.29	1.72	0.96	0.95

\* H' – Shannon's Index; D – Menhinick's Index; D' – Simpson's Index; J – Pielou's Index

**Table 2.** List of vascular epiphytes in sub-tropical forests (+ = Present; – = Absent).

Family/Taxa	Elevation			Phenology/ fertile period	Distribution	Conservation status
	Low	Mid	High			
<b>Acanthaceae</b>						
<i>Thunbergia coccinea</i> Wall. ex D.Don	+	+	+	Jul–Nov	TZ	LC
<i>Thunbergia lutea</i> T.Anderson	–	+	+	Jul–Oct	TZ	LC
<b>Apocyanaceae</b>						
<i>Hoya bella</i> Hook.	–	–	+	Oct–Nov	ICZ	NF
<i>Hoya latifolia</i> G.Don	+	+	–	Jul–Feb	TZ	VU
<i>Hoya linearis</i> Wall. ex D.Don	–	–	+	Aug–Nov	TZ	LC
<i>Hoya obcordata</i> Hook.f.	+	+	–	May–Jul	TZ	NF
<b>Araceae</b>						
<i>Colocasia affinis</i> Schott	+	+	–	Jul–Dec	TZ	LC
<i>Pothos scandens</i> L.	+	+	+	Dec–Jun	TZ	LC
<i>Rhaphidophora calophylla</i> Schott	+	+	+	Aug–Dec	TZ	NF
<i>Rhaphidophora hookeri</i> Schott	+	+	+	Mar–Jul	TZ	RR
<i>Scindapsus officinalis</i> (Roxb.) Schott	+	–	–	Feb–Jun	TZ	NF
<b>Aspleniaceae</b>						
<i>Asplenium phyllitidis</i> D.Don	–	–	+	Jun–Nov	TZ	LC
<i>Asplenium yoshinagae</i> ssp. <i>indicum</i> (Sledge) Fraser-Jenk.	–	–	+	May–Sep	TZ	LC
<b>Commelinaceae</b>						
<i>Cyanotis cristata</i> (L.) D.Don	+	+	–	Aug–Feb	TZ	LC
<i>Floscopa scandens</i> Lour.	+	–	–	July–Aug	TZ	EN
<b>Dioscoreaceae</b>						
<i>Dioscorea belophylla</i> (Prain) Voigt ex Haines	+	+	–	Oct–Jan	TZ	LC
<b>Gesneriaceae</b>						
<i>Aeschynanthus hookeri</i> C.B.Clarke	–	–	+	Jul–Aug	TZ	LC
<i>Lysionotus serratus</i> D.Don	–	–	+	Jul–Sep	TZ	LC
<b>Hypodematiaceae</b>						
<i>Leucostegia immersa</i> Wall. ex C. Presl	+	+	+	Jul–Sep	TZ	NT
<b>Lamiaceae</b>						
<i>Premna corymbosa</i> Rottler & Willd.	+	+	–	May–Jul	TZ	LC
<b>Lycopodiaceae</b>						
<i>Huperzia phlegmaria</i> (L.) Rothm.	+	+	–	Jul–Sep	TZ	EN
<i>Huperzia squarrosa</i> (G.Forst.) Trevis.	+	–	+	Jun–Sep	TZ	EN
<b>Moraceae</b>						
<i>Ficus sarmentosa</i> Buch.-Ham. ex Sm.	–	–	+	May–Jul	TZ	LC
<b>Nephrolepidaceae</b>						
<i>Nephrolepis cordifolia</i> (L.) C.Presl	+	+	+	Aug–Nov	TZ	LC
<b>Orchidaceae</b>						
<i>Aerides multiflora</i> Roxb.	+	+	–	Mar–Sep	TZ	NF
<i>Agrostophyllum planicaule</i> (Wall. ex Lindl.) Rchb.f.	+	–	–	July–Oct	TZ	NT
<i>Agrostophyllum stipulatum</i> ssp. <i>bicuspidatum</i> (J.J.Sm.) Schuit.	+	+	+	Mar–Jul	TZ	NF
<i>Bryobium eriaeoides</i> (F.M.Bailey) M.A.Clem. & D.L.Jones	+	+	–	Apr–Oct	TZ	NT
<i>Bulbophyllum careyanum</i> (Hook.) Spreng.	+	–	+	Oct–Feb	TZ	NF
<i>Bulbophyllum crassipes</i> Hook.f.	+	–	–	Sep–Dec	TZ	EN
<i>Bulbophyllum helenae</i> (Kuntze) J.J.Sm.	+	+	–	Oct–Feb	TZ	VU
<i>Bulbophyllum odoratissimum</i> (Sm.) Lindl. ex Wall.	–	–	+	Jul–Oct	TZ	LC
<i>Coelogyne flaccida</i> Lindl.	+	–	+	Mar–Jul	ICZ	NT
<i>Cymbidium aloifolium</i> (L.) Sw.	+	+	–	Apr–Jul	TZ	RR



<i>Cymbidium bicolor</i> Lindl.	+	–	–	Apr–Aug	ICZ	LC
<i>Cymbidium eburneum</i> Lindl.	+	+	–	Mar–Jul	ICZ	EN
<i>Dendrobium amoenum</i> Wall. ex Lindl.	+	–	+	May–Aug	TZ	NF
<i>Dendrobium aphyllum</i> (Roxb.) C.E.C.Fisch.	+	–	+	Mar–Jun	ICZ	RR
<i>Dendrobium bicameratum</i> Lindl.	+	+	+	Jul–Aug	ICZ	NF
<i>Dendrobium chrysanthum</i> Wall. ex Lindl.	+	–	+	Jul–Nov	ICZ	NF
<i>Dendrobium crepidatum</i> Lindl. & Paxton	+	+	–	May–Jul	TZ	EN
<i>Dendrobium nobile</i> Lindl.	–	–	+	Mar–Jul	TZ	VU
<i>Dendrobium pachyphyllum</i> (Kuntze) Bakh.f.	+	–	–	Mar–Jul	TZ	LC
<i>Dendrobium plicatile</i> Lindl.	–	–	+	Apr–Aug	TZ	NF
<i>Liparis viridiflora</i> (Blume) Lindl.	–	–	+	Oct–Feb	TZ	NT
<i>Panisea uniflora</i> (Lindl.) Lindl.	+	–	–	Apr–Jun	TZ	NT
<i>Papilionanthe teres</i> (Roxb.) Schltr	+	+	–	May–Jul	TZ	VU
<i>Rhynchostylis retusa</i> (L.) Blume	+	+	+	May–Sep	TZ	EN
<i>Thunia alba</i> (Lindl.) Rchb.f.	–	+	+	Jun–Sep	TZ	RR
<i>Uncifera obtusifolia</i> Lindl.	–	–	+	Aug–Oct	TZ	DD
<i>Vanda cristata</i> Wall. ex Lindl.	–	+	+	Apr–Aug	TZ	EN
<i>Vandopsis undulata</i> (Lindl.) J.J.Sm.	–	–	+	Apr–May	TZ	LC
<b>Piperaceae</b>						
<i>Peperomia heyneana</i> Miq.	+	–	–	May–Aug	TZ	LC
<i>Peperomia pellucida</i> (L.) Kunth	+	+	–	May–Aug	TZ	NT
<i>Peperomia tetraphylla</i> (G.Forst.) Hook. & Arn.	–	–	+	Feb–Jul	TZ	NT
<b>Polypodiaceae</b>						
<i>Drynaria quercifolia</i> (L.) J.Sm.	+	+	–	Jul–Dec	TZ	NT
<i>Goniophlebium amoenum</i> (Wall. ex Mett.) Bedd.	+	+	–	Aug–Nov	TZ	NT
<i>Lepisorus normalis</i> (D.Don) C.F.Zhao, R.Wei & X.C.Zhang	–	–	+	Aug–Nov	TZ	NT
<i>Loxogramme involuta</i> (D.Don) C.Presl	–	–	+	Aug–Oct	TZ	NT
<i>Pyrrosia costata</i> (Wall. ex C.Presl) Tagawa & K.Iwats.	+	+	–	Jul–Sep	TZ	NT
<i>Pyrrosia mannii</i> (Giesenh.) Ching	–	–	+	Jul–Oct	TZ	VU
<i>Pyrrosia nuda</i> (Giesenh.) Ching	+	+	–	Jul–Oct	TZ	NT
<i>Selliguea ebenipes</i> (Hook.) S.Linds.	–	–	+	Jul–Oct	TZ	NT
<i>Selliguea griffithiana</i> (Hook.) Fraser-Jenk.	–	–	+	May–Oct	TZ	NF
<b>Pteridaceae</b>						
<i>Vittaria elongata</i> Sw.	–	–	+	Jul–Oct	ICZ	LC
<b>Ranunculaceae</b>						
<i>Clematis buchananiana</i> DC.	+	+	–	Jul–Oct	TZ	NT
<b>Rubiaceae</b>						
<i>Neohymenopogon parasiticus</i> (Wall.) Bennet	–	–	+	Jun–Aug	TZ	LC
<b>Urticaceae</b>						
<i>Elatostema lineolatum</i> Wight	–	–	+	May–Jun	TZ	NT
<i>Pilea microphylla</i> (L.) Liebm.	+	+	–	Jun–Aug	TZ	LC
<b>Vitaceae</b>						
<i>Ampelocissus sikkimensis</i> (M.A.Lawson) Planch.	–	+	+	Jul–Oct	TZ	EN
<b>Zingiberaceae</b>						
<i>Globba multiflora</i> Wall. ex Baker	+	–	–	Aug–Nov	TZ	LC

\*TZ – Trunk Zone; ICZ – Inner Crown Zone; NT – Not Threatened, DD – Data Deficient, LC – Least Concern, VU – Vulnerable, EN – Endangered; NF – Not Found; RR – Rare.

species (Table 2). Of the total 21 families, the dicots were represented by 55% while 20% and 25% were monocots and ferns. Amongst dicots, Apocynaceae (4 spp.) was the largest family followed by Acanthaceae (2 spp.). Orchidaceae remained dominant within the monocots followed by Araceae and Commelinaceae with 5 and 2 species respectively.

Among orchids, there were large genera such as *Dendrobium* (8 spp.), *Bulbophyllum* (4 spp.) and *Cymbidium* (3 spp.). *Pyrrosia* (3 spp.), *Huperzia* (2 spp.),

*Selliguea* (2 spp.), and *Asplenium* (2 spp.) were dominant under the second largest family Polypodiaceae in terms of species number. Similarly, there were other species-rich genera in case of angiosperms excluding orchids such as *Hoya* (4 spp.) and *Peperomia* (3 spp.) while *Thunbergia* and *Rhaphidophora* were present each with only two species. Of the total 71 species, 58 species were herbs representing 82%. The climbers (10 spp.) accounted for 14% of the total taxa whereas only three species were shrubs (4%).

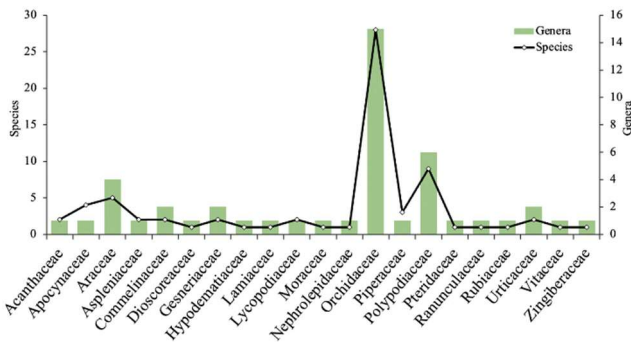


Fig. 2. Dominant families showing number of species and genera.

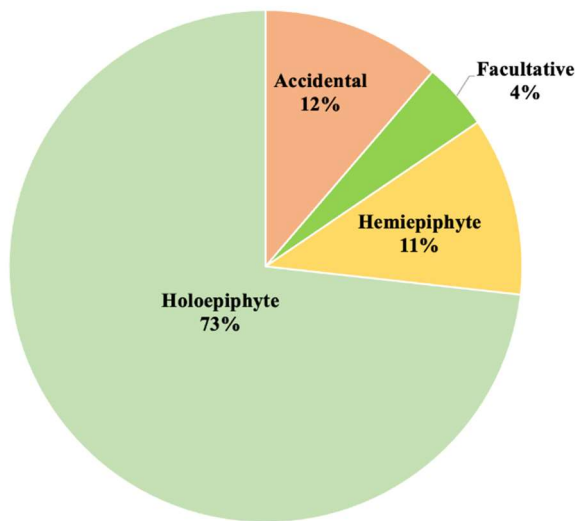


Fig. 3. Different life forms of vascular epiphytes.

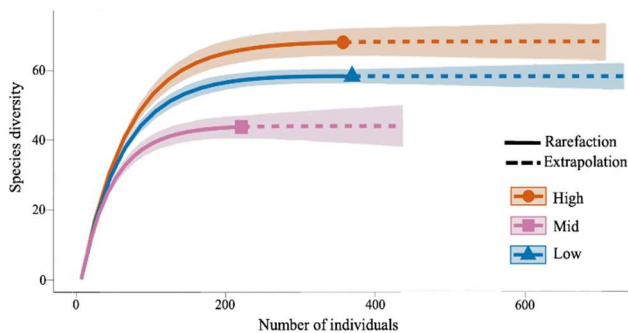


Fig. 4. Inter and extrapolated analysis of epiphyte diversity across the elevations.

The entire species recorded in this study were perennial, however, species like *Floscopa scandens* were occasionally annual in nature. Based on the life forms, holoepiphytes (52 spp.) were dominant representing 73% of the total species, of which orchids were dominant. Hemiepiphytes (8 spp.) accounted for 11% of the total species, with the species like *Ampelocissus sikkimensis*, *Ficus sarmentosa*, *Pothos scandens*, *Premna corymbosa*, *Rhaphidophora calophylla*, *R. hookeri*, *Scindapsus*

*officinalis* and *Thunbergia coccinea*. The other life forms were facultative (3 spp.) and accidental (8 spp.) representing 4% and 12% of the total species, respectively (Fig. 3). Species like *Colocasia affinis*, *Clematis buchananiana*, *Cyanotis cristata*, *Dioscorea belophylla*, *Floscopa scandens*, *Globba multiflora* and *Thunbergia lutea* were found to be grown as epiphytes accidentally while *Asplenium phyllitidis*, *A. yoshinagae* subsp. *indicum* and *Nephrolepis cordifolia* were recorded as facultative epiphytes. Phenology of flowering epiphytes reveals 37% of the total species bloomed in spring and summer, whereas 29%, 28% and 6%, respectively were known to flower in monsoon, autumn and winter seasons.

**Diversity indices**

The diversity indices for the recorded species were estimated across the low, mid and high elevations (Table 1). A low Shannon diversity index of the epiphytic community was obtained in mid elevations ( $H' = 3.05$ ) whereas the highest score was obtained from low elevations ( $H' = 3.46$ ) followed by high elevations ( $H' = 3.29$ ). The concentration of species richness (Simpson's index or  $D'$ ) was calculated as highest as 0.96 in both low and high elevations and lowest as 0.94 in mid elevations. Subsequently, the values of Menhinick's index ( $D$ ) varied from 1.94 in low elevations to 1.71 and 1.72 in mid and high elevations respectively. The score for Pielou's evenness index ( $J$ ) varied from 0 to 1 with 0.96, 0.94 and 0.96 in the respective elevations.

**Species richness and composition**

Our results showed that the highest species richness was found in low elevations (46 spp. belonging to 30 genera under 15 families) followed by high elevations (41 spp. under 30 genera and 16 families). Similarly, 34 species belonging to 28 genera and 15 families have been recorded from mid elevations. Overall, low elevations seem more diverse than mid and high elevations (Fig. 4). However, all three elevations had comparable diversity with entire elevational zone dominated by species of Orchidaceae while the members of Polypodiaceae increased with increasing altitude. Additionally, each elevation was dominated by herbaceous plants while a low number of shrubs had been observed. A slightly higher number of hemiepiphytes were found in the low elevations whereas only one or a few were present at both mid and high elevations. Furthermore, based on the Sorensen's index, vascular epiphytes in mid and high elevations showed the highest similarity of  $C_s = 0.67$  followed by the epiphytic community at low and mid ( $C_s = 0.373$ ) and the least similarity was observed in low and high elevational zones ( $C_s = 0.09$ ).

The number of families, genera and species plotted against the elevational gradient showed that species richness decreased towards mid-elevations while it increased towards

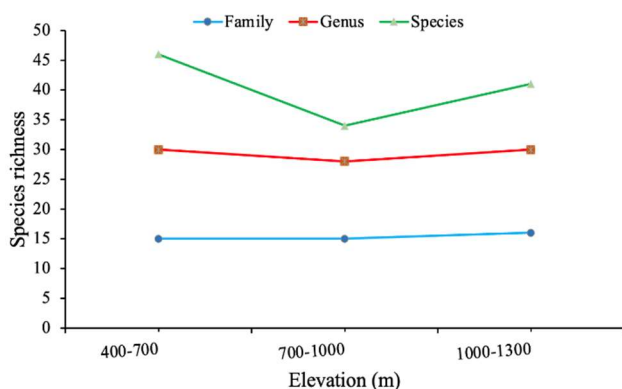


Fig. 5. Distribution of plant taxa from low to high elevations

low and high elevations (Fig. 5). In terms of composition, taxa like *Dendrobium pachyphyllum*, *Scindapsus officinalis*, and *Peperomia heyneana* were recorded only from low elevations (Table 2). However, other species such as *Dendrobium bicameratum*, *Leucostegia immersa*, *Nephrolepis cordifolia*, *Pothos scandens*, *Rhaphidophora calophylla*, *R. hookeri*, *Rhynchosstylis retusa*, *Thunbergia coccinea*, and *T. lutea* were distributed through the entire elevational zone. Similarly, *Asplenium phyllitidis*, *A. yoshinagae* subsp. *indicum*, *Aeschynanthus hookeri*, *Bulbophyllum odoratissimum*, *Dendrobium plicatile*, *Hoya linearis*, *Liparis viridiflora*, *Neohymenopogon parasiticus*, *Peperomia tetraphylla*, *Selliguea ebenipes* and *S. griffithiana*, were dominant only in high elevations. The lycophyte *Huperzia squarrosa* was observed only in mid elevations. The distribution pattern of species may be regulated by the site condition and biological peculiarities. Furthermore, epiphytic ferns and lycophytes were equally distributed in all low, mid and high elevations.

Several vascular epiphytes are increasingly threatened which may be due to anthropogenic activities, habitat fragmentation, over-exploitation, climate change, and increasing pollution in the natural habitats (Werner *et al.*, 2011). Our results also revealed that 23 out of the 71 taxa recorded were categorised under Least Concern representing 32%. Similarly, 23% (16 spp.) were Threatened. Furthermore, taxa such as *Ampelocissus sikkimensis*, *Bulbophyllum crassipes*, *Cymbidium eburneum*, *Dendrobium crepidatum*, *Huperzia phlegmaria*, *H. squarrosa*, *Rhynchosstylis retusa*, and *Vanda cristata* were Endangered representing 13% of the total species. Others such as *Cymbidium aloifolium*, *Dendrobium aphyllum*, *Rhaphidophora hookeri* and *Thunia alba* were classified as Rare (6%). Consequently, *Bulbophyllum helenae*, *Dendrobium nobile*, *Hoya latifolia*, *Papilionanthe teres* and *Pyrrosia mannii* were Vulnerable (7%) whereas *Uncifera obtusifolia* showed Data deficient (1%). However, the conservation status of 13 taxa (18%) was not found. Additionally, *Thunbergia lutea* was found to be endemic to Darjeeling region (Grierson and Long, 2001).

### Influence of host tree traits on species richness

The major host trees are *Callicarpa vestita*, *Castanopsis indica*, *Duabanga grandiflora*, *Engelhardia spicata*, *Ficus neriifolia*, *F. religiosa*, *Gmelina arborea*, *Lagerstroemia parviflora*, *Macaranga denticulata*, *Shorea robusta*, *Saurauia napaulensis*, *Schima wallichii* and *Tectona grandis*. Moraceae and Euphorbiaceae were the most species-rich families while Tetramelaceae, Lamiaceae and Lythraceae represented larger canopies. Some host trees like *Bridelia retusa*, *Dillenia pentagyna*, *Diploknema butyracea*, *Ficus benghalensis*, *Tetrameles nudiflora* had CBH more than 300 cm while host trees like *Callicarpa vestita*, *Eriobotrya dubia*, *Syzygium cumini* and *Macaranga denticulata* had girth less than 50 cm. Variation in the bark pH was also observed among tree species. The highest pH was estimated for *Acer thomsonii* (7.16) while the lowest for *Tectona grandis* (4.55).

Furthermore, host trees having rough bark texture harboured a maximum number of epiphytic species than host trees with smooth barks (Fig. 6). Trees like *Ficus neriifolia*, *Duabanga grandiflora* and *Saurauia napaulensis* could accumulate high diversity of epiphytes sheltering more than 15 species. The association of vascular epiphytic diversity depends on different host tree variables such as CBH, tree architecture, bark texture and canopy size. Our result showed that CBH was strongly correlated to epiphytic richness (Fig. 7A). The larger the CBH, the larger the surface area for epiphytes to establish. However, our result revealed that there was a very weak relationship between the host tree bark pH and vascular epiphytic richness (Fig. 7B). Furthermore, 90% of the total taxa were found to be grown in the trunk zone whereas only 10% were sheltered in the inner crown zone. Some host trees such as *Engelhardia spicata*, *Ficus benghalensis*, *F. neriifolia*, *Eriobotrya dubia* and *Shorea robusta* with maximum branching sheltered the majority of epiphytes whereas, host trees like *Macaranga denticulata* and *Syzygium cumini* with thin branching sheltered comparatively lesser species.

### Climatic variables determining vascular epiphyte distribution

The result of the Canonical Correspondence Analysis (CCA) showed the relationships between distribution of vascular epiphytes and climatic variables, such as mean annual temperature (MAT), mean annual precipitation (MAP) and mean annual relative humidity (MRH). The first axis explained 64.33% and the second axis explained 35.67% of the total variation in the data set (Fig. 8). The eigenvalues of these axes accounted for 0.14 and 0.08, respectively. MAP and MAT were closely related to Axis 1. The distribution of the species such as *Bulbophyllum crassipes*, *B. helenae*, *Bryobium eriaeoides*, *Colocasia affinis*, *Dioscorea belophylla*, *Drynaria quercifolia*, *Goniophlebium amoenum*, *Hoya obcordata*, *Huperzia phlegmaria*, *Peperomia heyneana*, *P. pellucida* and



Fig. 6. Vascular epiphytes (VE) growing in host tree with A: Rough bark. B: Smooth bark.

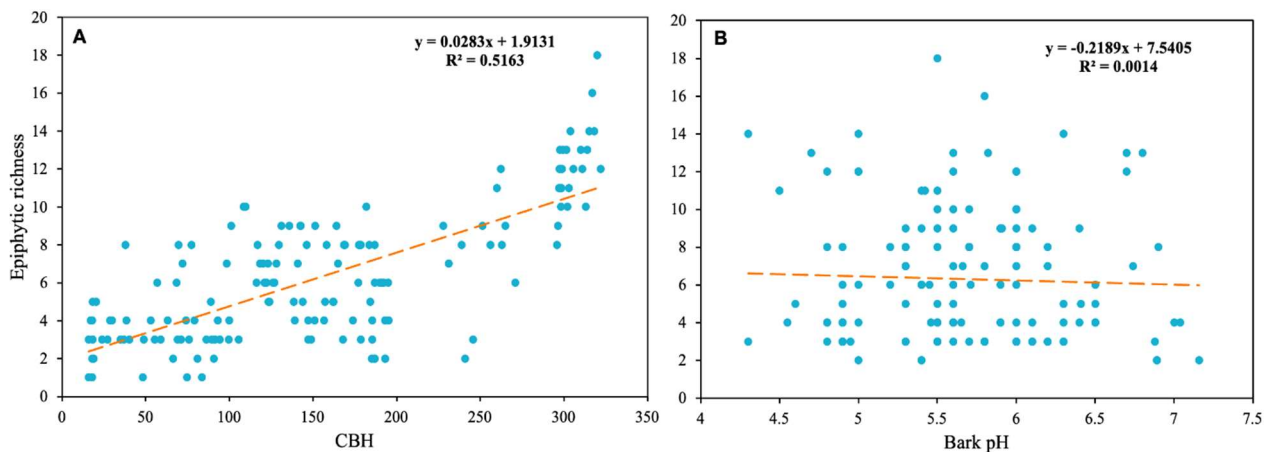


Fig. 7. Correlation of epiphytic richness with A: CBH. B: pH of host bark.

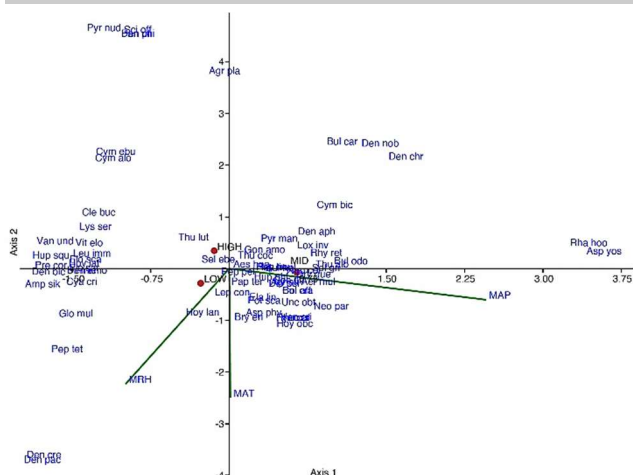
*Pyrrisia costata* on the first axis were predominantly found at low elevations while *Aeschynanthus hookeri*, *Asplenium yoshinagae* subsp. *indicum*, *A. phyllitidis*, *Bulbophyllum odoratissimum*, *Dendrobium aphyllum*, *D. nobile*, *Hoya linearis*, *Loxogramme involuta*, *Neohymenopogon parasiticus*, *Pyrrisia mannii*, *Selliguea griffithiana*, *S. ebenipes*, *Thunia alba*, *Uncifera obtusifolia* and *Vanda cristata* were found in high elevations. Furthermore, species like *Rhaphidophora hookeri* and *Asplenium yoshinagae* subsp. *indicum* was associated with high precipitation and low humidity (Fig. 8). *Ampelocissus sikkimensis*, *Cymbidium aloifolium*, *C. eburneum*, *Dendrobium amoenum*, *D. plicatile*, *Hoya latifolia*, *Huperzia squarrosa*, *Liparis viridiflora*, *Leucostegia immersa*, *Lysionotus serratus*, *Panisea*

*uniflora*, *Pyrrisia nuda*, *Scindapsus officinalis*, *Vandopsis undulata* and *Vittaria elongata* were related negatively to the first axis.

## DISCUSSION

The present study was focused on the vascular epiphytic community along an elevational range in the sub-tropical forests of Darjeeling eastern Himalaya. Our results showed a slightly U-shaped distribution pattern with decreasing trend in mid elevations i.e., from 700 to 1000 m. However, there was no difference in species richness in entire elevations. Conversely, the hump-shaped or “mid-elevation bulge” distribution pattern of vascular epiphytes were observed in other findings (Kreft





**Fig. 8.** Canonical Correspondence Analysis (CCA) showing the ordination of species and climatic variables in the first two axes.

*et al.*, 2004; Kromer *et al.*, 2005; Zhao *et al.*, 2015; Zhang *et al.*, 2015). The decreasing pattern of species richness in mid elevations could be attributed to the environmental variables, geographical area and topographic features. Additionally, this elevation was located in exposed areas with small host trees, resulting in reduced space for epiphytes to establish (Ding *et al.*, 2016). Besides, mid elevations of the present study area also experienced frequent disturbances including road construction, expansion of livelihood and other human interference, such as deforestation, plant collection for commercial and medicinal purposes and grazing. Our findings also showed that monocots were predominant in both low and high elevations. However, in case of dicots, a gradual decrease in species at mid elevation was observed. Our result did not reflect any species richness pattern for ferns in relation to elevations, it might be they were adapted morphologically and more flexibly that allowing them to grow across the entire elevational ranges with wide ecological amplitude. Our results showed that Orchidaceae was the most species-rich family as reported in other studies (Wang *et al.*, 2016; Ding *et al.*, 2016; Quiel and Zotz, 2021; Taylor *et al.*, 2022). Orchids are among the plants with the greatest ecological significance and have successfully colonised almost all habitats (Hsiao *et al.*, 2011). The life of an orchid in the canopy is very well adapted and they have roots with a high surface area for quick absorption of water and nutrients. Their secondary stems have the ability to retain water, allowing the plant to resist dry conditions. Another crucial factor for orchids being well flourished in forests is that they produce thousands of tiny seeds dispersed over large areas (Yang *et al.*, 2016; Zhang *et al.*, 2018).

As indicated in the previous studies, the development of the epiphytic community depends on the morphology of host tree, e.g. canopy, CBH, bark roughness and bark pH (Wang *et al.*, 2016; Getaneh and Gamo, 2016). Similarly, other studies also support that host tree

characters an important parameters for epiphytic species assemblage (Hietz, 1999; Callaway *et al.*, 2002; Adhikari *et al.*, 2012; Wang *et al.*, 2014). We found that CBH is closely related to vascular epiphytic abundance and species richness across host trees and different elevations. Tree sizes are known to have a huge effect on epiphytic diversity and composition (Bhattarai and Vetaas, 2003; Wang *et al.*, 2016; Timsina *et al.*, 2016). Older and larger host trees exhibit wider trunk and branch surfaces that allow the firm establishment of epiphytes (Callaway *et al.*, 2002; Woods *et al.*, 2015; Zhao *et al.*, 2015; Timsina *et al.*, 2016). Concurrently, our result also reflects that host tree with rough bark texture exhibited a maximum number of species as reported in other works (Getaneh and Gamo, 2016; Seshadri *et al.*, 2021). Rough bark has high water-holding capacity that retains moisture for a longer period of time providing better settlement of epiphytic seedlings (Callaway *et al.*, 2002; Timsina *et al.*, 2016). Therefore, host tree with rough bark serves as a suitable substrate for the attachment of epiphytes and furrowed bark enhance better moisture-holding capacity than smooth bark which often makes a poor host (Kellar *et al.*, 2006; Wyse and Burns, 2011). Furthermore, leaf size and host tree architecture remain an important factor for epiphytic diversity patterns as it influences light levels and wind movement (Cardelus *et al.*, 2006; Timsina *et al.*, 2016; Frati *et al.*, 2021). However, host tree bark pH was negatively associated with epiphytic abundance. On the contrary, other studies support the influence of pH on epiphytic taxa (Ghimire, 2008; Adhikari and Fischer, 2011). In this study, the epiphytes were observed to flourish well in the trunk zone as it provides conducive environmental conditions and sufficient area for epiphytes to grow (Trimanto and Danarto, 2020; Adhikari *et al.*, 2021). Furthermore, more humus and mosses in the trunk zone also serve as enough moisture for the ecesis and colonization of epiphytes (Hirata *et al.*, 2009; Wagner *et al.*, 2015). The vertical decline of epiphytic diversity from trunk zone to inner crown zone may be related to the decrease in humidity and increase in ultraviolet radiation and photon flux density along with the increasing canopy height of the hosts (Wang *et al.*, 2016).

Environmental variables have greatly influenced the distribution pattern of different life forms (Sahu *et al.*, 2019). Vascular epiphytes are known to be influenced by abiotic and biotic factors, however, the importance of direct and indirect effects on epiphytic distribution is poorly understood (Ding *et al.*, 2016). Furthermore, temperature, relative humidity, and rainfall are some important determinants of epiphytic species richness and abundance (Koster *et al.*, 2011; Benzing, 2004; Ding *et al.*, 2016). Similarly, light is another important factor responsible for the spatial pattern of epiphytes (Rosa-Manzano *et al.*, 2014; Petter *et al.*, 2016). Across three elevations, temperature, precipitation and relative humidity increase with increasing elevations. Generally,



altitude, mean annual rainfall and relative humidity seems to be crucial for vascular epiphytic abundance (Kreft *et al.*, 2004). Since epiphytes do not have direct contact with the ground, they rely on regular moisture inputs from fog and rainfall which are relayed to the host specificity that has potentially the greatest influence on epiphytes (Zotz and Hietz, 2001; Cardelus, 2007; Zhang *et al.*, 2015). We concluded that the variation in vascular epiphytic composition and diversity among study sites was related to climatic variables (mean annual precipitation and mean annual relative humidity) and structural variables (especially CBH). Conclusively, the real number of vascular epiphytes in the study area might be higher than the observed number in the present study. Hence, it is extremely important to protect large and old host trees and adequate management approaches should be implemented for the conservation of epiphytic species in the region.

## CONCLUSION

The present study suggests that the vascular epiphytic species richness varies along elevational and environmental gradients, presenting a slightly U-shaped pattern with a peak at low and high elevations. Overall, we found that the epiphytic diversity was determined by host tree traits, especially CBH and bark texture. Although the relationship between them is observed well, very little is known so far. Thus, the host-epiphytes associations should be studied in future at a greater scale. In conclusion, our findings would be seminal in providing a quantitative baseline for future research and the resulting details about distribution patterns of vascular epiphytes in study area would be the starting point in filling this knowledge gap.

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