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Terrestrial and epiphytic orchids exhibit different diversity and distribution patterns along an elevation gradient of Mt. Victoria, Myanmar

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ABSTRACT

Orchids have been long fascinating biologists and ecologists because of their remarkable range of life history strategies, floral and vegetative morphology, pollination syndromes, and symbiotic fungi. However, the diversity and distribution patterns of orchids remain unclear in several regions, seriously hindering the understanding of orchid diversity and their maintenance mechanisms. In this study, species richness, abundance, and environmental conditions of epiphytic and terrestrial orchids were investigated along an elevation gradient of Mt. Victoria, Myanmar, ranging from 600 to 3000 m with 200-m intervals. A binary species-based network was structured between epiphytic orchids and their hosts to further address the effect of hosts on orchid distribution. In total, 94 orchid species were recorded, including 58 epiphytic and 36 terrestrial orchids. A hump-shaped pattern of epiphytic orchid richness occurred along the elevation gradient, with the highest richness at ca. 2200 m, whereas terrestrial orchid richness follows a monotonous decrease. Both elevation and slope significantly affected the species composition and diversity of epiphytic and terrestrial orchids, while terrestrial orchids were also affected by herb coverage. The network between epiphytic orchids and their hosts exhibited a low level of connectance, and significant nestedness with a high level of modularity and specialization. Interactions in the network were heterogeneously distributed among hosts, as *Lithocarpus variolosus*, *Rhododendron arboretum*, and *Lyonia ovalifolia* hosted a wide variety of orchid species and hence played an important role in maintaining the diversity pattern of epiphytic orchids, while the bulk of species exhibited few interactions. Twenty epiphytic orchids (such as *Sunipia grandiflora*, *Liparis viridiflora*, *Porpax grandiflora* and *Liparis tsii*), which were only attached to specific host species, may be exposed to a high risk of extinction with the intensification of human activities. This study provides basic data for the conservation and management of orchids in Mt. Victoria, Myanmar.

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1. Introduction

Orchids have long fascinated biologists through their remarkable range of life history strategies, floral and vegetative morphology, pollination syndromes, *etc*. (Fay and Chase, 2009). As the major group of angiosperms with 29,485 species recorded worldwide (WFO, 2022), orchids are of great value in ornamental, medical, conservation, and evolutionary research (Zhang et al., 2018). They are found in almost all terrestrial ecosystems except polar and extremely arid desert regions, although most of them are mainly distributed in tropical regions (Dirzo and Raven, 2003; Kratochwil, 1999). This relatively high species diversity and wide distribution range of orchids may benefit from the family's evolution of pollinia, symbiotic associations with mycorrhizal fungi, colonization of epiphytic habitats, and Crassulacean Acid Metabolism (Givnish et al., 2015). In fact, although Orchidaceae are abundant and widely distributed, most orchid species are rare and endangered due to small population sizes, species-specific symbionts, and limited distributions (Cribb et al., 2003; Swarts and Dixon, 2009a). Thus, orchids are facing unprecedented levels of threat globally from habitat destruction and fragmentation, climate change, overcollection, and other human activities (Wraith and Pickering, 2019; Phillips et al., 2020). All wild orchids are protected by the Convention on International Trade in Endangered Species of Wild Fauna and Flora, accounting for more than 90% of all the plants protected by the Convention, making them the "flagship" group in plant conservation (Luo et al., 2003). Nonetheless, the conservation of orchids is impeded by a lack of biodiversity surveys. Additionally, the diversity and distribution of orchids remain unclear in several regions of the world, which has seriously hindered our understanding of orchids diversity and their maintenance mechanisms. Therefore, systematic investigation and assessment of orchids are necessary to identify species with high conservation value (Fay, 2018).

The relationship between species richness and elevation has been a core topic in biodiversity research (Acharya et al., 2011), which is ideal for understanding broad-scale patterns of species diversity and distributions, due to the short geographical distances and large climatic differences (Grytnes and Beaman, 2006). Two main patterns along with elevation have been documented: the monotonic decrease (Jacquemyn et al., 2005; Tusiime et al., 2007; Vázquez-García and Givnish, 2010; Timsina et al., 2021) and the hump-shaped pattern (Heaney, 2001; Bhattarai and Grytnes, 2004; McCain, 2005; Acharya et al., 2011; Djordjević et al., 2022). In addition, several ecological and biogeographical studies have focused on the identification of patterns and influencing factors of orchid species richness along geographic and environmental gradients (Acharya et al., 2011; Djordjević et al., 2022; Kuper et al., 2004; Timsina et al., 2021; Zhang et al., 2015b). For instance, orchid richness can exhibit a downward trend towards high elevations, mainly due to harsher climatic conditions, steeper terrain, less topsoil, or more rugged topography (Hu et al., 2022b; Timsina et al., 2021). Other findings have highlighted a hump-shaped pattern, probably caused by moderate relative air humidity, abundant precipitation and appropriate temperature, water and energy interact optimally, maximum productivity at the medium elevation gradient (Acharya et al., 2011; Djordjević et al., 2022; Zhang et al., 2015a). To date, little research has investigated the diversity and distribution of orchids along elevation gradients in the world; thus, the present study sets out to fill the gap and increase our knowledge on this topic.

About 18000 species (ca. 70% of orchid species all over the world) live on trees as epiphytes (Gravendeel et al., 2004). Indeed, epiphytic orchids are the main life form contributing to biodiversity in the tropics (Nieder et al., 1999; Swarts and Dixon, 2009b). For epiphytes, host attributes (e.g., architecture, tree size, bark texture, and physico-chemistry) are the important factors that may shape their distributions (Sayago et al., 2013; Francisco et al., 2018; Zarate-Garcia et al., 2020). Considering the survival and growth of epiphytic orchids mainly rely on their hosts, studies on commensal interaction networks between epiphytic orchids and their hosts may shed light on how hosts affect the diversity and distribution patterns of epiphytic orchids. However, to our knowledge, only two studies have focused on this topic (Silva et al., 2010; Zotarelli et al., 2019). Silva et al. (2010) assessed forty networks of epiphytic orchid-host tree species and found nested networks, resulting from differences in the abundance of host tree species. Zotarelli et al. (2019) focused on the influence of host characteristics on network structure and suggested that the generalist core trees represent a decisive factor in both nested and robust patterns. Therefore, host tree species need to be protected in conservation and restoration activities to prevent secondary extinctions (Francisco et al., 2021), and the analysis of epiphytic orchid-host networks is worthy of further exploration.

As a part of the Indo-Burma biodiversity hotspot, Myanmar has high biodiversity (Myers, 2000; Mittermeier et al., 2011). Mt. Victoria, as an alpine "sky island", is the third-highest mountain and a famous eco-tourism site in Myanmar. Unlike many other natural areas of Myanmar, Mt. Victoria contains a Holarctic floral species assemblage and is regarded as an important ecological refuge, attracting hordes of botanists and leisure tourists (Kurzweil et al., 2021; Tanaka, 2005). Despite Mt. Victoria's unique geographical location and irreplaceable ecological value, critical floristic inventories remain scarce in this region (Aung et al., 2020). Previous orchids studies in this region mainly have focused on species classification, species inventory and discoveries of new species (Aung et al., 2020; Kang et al., 2019; Zhou et al., 2018; Tanaka, 2005; Tanaka et al., 2010), while systematic analysis of orchids along elevation gradients and their relationship with host trees has never been reported. In this study, we investigated orchid communities along an elevation gradient (600–3000 m) on Mt. Victoria, Myanmar to (1) address orchid species richness pattern along an elevation gradient and identify the major drivers of such pattern, (2) structure the interaction network relationship between epiphytic orchids and their hosts, and (3) propose the conservation implications underlying these patterns. Survey data originating from this study will contribute to the conservation and management of orchids in Mt. Victoria, Myanmar.

2. Methods

2.1. Study area

Mt. Victoria (21˚12 N, 93˚35 E) is located in the southern part of Chin State, western Myanmar, near the borders with India and

Bangladesh and forms part of the Chin Hills-Arakan Yoma mountain range. Inscribed in 1997, the mountain and its foothills have been protected area status as the Natma Taung National Park, safeguarding its vast assemblage of plant and animal life (Kurzweil et al., 2021). At 3053 m above sea level (m a. s. l.), Mt. Victoria is the highest peak in Chin State, with rapid changes in forest type along a steep elevation gradient (Fig. 1).

The vertical distribution pattern was analyzed by 12 elevational zones from 600 m to 3000 m a. s. l. with an interval of 200 m. In accordance with Song et al. (2015), five plots (20 m × 20 m) were set up at each elevation zone, and a total of 60 plots were investigated.

2.2. Orchids investigation

Epiphytic orchids were investigated from all tree hosts in each plot, using portable long ladders and binoculars. Species richness and abundance of terrestrial orchids, however, were recorded on the whole forest floor of each plot. Most of the orchids were identified immediately in the field by senior orchid taxonomists and ecologists, but in cases of doubt, specimens were transported to the
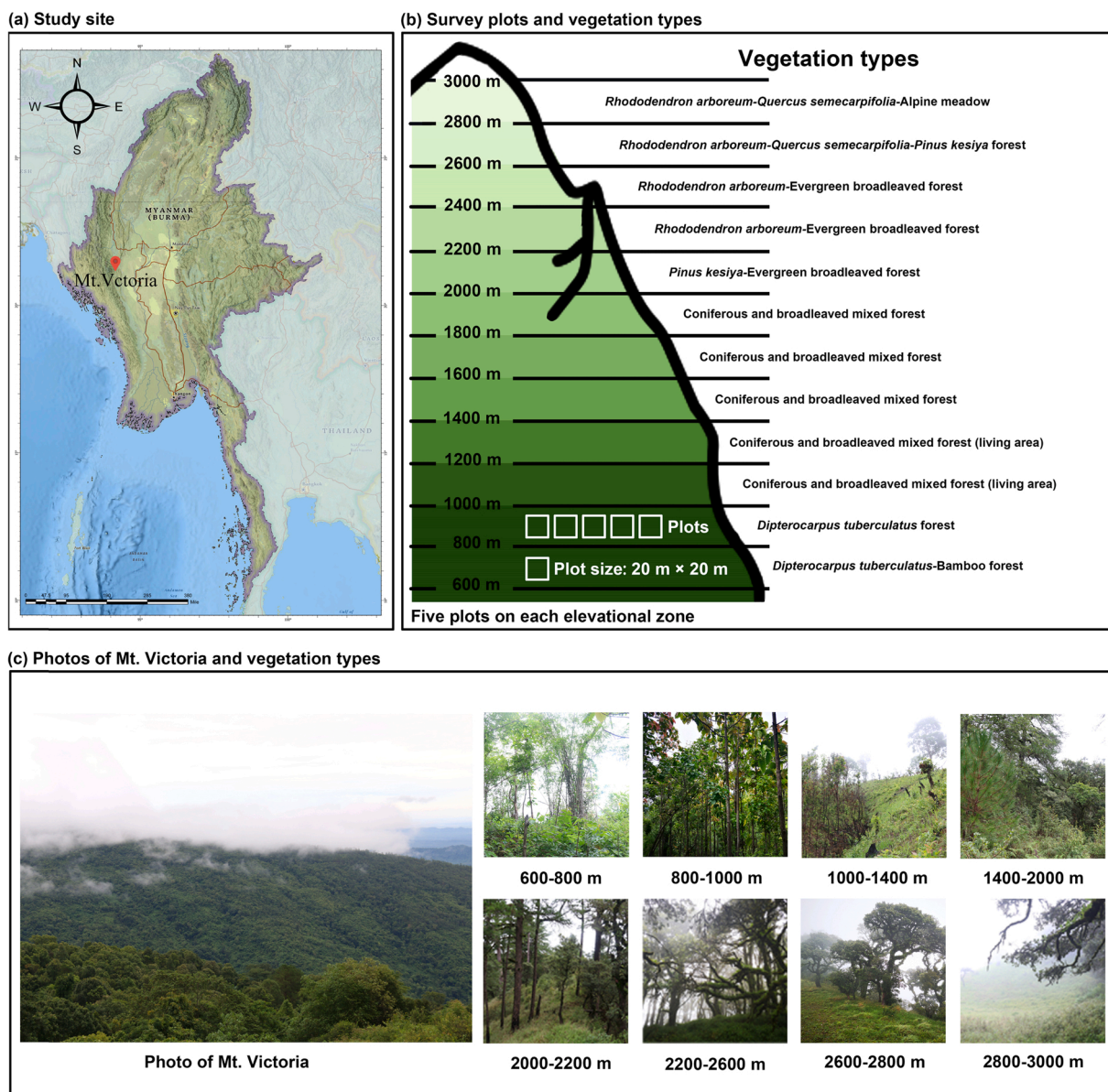

Fig. 1. Study site and experimental design. Notes: Orchids were investigated from 12 elevational zones with 200 m elevation intervals on Mt. Victoria, and five plots (20 m × 20 m) were randomly set for each elevation zone. (a) Study site. (b) Survey plot and vegetation types. The vegetation type was named by synthesizing all natural zones on each elevational zone. (c) Photos of Mt. Victoria and vegetation types.

laboratory for further inspection.

To address the major drivers of the species richness pattern of orchids, we measured environmental factors including topographic parameters (elevation, slope, and aspect) and stand characteristics (tree coverage, shrub coverage, and herb coverage). Tree coverage, which refers to the percentage of the above-ground vertical projection area of the tree layer over the plot area (20 m × 20 m), was measured using a quantitative approach suggested by Gao et al. (2006). In each plot, five shrub subplots (5 m × 5 m) and five herb subplots (1 m × 1 m) were set at the four corners and the center of each plot (20 m × 20 m). Shrub coverage and herb coverage were then calculated as the mean values of the estimated coverages of the five subplots. A portable compass (pauloneDC45) was used to measure the slope and aspect of the sampled plots.

The survey regions were subdivided into seven vegetation types based on different vertical natural zones along an elevation gradient, i.e., *Dipterocarpus tuberculatus*-bamboo forest, *Dipterocarpus tuberculatus* forest, coniferous and broadleaved mixed forest, *Pinus kesiya*-evergreen broadleaved forest, *Rhododendron arboretum*-evergreen broadleaved forest, *Rhododendron arboretum-Quercus semecarpifolia-Pinus kesiya* forest, *Rhododendron arboretum-Quercus semecarpifolia*-subalpine meadow (Fig. 1b). Among the vegetation types, Kanpetlet town, which had an elevation range of 1000–1400 m with the most populated area, was marked as a living area since the coniferous and broadleaved mixed forest in this elevation range was obviously different from the one in the range of 1400–2000 m (Fig. 1c).

Nomenclature followed the taxonomic system of the World Checklist of Orchidaceae (Govaerts et al., 2022). During the species identification process, we only considered specimens identified at the species level. Varieties and subspecies were treated as individual species in the diversity estimates. All information concerning the collector, collector's number, collection date, taxonomy, locality, and habitat were copied from the herbarium labels and entered into a relational database.

2.3. Statistical analysis

Importance value (IV) of orchids was calculated using the following formula:

$$IV = (R_{fre} + R_{abu}) / 2 \times 100\%$$

Where, R_{fre} is the relative frequency of a certain species, and R_{abu} refers to the relative abundance of a certain species.

The 'vegan' package (ggplot2) was used for drawing richness curves (Oksanen et al., 2020). Dynamic curve fit equations were created using SigmaPlot 14.0 (Systat Software Inc., San Jose, CA, USA). The species richness pattern of epiphytic orchids along elevation was fitted using peak regression based on a log-normal distribution with four parameters, while polynomial regression based on linear distribution with two parameters was performed on terrestrial orchids. Differences in species richness of orchids among elevational zones were tested using one-way analysis of variance (ANOVA). Non-metric multi-dimension scaling (NMDS) was used to visualize community composition and potential drivers of orchids. Data were organized into a segment by species matrix and a segment by environmental factors (Elevation, Slope, Tree cover, Shrub cover and Herb cover) matrix, with cells filled with the frequency of each species. The quality of the NMDS result was evaluated using the stress coefficient, with < 0.2 corresponding to a usable biplot ordination plot, < 0.1 corresponding to a good ordination, and < 0.05 corresponding to an excellent representation (Clarke, 1993). Considering the habitat of different life forms of orchids is totally different from each other, the NMDS ordination of the whole data set clustered species into two distinct groups, including epiphytic and terrestrial orchids. The correlation between the species composition of orchids and environmental factors was computed using the envfit function in the 'vegan' package.

A matrix describing the interactions of the entire surveyed site was constructed, with epiphytic orchids in rows and their host trees in columns. A value in the cell represented the number of individuals of epiphytic orchids on the host species. Interspecific interactions between epiphytic orchids and their host were visualized as networks, in which species and interactions were depicted as nodes and pair links, respectively. The following four characteristics of network structure were calculated: (i) Connectance, to measure network complexity (number of observed interactions divided by the total possible interactions) (Dunne et al., 2002; Tusiime et al., 2007). (ii) Nestedness, assessed with the NODF (nestedness metric based on overlap and decreasing fill) varying from 0 to 100 (Almeida-Neto et al., 2008). (iii) Modularity, calculated by Q index to measure the strength of the division ranging from 0 (no particular structure) to 1 (completely modular network) (Beckett, 2016). (iv) Specialization, measured by frequency-based index H_2' (standardized two-dimensional Shannon entropy); with $0 \le H_2' \le 1$, i.e., 0 for no specialization and 1 for perfect specialization (Bluethgen et al., 2006). Finally, we compared these values with those obtained from the null model to assess the significance of observed data. All metrics were obtained using the 'bipartite' package (Dormann, 2011) and the 'igraph' package (Csardi and Nepusz, 2006). The analyses were performed in R statistical software version 4.1.1 (R Core Team, 2021).

3. Results

3.1. Species composition and richness patterns of orchids and the drivers

Overall, we recorded 94 species belonging to 39 genera (Supplementary Table 1), including 58 epiphytic orchids and 36 terrestrial orchids. Among these orchids, *Coelogyne occultata*, *Trichotosia dasyphylla*, *Nervilia crociformis*, *Nervilia mackinnonii*, *Dendrobium longicornu*, *Eulophia graminea*, *Bulbophyllum reptans*, and *Peristylus goodyeroides* were the dominant orchid species of the study region. *Dendrobium* (12 species) and *Bulbophyllum* (7 species) were the two epiphytic genera with a higher number of species. The survey also documented two endemic epiphytic orchid species in Myanmar, i.e., *Coelogyne victoria-reginae* and *Liparis casseabria*.

A significant difference in orchid richness occurred at different elevational zones for both epiphytic and terrestrial groups (Supplementary Table 2). The epiphytic species exhibited a significant peak regression with the elevation gradient (P < 0.001), while the terrestrial orchids revealed a monotone-decreasing linear regression with the elevation gradient (P < 0.001). The species richness of epiphytic orchids presented a "hump-shaped" pattern which increased from the lowland plain at the lowest elevation (600 m) to a peak value (humid forest) at ca. 2200 m, then decreased towards the higher elevations (Fig. 2).

The two main axes of variation in species composition of the whole study region were associated with elevation, slope, aspect, tree cover, shrub cover and herb cover (Table 1). Both elevation and slope had significant effects on the composition of epiphytic and terrestrial orchids, and herb coverage significantly affected the composition of terrestrial orchids (Fig. 3).

3.2. Interaction network analysis of epiphytic orchids and their hosts

The interaction network showed 17,370 connections between host trees (23 species) and epiphytic orchids (58 species) (Fig. 4, Supplementary Table 3). Based on network analysis, the orchid-host trees assemblage exhibited a non-random pattern (Table 2). Each epiphytic orchid species was on average attached to two host species (generality = 2.0029, P < 0.001), and an average of two orchid species interacted with each host species (vulnerability = 2.2095, P < 0.001). The network displayed low connectance (C = 0.1432), and significant nestedness (NODF = 30.3929) with high modularity (Q = 0.3490) and specialization (H_2' = 0.8272) (Table 2, Supplementary Figure 1). The most abundant orchid species (*Coelogyne occultata*) were represented by a total of 10,804 connections (62.2% of the total) with host species *Quercus semecarpifolia* and *Rhododendron arboreum*. However, 20 epiphytic orchids only interacted with their specific host (i.e., host specificity) and together contributed only 1.7% of the total connections. The generalist orchid species *Dendrobium longicornu* colonized 16 host species (69.6% of the species), while the host species, *Lithocarpus variolosus,* was occupied by 25 epiphytic orchid species, followed by *Rhododendron arboreum* (20 orchid species) and *Lyonia ovalifolia* (18 orchid species).

4. Discussion

4.1. Orchids diversity and distribution pattern

This study represents the first systematic analysis of the diversity and distribution patterns of orchids on Mt. Victoria, Myanmar. It documents a high diversity of orchids and a hump-shaped richness pattern of epiphytic orchids along an elevation gradient in the Natma Taung National Park. In a recent assessment, 227 orchid species have been recorded in the whole Chin State (Aung et al., 2020), and a total of 94 orchid species were recorded in this investigation, accounting for 41.4% of all orchid species in Chin State. We speculated that more orchid species exist on Mt. Victoria compared to previous records, considering that our data collection was based on ground surveys while inevitably neglecting some epiphytic orchids anchored in the upper canopy (Shen et al., 2022). This bottom-up approach may underestimate the number of epiphytic orchid species, although long ladders and binoculars were used to record as many epiphytic orchid species as possible. Future research should expand this data set to include orchids from upper canopies using method such as single rope technique.

According to the field observation, the two endemic species, *Coelogyne victoria-reginae* and *Liparis casseabria* detected are likely adapted to the local environmental conditions. These unique plants, which are part of Myanmar's orchid species pool, provide the raw material for both conservation efforts and scientific experiments (Štípková and Kindlmann, 2021). Moreover, new orchid species have been discovered in the study area (Wang et al., 2022; Yukawa et al., 2010; Zhou et al., 2018), implying the richness of orchids on Mt.
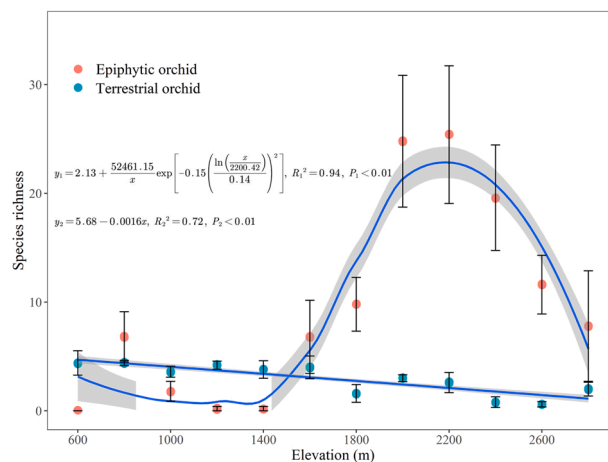

Fig. 2. Species richness patterns of orchids along an elevation gradient of Mt. Victoria, Myanmar. Note: The gray ribbon represents the standard error, and the interval is not generated as a result of the extremely low standard errors between 800 and 1400 m (see Supplementary Table 2).

Table 1

Factors influencing species composition and distribution patterns along an elevation gradient ranging from 600 to 3000 m with 200 m elevation interval of Mt. Victoria.

Life forms	Factor	NMDS1	NMDS2	R^2	P
Epiphytic orchid	Elevation	0.88348	0.46846	0.7966	**0.001**
	Slope	0.59134	0.80642	0.2744	**0.006**
	Aspect	-1.00000	0.00038	0.0632	0.383
	Tree cover	0.99906	0.04331	0.0304	0.609
	Shrub cover	-0.05463	0.99851	0.111	0.144
Terrestrial orchid	Elevation	0.93874	0.34464	0.7623	**0.001**
	Slope	0.61186	0.79097	0.1829	**0.010**
	Aspect	-0.89142	0.45317	0.0541	0.270
	Tree cover	-0.06068	0.99816	0.1408	0.478
	Shrub cover	-0.91525	0.40288	0.0116	0.762
	Herb cover	0.88810	-0.45965	0.1935	**0.005**

Note: Permutation = 999, with 999 random permutations to test the significance of each environmental variable.
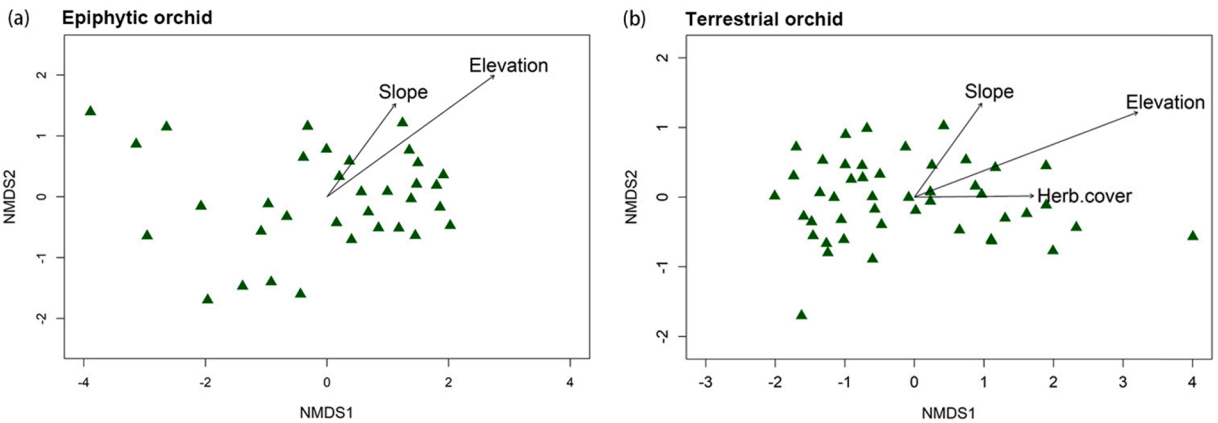

Fig. 3. NMDS ordinations of orchid sample plots along an elevation gradient of Mt. Victoria, Myanmar. Note: Sample plots of orchids are shown in green triangles. (a) NMDS ordination (stress = 0.0816) of sample plots of epiphytic orchid. (b) NMDS ordination (stress = 0.0869) of sample plots of terrestrial orchids. The arrows represent the remaining environment variables (elevation, tree cover, shrub cover, herb cover, canopy height and slope) after the Spearman correlation analysis.
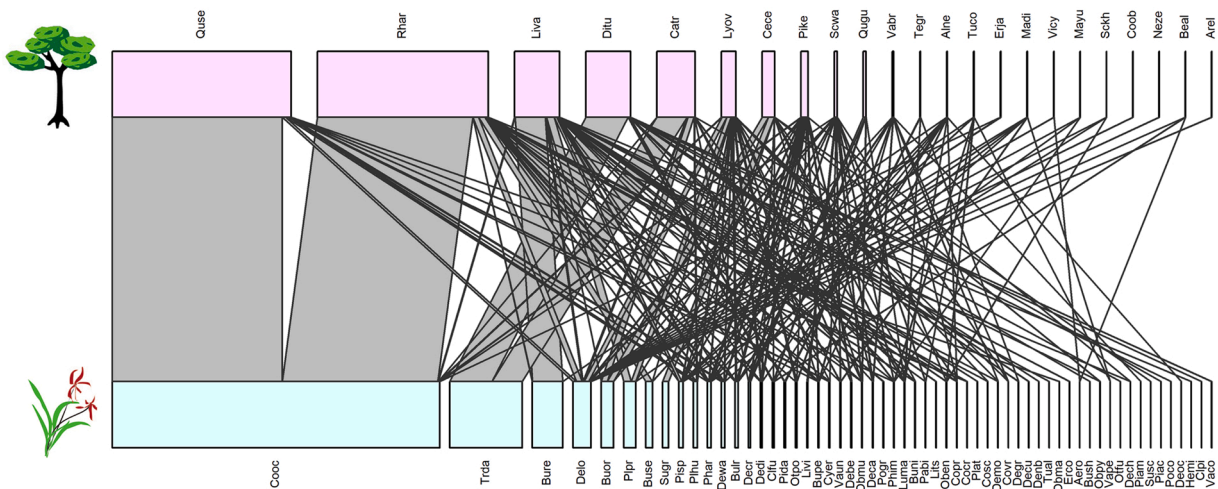

Fig. 4. The network between epiphytic orchids and their hosts of Mt. Victoria, Myanmar. Note: The purple rectangles at the top represent epiphytic orchids, while the blue rectangles at the bottom are hosts. The width of a rectangle represents the relative frequency of interaction among species. The name of each rectangle is a code of epiphytic orchids and hosts (see detail in Supplementary Table 3).

Table 2

Species- and network-level indices of the commensal network between epiphytic orchids and their hosts of Mt. Victoria, Myanmar.

Species-level index		Network-level index	
Number of tree species	23	Connectance (C)	0.1432 (P < 0.001)
Number of tree individuals	575	Nestedness (NODF)	30.3929 (P < 0.001)
Number of orchid species	58	Modularity (Q)	0.3490 (P < 0.001)
Number of links	17,370	Generality	2.0029 (P < 0.001)
		Vulnerability	2.2095 (P < 0.001)
		Specialisation (H_2')	0.8272 (P < 0.001)
		Number of modules	5

Note: The statistical significance of observed network metrics was tested using the null model that generated 1000 random networks in which the number of nodes and interactions are given by the observed networks.

Victoria and further systematic and detailed investigation is needed.

Our results also show that the species richness of epiphytic orchids on Mt. Victoria presented an obvious "hump-shaped" distribution pattern, consistent with several related studies (e.g., Acharya et al., 2011; Zhang et al., 2015a). According to the results of NMDS analysis, elevation significantly influenced the distribution pattern of orchids (Table 1, Fig. 3). Elevation was the most crucial factor affecting the diversity and distribution patterns of orchids, perhaps because several environmental factors changed with elevation, such as average temperature, water vapor pressure, precipitation. (Korner, 2007; Ye et al., 2021). Air humidity is the most important environmental factor determining epiphyte diversity from ecophysiological respect (Kuper et al., 2004; Taylor and Burns, 2016; Quiel and Zotz, 2021). Highest air humidity usually occurs at mid-elevations, with a dramatic decline in the lowlands, and a moderate decline at high elevations (Kromer et al., 2005; Salas-Morales et al., 2015; Song et al., 2015). Normally, epiphyte diversity is relatively high in the elevation range of 1000–2000 m (Acharya et al., 2011; Zhang et al., 2015a). However, an abrupt low diversity of epiphytic orchids occurred in the elevation range of 1000–1400 m (Fig. 2), which might be caused by the presence of anthropogenic activity in the surrounding forests, in the form of timber, food, folk medicine, farming, household goods, *etc*. Following repeated clearance from shifting cultivation, natural forests in this region largely give way to severely degraded secondary forests (MBG, 2022), resulting in unsuitable habitats for epiphytic orchids.

Species richness of terrestrial orchids, however, exhibited a monotonous decrease trend along with the increasing elevations (Jacquemyn et al., 2005; Timsina et al., 2021), although a hump-shaped relationship occurred along the Himalayan elevation gradient (Acharya et al., 2011). The decline of orchid diversity towards high elevations has been attributed to harsher climatic conditions, narrower habitat areas, higher propagule pressures *etc*. (Jacquemyn et al., 2005; Timsina et al., 2021). Moreover, relatively low temperatures in high-elevation regions can retard soil formation and plant growth, while the harsh conditions including intense solar radiation and large diurnal temperature variations between day and night exceed the limits of most species' tolerance (Qu et al., 2012). Our results further show that herb coverage was positively correlated with elevation, which may enhance the competition for light, space and nutrients between terrestrial orchids and other herbage. Epiphytic orchids, however, escape from the ground and grow on trees, herb coverage, thus not affecting their distributions. Slope is another key environmental factor that influenced the elevation richness patterns of terrestrial orchids, which not only affects the stability of geomorphology but also soil conditions (Chen et al., 2006; Shen and Fang, 2001). Soil water and nutrients are lower and soil surface texture is coarser at upper slope positions (Takahashi and Murayama, 2014; Halbritter et al., 2018).

The elevation richness pattern was significantly different between the epiphytic and the terrestrial orchids, because orchids of various life forms evolved and survived in totally heterogeneous habitats, and their growth and reproduction can be controlled by different environmental factors. Epiphytes evolve high diversity in the complex forest canopies and depend on their host trees for survival (Hu et al., 2022a; Silva et al., 2010; Zotz, 2013). As epiphytes grow in the air, they rely more on the atmosphere for water and nutrients and are very sensitive to human disturbances (e.g., deforestation, illegal collection, overharvesting) and global changes (e.g., global warming, drought, and nitrogen deposition) (Song et al., 2011, 2012; Shi et al., 2017). However, the terrestrial counterparts growing on the forest floor mainly relied on soil matrix for water and nutrient resources, and were prone to be affected by either microenvironment changes in the understory (e.g., herb coverage, slope) or macroclimate change in the geographical areas (e.g., latitude, elevation) (Qu et al., 2012).

4.2. Characteristics of the epiphytic orchid-host network

A total of 58 epiphytic orchid species were recorded on 23 host species, accounting for 61.7% of the total orchids. At a community-wide level, the epiphytic orchid-host network exhibited a significantly nested and modular structure with a low level of connectance and a high level of specialization. Consistent with many other commensal networks between epiphytes and their hosts (Sayago et al., 2013; Ceballos et al., 2016; Francisco et al., 2018; Zotarelli et al., 2019), the low connectance indicates that the majority of epiphytic orchids tend to grow on a few host species. Furthermore, differences in the abundance of host species contribute to nested patterns of epiphytic orchid-host trees network (Piazzon et al., 2011). A significant nestedness in this study was similar to the result of Cortes-Anzures et al. (2020), which reported that the most abundant trees tend to host the majority of epiphytic orchids. In ecosystems, networks with nested structures maintain biodiversity and improve network robustness by reducing interspecific competition and lowering the extinction risk of specialized species (Bascompte et al., 2003; Burgos et al., 2007; Song et al., 2017).

Unexpectedly, compared with previous analyses of 12 networks between vascular epiphytes and hosts in tropical and subtropical

forests, the current result shows a higher value of modularity (Naranjo et al., 2019). The modular structure suggests that species within modules are more linked to each other than to species among modules (Naranjo et al., 2019), hence, high modularity can enhance network stability and buffer the effects of secondary extinctions by retaining the influence of perturbations within a single module and minimizing the influence on other modules (Stouffer and Bascompte, 2011). In addition, the epiphyte-orchid network in this study was more specialized than other epiphyte-host networks (0.084 in Ceballos et al., 2016; 0.30 in Francisco et al., 2018; 0.24 in Sayago et al., 2013; 0.50 in Zhao et al., 2015). High specialization is common in antagonistic relationships because of the preference of specialists for habitat (Ravigne et al., 2009; Wagner et al., 2015), while the low level of specialization appears as a common property of epiphyte-host networks. For epiphytic orchid-host networks, however, the relatively high specialization results from the special environmental requirements of orchid growth, which can only be provided by few host species. Here, more than one-third of epiphyte orchid species grew exclusively on the specific host, and the intensive host preferences of these epiphytic orchids reinforced the degree of network specialization.

Interactions in the network were heterogeneously distributed among hosts at a species level. As generalists, host species such as *Lithocarpus variolosus*, *Rhododendron arboretum*, and *Lyonia ovalifolia* mainly hosted epiphytic orchid species and maintained most of the interactions in the network, indicating that several hosts were more connected than our expectation. Indicative characteristics of hosts such as size, abundance, architecture and physicochemical property, may explain the heterogeneous distribution of epiphytes (Wolf, 1994; Wester et al., 2011; Timsina et al., 2021). Our previous research indicated that tree size is the most important factor (Shen et al., 2022). In fact, large host trees (with a big diameter at breast height) usually played an important role in the studied commensal orchid-host trees network structure, because larger trees provide greater surface area exposed to receive epiphytes, more variable microhabitat, better bark quality, and greater exposure to humidity and light (Francisco et al., 2018; Shen et al., 2022; Zotarelli et al., 2019). In addition, host abundance also affects the network structure. In this study, *L. variolosus*, *R. arboretum* and *L. ovalifolia*, as the most common species among sampled trees, hosted most of the epiphytic orchid species and maintained most of the interactions in the network as suggested by previous studies in other areas (Hu et al., 2021; Calatayud et al., 2017). Additionally, physiological characteristics, such as allelopathic compounds, the lifespan of branches, and the deciduousness of host trees, may also limit the establishment of epiphytes to various degrees (Cortes-Anzures et al., 2020). Hosts carrying more epiphytic species play an important role in supporting the robustness and diversity of the network (Gonzalez et al., 2010). Consequently, the epiphytic orchids from this study indicate obvious host specificity, instead of a random distribution pattern in the studied network.

4.3. Conservation implications for orchids

The results of this study have three significant implications for orchid conservation. Firstly, the two detected endemic species, *C. victoria-reginae* and *L. casseabria,* should be seriously taken into consideration since endemic species are obviously of special importance in plant conservation and no large distribution area exists for their survival (Kurzweil et al., 2021). As a result, without protection, endemics in hotspots are likely to face serious threats or even vanish in the near future (Fay, 2018). As endemic species, *C. victoria-reginae* and *L. casseabria* were discovered in a relatively narrow area. Consequently, the most important measure to conserve these endemic species is to protect the suitable habitat, i.e., the large-sized host trees and the unspoiled forests where they can survive.

Secondly, low species richness of total orchid species had been detected in low-elevation areas, which strongly coincided with the presence of living area on Mt. Victoria (< 1400 m in this study). Thus, on the one hand, population aggregation means an increase in the illegal collection of orchids, especially beautiful, rare epiphytic orchids in the nearby forests, which could directly reduce the richness of epiphytic orchids (Ye et al., 2021) and hinder the in situ conservation of orchids (Fay, 2018; Swarts and Dixon, 2009b; Wraith and Pickering, 2019). On the other hand, we found frequent human activities such as logging and land use change in low elevations during our field expedition, which induced extensive forest degradation or destruction. High-intensity deforestation would inevitably affect the commensal interaction of orchid-host trees, leading to a dramatic decline in the diversity of epiphytic orchid species. Accordingly, ecological restoration of degraded forests and ecological tourism should be encouraged in the lowland rural area to achieve harmony between economic development and ecological protection towards the sustainable development of tropical regions.

Thirdly, some host species (e.g., *L. variolosus*, *R. arboretum* and *L. ovalifolia*) provided suitable habitats for many epiphytic orchids species and hold several interactions in the network. Similarly, in a study of 105 epiphytic orchid species, ca. 40% are associated with less than five host tree species (Silva et al., 2010). The loss of these important host trees would lead to a dramatic decline in orchid diversity. Thus, forest management measures such as selective logging should omit these tree species. Moreover, 20 epiphytic orchids, including *S. grandiflora, L. viridiflora, P. grandiflora and L. tsii*, were only attached to specific host species probably due to the selection of host characteristics. Considering that these epiphytic orchids are at risk of extinction once the specific tree species are lost (Colles et al., 2009; Hu et al., 2021), the high level of host preference does not conduct to the stability of the network, calling for special protection of these specific hosts. On the contrary, *Dendrobium longicornu*, as a generalist, can likely attach to most tree species. This species can maintain long-term stable existence in the network by regulating interactions with other hosts when one host disappears (Vizentin-Bugoni et al., 2020), although it was weakly connected to each host.

5. Conclusions

A total of 94 orchid species were recorded along an elevation gradient ranging from 600 to 3000 m on Mt. Victoria, comprising 58 epiphytic and 36 terrestrial orchids. Species richness of epiphytic orchids exhibited a hump-shaped pattern (peaked at ca. 2200 m), while terrestrial orchids showed a monotonic decreasing trend with increasing elevations. The network between epiphytic orchids and

their hosts exhibited low connectance and significant nestedness, with high levels of modularity and specialization. Effective forest management and conservation in these areas should focus on tree species such as *Lithocarpus variolosus*, *Rhododendron arboretum* and *Lyonia ovalifolia*, because their loss may lead to a sharp decline in epiphytic orchid diversity. To comprehend the mechanisms influencing the distribution patterns of orchids, future studies should take into account more microclimate data. Additional research is also required to identify the mechanisms underlying the biases in orchid distribution towards particular host tree species.

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CRediT authorship contribution statement

QL, LS, and YYA conceived the research idea; QL led the data collection; YYA, LS, QL, and HXH were involved in statistical analyses and interpretations; and YYA, LS, and QL drafted the manuscript with input from other co-authors.

Declaration of Competing Interest

The authors declare that there are no known competing financial interests or personal relationships that will influence the current work reported in this paper.

Data Availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02408.

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