

Diversity and species of vascular epiphytes in Tingana, the highest flooded forest in Peru

Yakov Quinteros-Gómez^{1,4}, Betty Millán^{1,2}, Doris Gómez-Ticerán³, Franco Angeles-Alvarez¹, Abel Salinas-Inga¹, Jehoshua Macedo-Bedoya¹, Sergio Olórtegui Chamolí⁵, Ángel Balbuena-Serrano⁶

¹ Faculty of Biological Sciences, ² Natural History Museum (Department of Gymnosperms and Monocotyledons) and

³ Faculty of Mathematical Sciences, National University of San Marcos, Lima, Peru

⁴ Graduate School, Norbert Wiener Private University, Lima, Peru

⁵ CIFFA PERU, Moyobamba, San Martin, Peru

⁶ National Technological Institute of Mexico - Technological Institute of Toluca, Metepec, Mexico State, Mexico

SUMMARY

A variety of ecosystems can be found on the eastern flank of the Peruvian Andean-Amazonian piedmont. Amongst these, seasonally flooded forests (which include many peatlands) have attracted scientific attention because of the ecosystem services they provide. Our research was conducted in the Tingana flooded forests situated in the Alto Mayo Valley, San Martin (Peru). The canopies and branches of phorophytes (epiphyte-bearing plants) located within fourteen 20×20 m plots at two study sites were accessed using climbing equipment, and 107 epiphytic species were recorded. The epiphyte genera with the highest diversity were *Epidendrum* (15 species), *Asplenium* (7 species), *Anthurium* (6 species) and *Peperomia* (5 species), and the phorophyte with the highest epiphyte diversity was *Ficus trigona*. The richness estimators (Chao1 and ACE) accounted for >75.3 % of the species present, with Stratum III being the most abundant and diverse. Demographic studies will be needed to comprehend the potential consequences of climate change for the epiphyte communities of flooded forests as they recover from disturbance.

KEY WORDS: Alto Mayo Valley, orchids, phorophyte, strata, climate change

INTRODUCTION

Epiphytic species are important in tropical forests because they represent about 10 % of the ecosystem's diversity, the most abundant families being Orchidaceae, Bromeliaceae and Araceae (de la Rosa-Manzano *et al.* 2019, Taylor *et al.* 2021). They participate in nutrient and water recycling (Bruijnzeel & Veneklaas 1998) and are essential for ecosystem dynamics, providing food and habitats (from ground level to the canopy) for a wide range of organisms including invertebrates, insects, birds and mammals (Barthlott *et al.* 2001, Ceja *et al.* 2008, Gómez-González *et al.* 2017).

On the eastern flank of the Peruvian Andean-Amazonian piedmont we find a great variety of ecosystems including seasonally flooded forests, which are amongst the most diverse as well as the most disturbed by human activities (Alvarez-Montalván *et al.* 2021). Many of them are peatlands. Their diversity is influenced by climatic conditions and geomorphology, as well as by the duration and level of flooding (Casanova & Brock 2000).

Amazonian flooded forests have attracted special attention from the scientific community on account of the ecosystem services they provide (Quinteros-Gómez *et al.* 2021); especially soil formation, primary productivity, carbon sequestration and climate change mitigation (Meister *et al.* 2012, Quinteros-Gómez *et al.* 2023).

Forests that include oligarchic and hyper-dominant species, occurring in subtropical and tropical climates with annual rainfall greater than 1,000 mm, are favourable for the development of vascular epiphytes (Hurtado 2017, Nadkarni & Kohl 2019). The greatest richness of these taxa is found in montane rain and cloud forests (mountain mesophilic forest; Hurtado 2017) between 1,000 and 2,000 m a.s.l. which provide highly favourable conditions in terms of temperature and relative humidity (Krömer *et al.* 2005, Mondragón-Chaparro *et al.* 2006, Ceballos 2023).

The distribution of epiphytes in a plant community is associated with microclimatic conditions (Leimbeck & Balslev 2001), physiological-mechanical factors (Nieder *et al.*

1999), canopy properties (Rojas & Sánchez 2015) and phorophyte-specific characteristics (Granados-Sánchez *et al.* 2003, Jiménez-López *et al.* 2017). In each phorophyte (epiphyte-bearing plant), the formation of different types of substrate for epiphytes occurs through the decomposition of parts of the phorophyte and parts of epiphytes (Jiménez-López *et al.* 2017), with ants being the main agents (Griffiths *et al.* 2018).

To evaluate the presence or absence of epiphytes, phorophytes are typically divided into five vertical zones or strata, taking into account the aerial roots, trunk and crown (Johansson 1974). Differences in the vertical distribution of epiphyte abundance and richness have been observed between host trees and between their respective strata (Álvarez *et al.* 2018) with Strata III and IV being preferred (Mora-Olivo *et al.* 2018). The horizontal distribution of epiphytes also varies among forests, vegetal formations and phorophytes (ter Steege & Cornelissen 1989).

The updated flora of vascular epiphytes for Peru lists 2,462 species belonging to 25 botanical families, of which the most diverse are the Orchidaceae, Bromeliaceae and Piperaceae, with 112, 108 and 96 species, respectively. Indeed, the first two account for 73.4 % of the country's vascular epiphyte richness, with the highest number of endemisms recorded at altitudes of 1,500–2,000 m a.s.l. (Mondragón-Chaparro *et al.* 2024). The most representative phorophyte families are Fabaceae, Moraceae, Rubiaceae and Euphorbiaceae (Hurtado 2017).

The San Martín region hosts 24 % of the country's rice production and 42 % of the region's rice cultivation is concentrated in the Alto Mayo Valley (MIDAGRI 2021), resulting in a constant search for fertile soils which has led to the deforestation of floodplain forests. Epiphyte species respond to forest fragmentation in different ways depending on the intensity of land use (León-Alfaro 2019) and exactly how opening of the canopy affects microclimate and the incidence of light on the plant community beneath (Martínez-Meléndez *et al.* 2008, Plateros-Gastélum *et al.* 2018). The selective extraction of species that are favoured for cultivation as ornamental plants - especially orchids and bromeliads - also seriously affects epiphyte diversity (Francisco-Ventura *et al.* 2018).

There have been few studies on epiphytes in Peru, and even fewer in Andean-Amazonian piedmont localities such as Tingana. The objectives of this research were to determine epiphyte richness and the relationship between phorophyte strata and epiphyte diversity in two floodplain forests in the Alto Mayo Valley. We expected that the results would confirm the hypothesis that greater epiphytic richness is found

in areas with larger trees (better conserved areas) and closer to the river.

METHODS

Study area

The study was carried out between August 2022 and April 2024 in two fragments of different types of flooded forest (*Mauritia flexuosa* swamp forest “aguajal” and *Ficus trigona* swamp forest “renacal”) in the Andean-Amazonic piedmont (eastern slope) within the Alto Mayo Valley, in the Water Association Aguajal Renacal del Alto Mayo (ADECARAM Tingana, ecotourism; 05° 54' 17.9" S, 77° 07' 07.5" W; Figure 1). The climate is humid subtropical with annual mean temperature 22.8 °C and annual precipitation 1,265 mm (PEAM 2004). The soils of the Alto Mayo flooded forest are characterised by peat deposits accumulated since the Quaternary (Alva-Hurtado *et al.* 1992).

Tingana is located in a transition area between the low-lying flooded zone of the central Huallaga and the mountain forests of the eastern Peruvian Andes (Quinteros-Gómez *et al.* 2023). It comprises a series of flood-prone areas rich in biomass and carbon sequestration at an elevation of 850–890 m a.s.l. There is a ubiquitous presence of dominant phorophytes bearing taxonomically and ecologically distinct epiphytic communities. The forest structure is characterised by tall trees and palms that form an emergent canopy which can reach up to 25 m in height. Species from the genera *Mauritia*, *Euterpe*, *Coussapoa*, *Virola*, *Symphonia*, *Ficus*, *Clusia* and *Nectandra* contribute to this emergent layer, with the latter hosting a high diversity and abundance of vascular epiphytes, notably ferns, orchids, bromeliads and Araceae (Quinteros-Gómez *et al.* 2021, 2023).

Selection of study sites

Two study/collection sites (where epiphytes were present) were identified, selecting the largest trees in each case. The *Mauritia flexuosa* swamp forest (Ma) study site was located in open canopy swamp forest dominated by *M. flexuosa* and *Euterpe precatoria*, with palms taller than 20 m. The *Ficus* swamp forest (Fi) site was located adjacent to the Avisado River in forest dominated by *Coussapoa trinervia*, *F. trigona* and *Virola elongata* trees with diameter at breast height (DBH) > 30 cm. Both sites were subject to repeated flooding events caused by the Avisado and Mayo rivers, with flood levels exceeding 3 m during wet seasons (February and April; Börner & Zimmermann 2003).

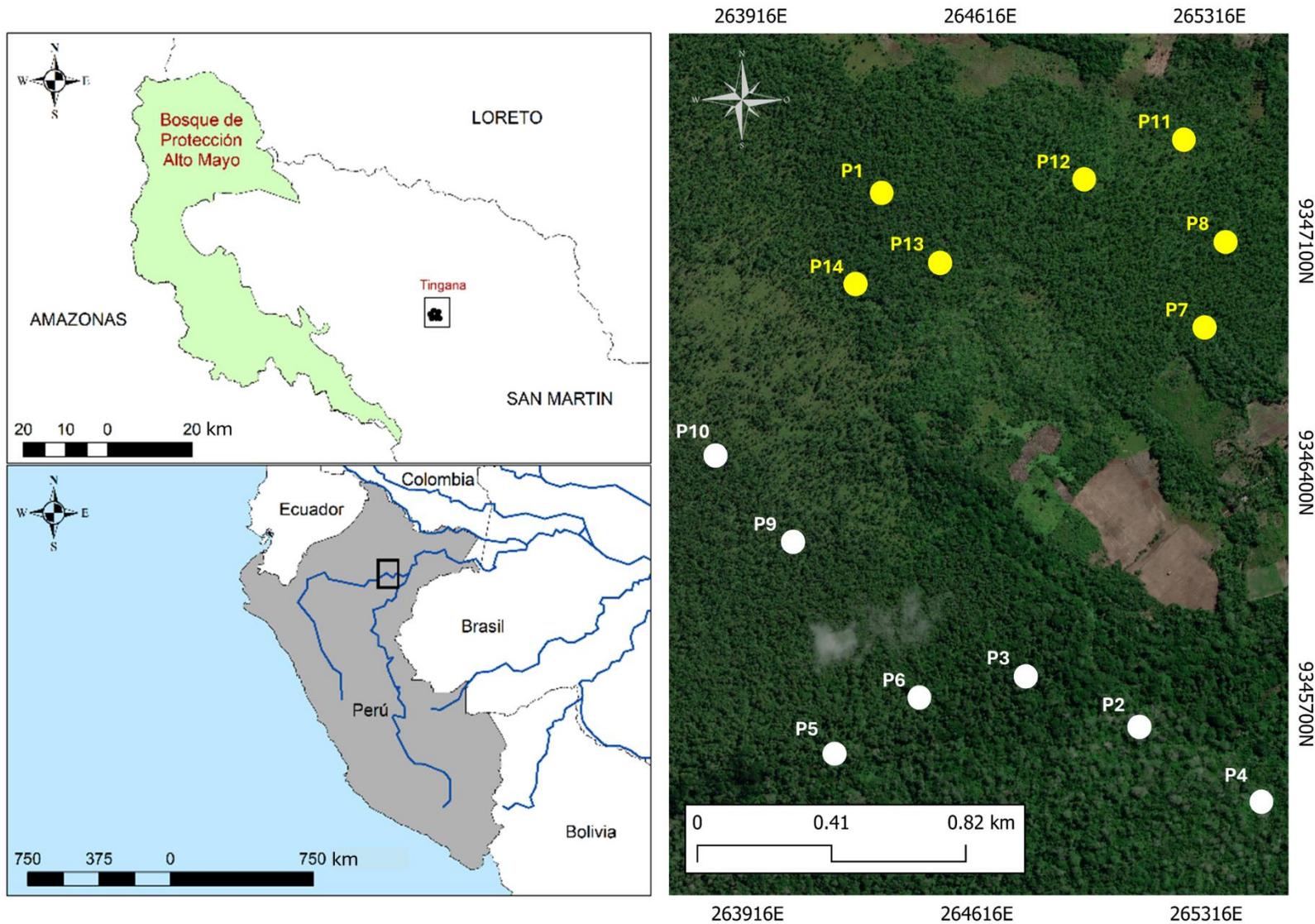


Figure 1. Map of the study area in San Martín region, Peru (left), showing (right) the locations of sampling plots in the Ma (yellow symbols) and Fi (white symbols) study sites.

Within each of the study sites we established seven plots of size 20×20 m, which were at least 100 m distant from one another. We sampled all potential hosts within each plot that met the following criteria:

- i) individual trees with diameter at breast height (DBH) ≥ 30 cm and height ≥ 20 m;
- ii) shrubs with DBH ≥ 5 cm; and
- iii) palms with height ≥ 15 m and DBH ≥ 15 cm.

These criteria were chosen to include only adult individuals, which are associated with increased colonisation by epiphyte species (Gradstein *et al.* 2003). Hosts with branches inclined at more than 45° were excluded for safety reasons (Pos & Slegers 2010).

To access the host canopies and branches, a climbing team used the 'single rope technique' (Anderson *et al.* 2015), which utilises multiple attachment points between climber and rope to reduce the risk of falls (ANSI 2012). The height of each host was estimated using a Suunto clinometer and locations were determined with a GPS Magellan Xplorist 310 (Lamprecht 1990). We recorded all species of vascular epiphytes on shrubs and palms using binoculars (Bushnell PowerView 20 × 50 mm) from different spots on the ground (Malizia 2003, Krömer & Gradstein 2016). Additional observations to help characterise the Tingana epiphytes were made during extensive walking and canoeing in the forest between study sites.

Sampling

We collected data about the abundance and vertical stratification of epiphytes, following Johansson (1974). Johansson's scheme is based on the principal structures of the host, and not on absolute height (Zotz 2007). The specimens for each stratum were collected carefully (not duplicated) and labelled for taxonomic identification purposes. Depending on the epiphyte species, we considered individuals, rosettes or sheets as vegetative units (Heitz *et al.* 1997, García 2012). Botanical nomenclature was based on W3-Tropicos (www.tropicos.org). The conservation status of recorded species was noted according to the Red List criteria, CITES categories (I, II, III) and the Peruvian categorisation of threatened flora species (Decreto Supremo N° 043-2006-AG).

Data analysis

The χ^2 test was performed to determine whether richness and abundance differed significantly between sampling areas. Community studies usually report a high number of rare species that are found only once (singletons) or twice (doubletons),

suggesting that some species in the community may not be represented in the sample and that the sampling effort might be insufficient to register all species (Moreno *et al.* 2011). To avoid this methodological problem, species accumulation curves were constructed to visualise the sampling effort per phorophyte. For this purpose, the ACE and Chao1 estimators (Colwell & Coddington 1994) were determined using the EstimateS 9.1.0 program (Colwell 2013).

We also developed a bipartite graph using the ggplot2 library (Wickham *et al.* 2016) to determine the preferences of epiphyte species across the Tingana phorophytes, with nodes representing epiphyte species (left) and host species (right). The bipartite graph was produced in R version 4.0.4 (R Core Team 2021).

A multivariate clustering analysis was performed using the Bray-Curtis distance (9999 permutations), considering the abundance of epiphyte species per stratum. Abundance data were transformed using Ln (x+1) (Hammer *et al.* 2001). We also performed correlation tests for epiphyte species richness and abundance against phorophyte height, DBH and abundance. Finally, a Mantel test, based on Monte Carlo permutation methods (Chao *et al.* 2005) considering two data distance matrices data and the Jaccard and Sorensen beta diversity indices were calculated using the program XLStat 2023.

RESULTS

Floristic richness and composition

In total, we found 107 species (76 species in plots) belonging to 12 families and 50 genera (see Table A1 and Figure A1 in the Appendix). Of these, 42 species were found in the Ma study site and 77 in the Fi study site. The best represented families were Orchidaceae (55 species), Polypodiaceae (15 species) and Araceae (11 species), which together accounted for 75.7 % of total richness. The most diverse genera were *Epidendrum*, *Asplenium*, *Anthurium* and *Peperomia* with 15, 7, 6 and 5 species respectively.

A total of 71 phorophytes were sampled in the plots, and 2,593 epiphytic individuals were recorded. The plots in Fi had significantly greater richness and abundance of epiphytes than the plots in Ma. Statistically significant differences were found between the sampling areas for richness ($t = -3.24$; $P < 0.01$) and abundance ($t = -3.67$; $P < 0.01$).

On average, the number of phorophytes recorded was 6.8 ± 2.34 per plot (Ma: 7 ± 2 ; Fi: 6.57 ± 2.57). The greatest number of epiphyte species documented in a single plot was 37, in Fi (Plot 3); while the

smallest number was eight, in Ma (Plots 1 and 7). The highest abundance (559 and 704 individuals, respectively) was found in Plots 5 and 6, located in the Avisado riverbed. Plots 2 and 3 (in Fi) had lower abundance but the highest diversity levels (Table 1).

The plots exhibited a high richness of epiphyte species, as revealed by non-parametric value estimators. Our sampling covered approximately 75.3 % and 79 % of the observed cases according to the ACE and Chao1 estimators, respectively. Additionally, the fit curves showed close fit values (ACE $R^2 = 0.6856$, Chao1 $R^2 = 0.8856$, Figure 2). Thirty-one additional species were observed during extensive walking and canoeing in the forest between study sites, indicating they have limited distribution and making them rare species. These species were not recorded within the plots and were not directly related to the sampling design.

Phorophyte specificity

Twelve species were reported as phorophytes in Tingana (Table 2). Plots 1 and 12 identified *Euterpe precatória* and *M. flexuosa* palms, as well as two woody species (*Symphonia globuifera* and *Simira rubescens*), as phorophytes. The epiphyte with the greatest presence on these hosts was *Anguloa uniflora* (Orchidaceae). The remaining plots had only woody species, small trees or shrubs as phorophytes (one plot had no reported epiphytes). *F. trigona* had the highest number of epiphytes, comprising 2,469

individuals and 68 species distributed on 48 phorophytes (Figure 3). It is suggested that *F. trigona* is a generalist host species (typically colonised by a wide variety of epiphytic species). Epiphytic species displayed a preference for Fi.

Vertical stratification

Abundance exceeded 50 individuals for nine epiphyte species. The most abundant species was *Peperomia obtusifolia* with 1,188 individuals, representing 90 % of the records in Stratum III. This stratum accounted for 79.7 % of the epiphyte abundance in Tingana (Figure 4). Three epiphyte species (*Vriesea* sp., *Ludovia integrifolia*, *Epidendrum schizoclinandrium*) were found exclusively in Stratum I, while seven were reported for Stratum II and 13 for Stratum III. Finally, nine exclusive taxa were reported for Stratum IV, while no epiphytes were reported for Stratum V (most exposed to solar radiation),

Strata II and III were the most similar to one another (SI=0.51) and jointly contributed 35.5 % of the total number of epiphytes recorded in the plots. Strata I and IV were the least similar, sharing only six species, namely: *Asplenium auritum* Sw., *Dichaea pendula* (Aubl.) Cogn., *Pecluma plumula* (Humb. & Bonpl. ex Willd.) M.G. Price, *Phlegmariurus linifolius* (L.) B. Øllg., *Prosthechea fragrans* (Sw.) W.E. Higgins and *Sobralia candida* (Poepp. & Endl.) Rchb. f.

Table 1. Epiphyte richness and abundance in Ma and Fi plots.

Site	Plot	Richness	Abundance
Ma	P1	8	58
Fi	P2	27	394
Fi	P3	37	454
Fi	P4	22	168
Fi	P5	11	559
Fi	P6	10	704
Ma	P7	8	19
Ma	P8	16	38
Fi	P9	15	94
Fi	P10	13	95
Ma	P11	1	1
Ma	P12	1	1
Ma	P13	2	8
Ma	P14	0	0

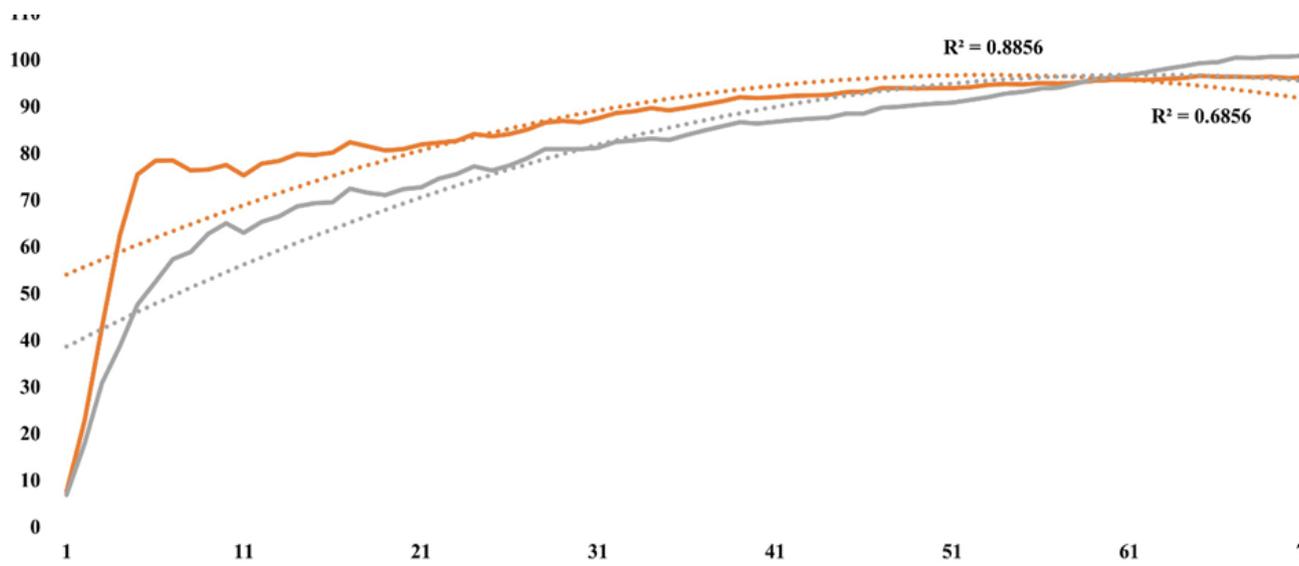


Figure 2. Species accumulation curves ($p < 0.05$) of epiphytes in 71 sampling units (phorophytes) in the flooded forests of Tingana, Peru. The solid lines correspond to the estimators and the dotted lines to the respective polynomial fits. The ACE estimator is shown in orange, and the Chao1 estimator in grey.

Table 2. Phorophytes reported in Tingana, Alto Mayo Valley, Peru.

Scientific Name	Family	Species code
<i>Virola elongata</i> (Benth.) Warb.	Myristicaceae	1
<i>Ficus trigona</i> L.f.	Moraceae	2
<i>Euterpe precatoria</i> Mart.	Arecaceae	3
<i>Simira rubescens</i> (Benth.) Bremek. ex Steyerm.	Rubiaceae	4
<i>Symphonia globulifera</i> L.f.	Clusiaceae	5
<i>Miconia poeppigii</i> Triana	Melastomataceae	6
<i>Trichilia</i> sp.	Meliaceae	7
<i>Oxandra sphaerocarpa</i> R.E. Fr.	Annonaceae	8
<i>Nectandra pulverulenta</i> Nees	Lauraceae	9
<i>Sloanea robusta</i> Uittien	Elaeocarpaceae	10
<i>Mauritia flexuosa</i> L.f.	Arecaceae	11
<i>Hura crepitans</i> L.	Euphorbiaceae	12

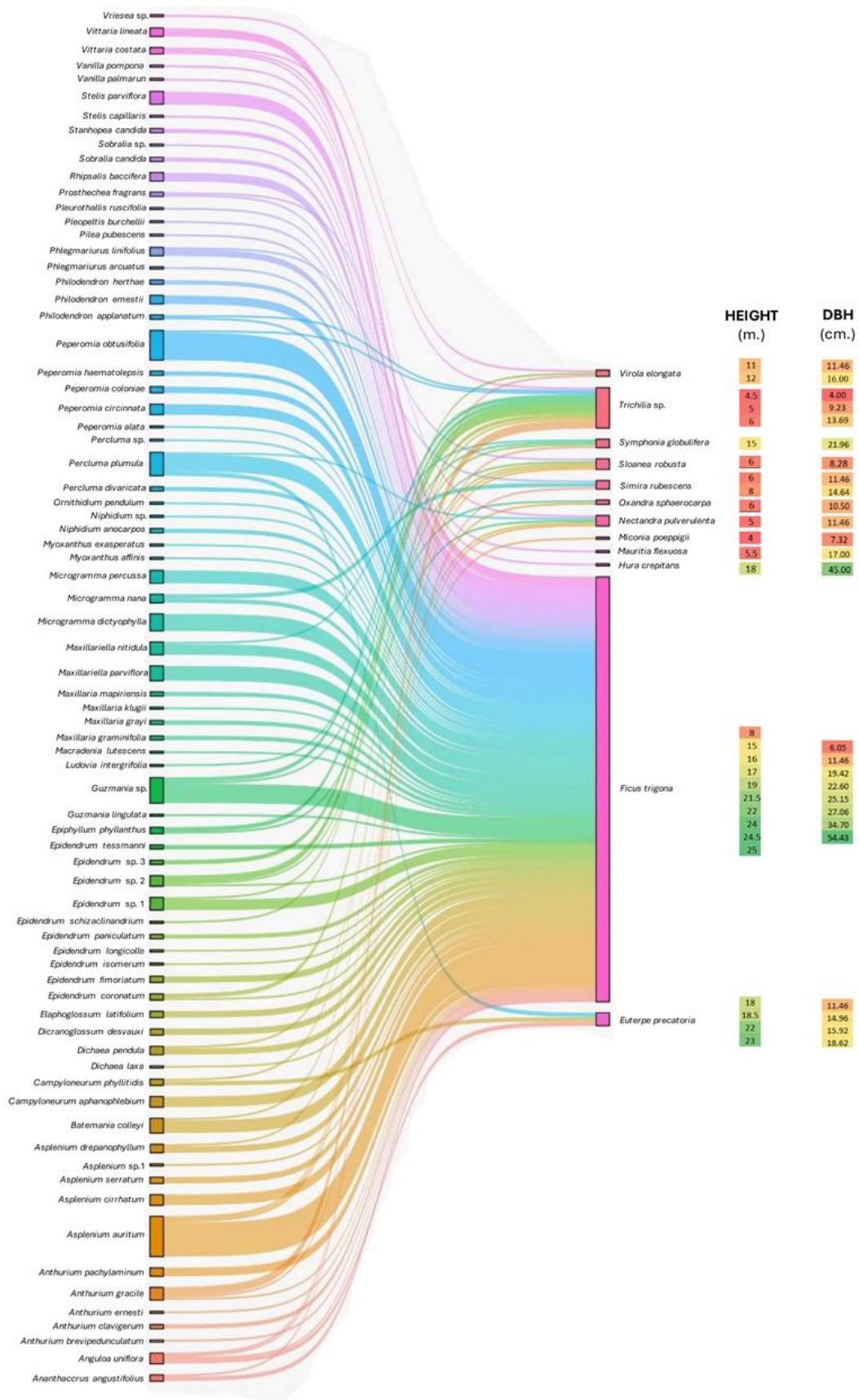


Figure 3. Bipartite network diagram showing the interaction between epiphyte species (left) and phorophytes (right) in Tingana, Alto Mayo Valley, Peru.

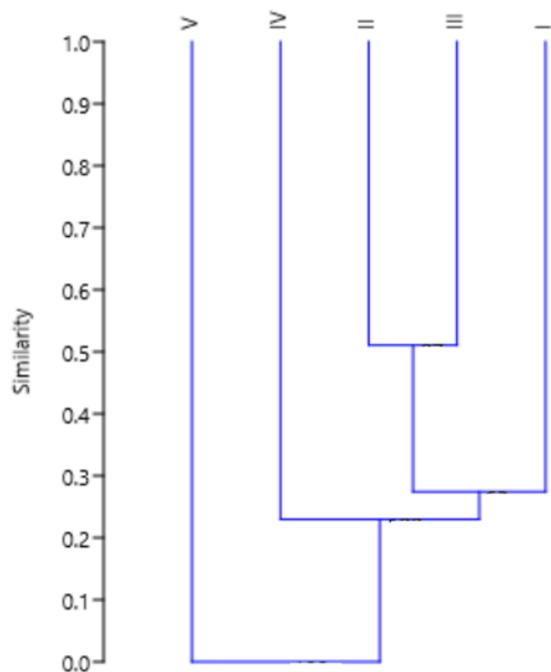


Figure 4. Cluster analysis (UPGMA) showing the similarity relationship, as calculated by the Bray Curtis index, amongst phorophyte strata in Tingana.

Relationship between host variables and epiphyte richness and abundance

The abundance of epiphytes increased with the diameter ($P < 0.05$; $R = 0.44$) and height ($P < 0.05$; $R = 0.45$) of the phorophyte. Richness also showed significant relationships with both phorophyte variables (DBH: $P < 0.05$, $R = 0.65$; height: $P < 0.05$, $R = 0.48$; Figure 5). The Mantel test suggests that

there are no significant correlations relating to geographical distance and floristic similarity between plots (Jaccard index: $R^2 = 0.1283$; $P > 0.001$; Sorensen index: $R^2 = 0.1107$; $P > 0.001$).

DISCUSSION

Epiphyte biodiversity in Tingana

The importance of epiphyte biodiversity in the Tingana forest lies in its ability to diversify microhabitats, which in turn favours the presence of various arthropods (Troya *et al.* 2012, Luna-Castañeda *et al.* 2023). Additionally, in the dynamic ecosystem of the flooded forest, epiphytes play a fundamental role in capturing nutrients and regulating the hydrological cycle, as they do not depend on the soil for their sustenance. Epiphytes can serve as indicators of the ecosystem's health through their sensitivity to atmospheric pollution (Krömer *et al.* 2014).

The Fi forest in Tingana proved to be more diverse than Ma, with 95.2 % of the individuals found concentrated in the seven plots. The onset of the rains allows epiphytic species to increase their abundance rapidly. In fact, during the months of February and March, their splendour is enhanced (branches densely covered with epiphytes), especially on the Renaco trees (*F. trigona*), which reach heights of more than 20 m (Börner & Zimmermann 2003) and form a dense closed canopy (Quinteros-Gómez *et al.* 2021) amongst individuals of the families Moraceae, Myristicaceae, Meliaceae and Arecaceae in the areas surrounding the Avisado riverbed.

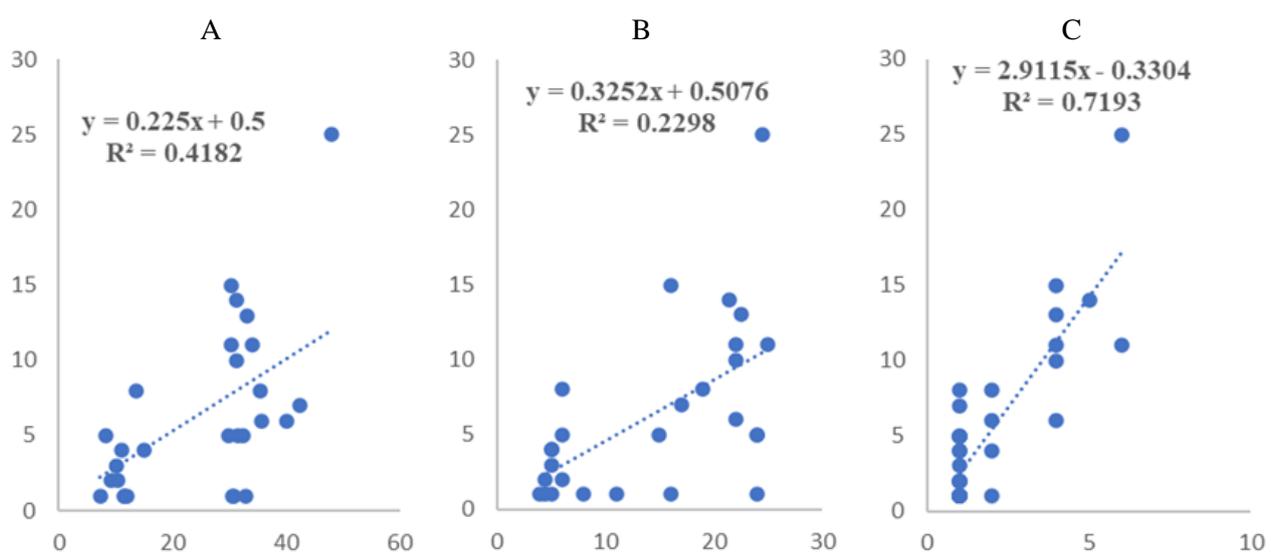


Figure 5. Relationships between phorophyte variables and epiphyte richness ($p < 0.05$). A: DBH vs. richness; B: height vs. richness; C: number of phorophytes vs. richness.

The sampling areas in Tingana are surrounded by extensive territories where the use of space and change of land use to agriculture (rice and coffee) or cattle ranching provide evidence for deterioration of the ecosystem. Disturbances such as deforestation and selective extraction of epiphytes lead to the establishment of vegetation mosaics with their own peculiar dynamics (Gayá 2014). Tingana's seasonally flooded forests are remnants of natural habitat where 107 epiphytic species have become concentrated and are, thus, more diverse than other Amazonian floodplain forests that have been studied. For example, Quaresma *et al.* (2017) reported a total of 96 species in várzea and igapó ecosystems. The Tingana forests also exhibit greater species richness than other Peruvian ecosystems; e.g., 48 species have been reported along an altitudinal gradient (1100–2200 m a.s.l.) in the Huancabamba highlands of Piura (Benavente *et al.* 2020) and 80 species in the montane forests of Madre de Dios (Vera 2017).

The most important families of vascular epiphytes in Tingana were Orchidaceae, Polypodiaceae and Araceae, which coincides with the report of 56 epiphytic orchids from Quaresma *et al.* (2017). Orchidaceae was also the most abundant family in the eastern montane forests of Madre de Dios (76 species; Vera 2017), as well as in the premontane humid forests of Piura and the relict forest of Cajamarca, where 30 and 17 orchid species, respectively, were reported (Benavente *et al.* 2020, Juárez *et al.* 2005).

Four species: *Epiphyllum phyllanthus* (L.) Haw., *Rhipsalis baccifera* (Sol.) Stearn, *Vanilla odorata* C. Presl. and *Vanilla pompona* subsp. *gandiflora* (Lindl.) Soto Arenas were found on the Red List. Fifty-four orchids were found in CITES Appendix II and only one species, namely *Phragmipedium warscewiczii* (Rehb. f.) Christenson in Appendix I. Four of the orchid species recorded (*Chaubardia klugii* (C. Schweinf.) Garay, *Gongora atropurpurea* Hook., *Masdevallia weberbaueri* Schltr. and *Stanhopea candida* Barb. Rodr.) were listed as Vulnerable according to DS N° 043-2006-AG.

The Chao1 and ACE indices confirmed that the sampling effort applied in Tingana was sufficient, confirming over 75.3 % of estimated species in the plots. We consider that the method of climbing into the canopies and all upper parts of the hosts was very important for this result, because it improved the accuracy of recording (Krömer *et al.* 2020).

Phorophyte preference

The richness and abundance of epiphytes was biased towards one tree species (*F. trigona*). This allows us to confirm that there is a preference for one

phorophyte (Vergara-Torres *et al.* 2021), since high levels of colonisation could be observed on it. The opposite was the case for palm trees (very abundant in the study area), since *Mauritia flexuosa* and *Socratea exorrhiza* showed low and zero colonisation by epiphytes, while *Euterpe precatoria* proved to be a good host only for some individuals of *Anguloa uniflora*, *Campyloneurum phyllitidis*, *Pecluma plumula*, *Phlegmariurus linifolius*, *Microgramma nana* and *Campyloneurum phyllitidis*. In fact, not all trees seem to be good hosts. A good host has thick, horizontal branches and rough bark covered with lichens and mosses, which begins to crack and decompose, facilitating colonisation by epiphytes (Nadkarni 2000, López-Villalobos *et al.* 2008, Wyse & Burns 2011, Staniaszek-Kik *et al.* 2019). In this sense, *F. trigona* branches are conducive to colonisation (Trejo-Cruz *et al.* 2021), which explains the presence of a great variety of epiphytes on individuals of *F. trigona* in Tingana.

Another important characteristic of *F. trigona* is its ability to strangle other trees. These plants are classified as hemiepiphytes because their initial development takes place epiphytically on other plants before they establish on the ground, branch and develop to their full extent (Niles 2015). The diversity of epiphytes colonising individuals of *F. trigona* in Tingana was similar to that found on other *Ficus* species in Ecuador (Köster *et al.* 2011) and Brazil (Gonçalves & Waechter 2002), where 62 and 77 epiphytic species were reported, respectively. *Ficus* are good indicators because through them it is possible to detect changes in the composition, structure and diversity patterns of epiphytic species (Gonçalves & Waechter 2002); moreover, they contribute to the maintenance of epiphytic diversity (Trejo-Cruz *et al.* 2021) in areas with different levels of anthropic activity.

The genus *Peperomia* was the most abundant (1,388 individuals). This contrasts with a significant number of species (42 % of the total) that reported one (singletons) or two (doubletons) individuals and are therefore considered rare species. The species of the genus *Peperomia* are characterised by being succulent and terrestrial (occasionally epiphytic), with creeping stems and a large number of adventitious roots (Callejas & Betancur 1997). They also have an adaxial tissue that stores a large amount of water and allows them to adapt to xerophytic environments through morphological and physiological adaptations, such as Crassulacean Acid Metabolism (Hietz & Hietz-Seifert 1994). They are also an important group in humid forests, where they are mainly found as epiphytes in the understorey (Krömer *et al.* 2007).

Peperomia obtusifolia was the most abundant species in Tingana. This species has a wide distribution covering Mesoamerican and South American territories, being reported as epiphytic and rupicolous (Vergara-Rodríguez 2013). It can develop in nutrient-poor soils and adapt to different light levels from the understorey (as in Tingana) to areas with indirect light. Indeed, *P. obtusifolia* has the ability to change the morphodistribution of its chloroplasts to adapt to different solar irradiance conditions (Di Benedetto 2004). It also has great plasticity to adapt to a wide variety of habitats from deciduous forests and oak forests to mangroves and tropical rainforests at altitudes ranging from sea level to 1,600 m (Vergara-Rodríguez 2013). *P. obtusifolia* produces small flowers and fruits (berries) that contain many easily dispersed seeds, allowing it to colonise a wide variety of habitats.

Ferns, which are abundant, possess trichomes that perform a crucial function in water absorption and retention. Additionally, they provide protection against herbivores (Granados-Sánchez *et al.* 2008). Another important characteristic of ferns is their ability to survive periods of drought due to their poikilohydric capacity and then to regrow (as resurrection plants; Ceja *et al.* 2008) due to the osmoprotective action of trehalose (Iturriaga *et al.* 2009), which also plays a vital role in different stages of plant growth (Mascorro-Gallardo *et al.* 2005).

Orchid seeds can float for long periods owing to their small size, the morphology of their fruits, and their large internal air spaces. This facilitates long-distance dispersal (Arditti & Ghani 1999).

Vertical stratification

The epiphytes occupied various strata with different levels of solar exposure. Strata II and III of the host showed the greatest richness of epiphytes, while the Orchidaceae family and the genera *Epidendrum*, *Maxillaria* and *Sobralia* were the most diverse genera (Quaresma *et al.* 2017). Both strata were also regarded as the most diverse in Antioquia's montane moist forests and the Caribbean plain's tropical dry forests, both in Colombia (Alzate & Cardona 2000, Mercado-Gómez *et al.* 2023). However, variations in abundance and richness have been observed among hosts of the same community (Álvarez *et al.* 2018), with epiphytic species showing a preference for Strata III, IV and V (Martínez-Melendez *et al.* 2008) whereas Mora-Olivo *et al.* (2018) suggest Strata III and IV are preferred. Both studies confirm that Stratum I has the lowest diversity.

The microclimatic gradient varies depending on characteristics of the host and vertical stratification, resulting in a diverse range of habitats from the

understorey to the emergent canopy (Mendieta-Leiva *et al.* 2020). The preference for Strata II and III is likely to be specific to the forests of Tingana and is linked to the proximity of the river, availability of water resources, and the prevalence of certain hosts (especially *F. trigona*). Therefore, further studies are required to establish distribution patterns and behaviour relating to abiotic variables (Leimbeck & Balslev 2001) and forest cover (Rojas & Sánchez 2015).

In line with our expectations, richness and abundance were correlated with the host variables diameter at breast height (DBH), height, and number of phorophytes. Consistent with the findings of Jiménez-López *et al.* (2017), height exhibited the weakest correlation with richness while DBH and number of phorophytes showed the strongest correlations. Hosts (such as *F. trigona*) with larger DBH and more branches increase the abundance and richness of epiphytes by offering a larger surface area for colonisation (Flores-Palacios & García-Franco 2006, Jiménez-López *et al.* 2017). The host's size and consequently larger surface area, along with its increased longevity, directly enhance the abundance of epiphytes (Woods *et al.* 2015). As a result, the role of such hosts in preserving diversity is significant.

The diversity of epiphytes in the forests lining the Avisado River in Tingana is significant when compared to the number of woody and palm species (DBH > 10 cm) present in these floodplains (52 species; Quinteros-Gómez *et al.* 2023). It is apparent that both the epiphytes and their primary host (*F. trigona*) require attention for conservation purposes, particularly as the host is inhabited by 79 % of the epiphytes found in these flooded forests. This is in addition to the urgent need for conservation of these forests due to the ecosystem services they offer and their significant carbon reserves in the aerial biomass of the vegetation (Quinteros-Gómez *et al.* 2023). It is vital for governments to exercise greater attention and control to prevent forest fragmentation from adversely affecting the diversity of tree communities (Krömer *et al.* 2014). In addition, there is a need for further research on epiphyte communities in flooded forests to comprehend the potential effects of climate change on these populations.

According to Mantel's test, there was no relationship between geographic distance and similarity between plots. It is not possible to conclude that the closest plots were the most floristically similar, indicating that the proximity of plots does not affect the proportion of shared species which is, therefore, not restricted by any limitation on dispersal at the between-plot scale (Benavides *et al.* 2005).

In contrast to findings from other studies (Benavides *et al.* 2011), floristic similarity within each plot did not tend to result in a high Mantel correlation with geographic distance. This indicates that geographic distance and diversity are not confined or restricted to particular regions, implying that communities in closer proximity do not necessarily possess identical traits. This agrees with Duque *et al.* (2002), who discovered that, in the Colombian Amazon, the floristic composition of epiphytic species differs regardless of the distance between plots. Similarly, the research conducted by Leal-Pinedo & Linares-Palomino (2005) also contends that diversity between plots is not influenced by geographic distance.

Selective extraction and over-collection of epiphytes for commercial purposes is a significant factor affecting these communities (Flores-Palacios & Valencia-Díaz 2007). In Tingana, over-exploitation of vanilla beans in the last five years has resulted in a lower density of individuals and a deterioration in pod quality (Quinteros-Gómez *et al.* 2024). Changes in rainfall patterns and longer drought exposure due to global warming (Foster 2001) also affect epiphyte diversity and abundance. Orchids and bromeliads are the primary targets of extraction (for their highly attractive flowers) and have a significant commercial value in local markets and nurseries. In recent times, the surge in demand for vanilla has resulted in targeted extraction of these species for commercial trade and collection of genetic material for vanilla cultivation that has affected the Tingana forests as well. Our proposal is to use already fallen hosts (Krömer *et al.* 2018) for commercial purposes.

Although the Tingana forests are fragmented, their richness suggests good conservation status of these ecosystems, which are recovering from the effects of deforestation, hunting and unsustainable resource extraction prior to establishment of the Tingana conservation concession (Quinteros-Gómez *et al.* 2023). It is essential to carry out demographic studies on key species in order to obtain reliable and representative information in the medium term. This will allow us to determine the extent to which climate change is affecting these communities.

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AUTHOR CONTRIBUTIONS

YQG, BM and DGT conceived and designed the study. YQG, SOC and FAA coordinated the fieldwork. FAA, ASI, JMB and SOC carried out the fieldwork, tree climbing, counting and collection of material. ABS carried out the georeferencing of the plots and the elaboration of maps for the fieldwork and the manuscript. BM, ABS and YQG participated in taxonomic determination. DGT, FAA and ASI prepared the database and performed the statistical analyses. JMB and YQG interpreted the results and wrote the first draft of the manuscript. All authors contributed to the review and approval of the final manuscript.

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Author for correspondence: Dr Yakov Quinteros-Gómez, Facultad de Ciencias Biológicas, Universidad Nacional Mayor de San Marcos (UNMSM), Calle Germán Amezcaga 375, Cercado, Lima, Perú.
Tel: +51 991652330; E-mail: yquinterosg@unmsm.edu.pe



Appendix

Table A1. List of epiphyte families and species recorded in Tingana, Alto Mayo Valley, their associated phorophyte species (see Table 2), abundance per stratum and conservation status. IUCN Categories: EN=Endangered, VU=Vulnerable, LC=Least Concern; superscripts: a=IUCN Red List, b=Peruvian LSA N° 043-2006-AG.

Family	Species	Phorophyte species	Number of phorophytes	Stratum					IUCN Category	CITES Appendix
				I	II	III	IV	V		
Araceae	<i>Anthurium brevipedunculatum</i> Madison	2	1	0	0	0	4	0		
	<i>Anthurium clavigerum</i> Poepp.	2	2	0	0	3	0	0		
	<i>Anthurium ernesti</i> Engl.	2	1	0	7	0	0	0		
	<i>Anthurium gracile</i> (Rudge)	2,6,7,	6	0	1	8	1	0		
	<i>Anthurium kunthii</i> Poepp. *	1	-	0	0	0	0	0		
	<i>Anthurium pachylaminum</i> Croat	2	4	0	24	0	3	0		
	<i>Philodendron applanatum</i> G. M. Barroso	2, 7	2	0	0	2	3	0		
	<i>Philodendron ernestii</i> Engl.	2	4	0	3	3	0	0		
	<i>Philodendron herthae</i> K. Krause	2	2	0	4	0	4	0		
	<i>Philodendron linnaei</i> Kunth *	3	-	0	0	0	0	0		
<i>Philodendron</i> sp.1 *	3	-	0	0	0	0	0		II	
Aspleniaceae	<i>Asplenium auritum</i> Sw.	2, 8, 9, 10	12	13	82	91	4	0		
	<i>Asplenium cirrhatum</i> Rich. ex Willd.	2	5	0	5	21	0	0		
	<i>Asplenium drepanophyllum</i> Kunz	2, 9	4	0	16	2	0	0		
	<i>Asplenium hallii</i> Hook. *	3	-	0	0	0	0	0		
	<i>Asplenium serratum</i> L.	2	3	0	18	14	0	0		
	<i>Asplenium</i> sp.1	2	1	0	0	2	0	0		
	<i>Asplenium sulcatum</i> Lam. *	3	-	0	0	0	0	0		
Bromeliaceae	<i>Guzmania lingulata</i> (L.) Mez	2	1	0	0	3	0	0		
	<i>Guzmania</i> sp.1	2, 7, 8,	12	0	14	35	0	0		
	<i>Guzmania tarapotina</i> Üle *	1	-	0	0	0	0	0		
	<i>Vriesea</i> Lindl.	1	1	6	0	0	0	0		

Family	Species	Phorophyte species	Number of phorophytes	Stratum					IUCN Category	CITES Appendix
				I	II	III	IV	V		
<i>Cactaceae</i>	<i>Epiphyllum phyllanthus</i> (L.) Haw	7, 9	3	0	0	2	1	0	LC ^a	
	<i>Rhipsalis baccifera</i> (Sol.) Stearn	2	4	0	0	3	1	0	LC ^a	
<i>Cyclanthaceae</i>	<i>Ludovia integrifolia</i> (Woodson) Harling	5	1	1	0	0	0	0		
<i>Dryopteridaceae</i>	<i>Elaphoglossum latifolium</i> (Sw.) J. Sm.	2	3	0	7	18	0	0		
<i>Lycopodiaceae</i>	<i>Phlegmariurus arcuatus</i> (B. Øllg.) B. Øllg.	2	1	0	0	0	8	0		
	<i>Phlegmariurus linifolius</i> (L.) B. Øllg.	2, 4	4	1	7	0	4	0		
	<i>Acianthera ciliata</i> (Knowles & Westc.) F. Barros & L.R.S.Guim. *	6	-	0	0	0	0	0		II
	<i>Acianthera</i> sp.1 *	6	-	0	0	0	0	0		II
	<i>Anguloa uniflora</i> Ruiz & Pav.	2, 3, 4, 5	5	27	8	0	0	0		II
	<i>Batemannia colleyi</i> Lindl.	2, 10	6	19	1	13	0	0		II
	<i>Camaridium vestitum</i> (Sw.) Lindl	2	6	0	30	15	7	0		II
	<i>Catasetum saccatum</i> Lindl. *	1	-	0	0	0	0	0		II
	<i>Chaubardia klugii</i> (C. Schweinf.) Garay	2	1	0	2	0	0	0	VU ^b	II
	<i>Coryanthes</i> sp.1 *	6	-	0	0	0	0	0		II
<i>Orchidaceae</i>	<i>Cyrtopodium</i> sp.1	2	2	0	0	12	0	0		II
	<i>Dichaea laxa</i> (Ruiz & Pav.) Poepp. & End	2	1	0	0	0	6	0		II
	<i>Dichaea pendula</i> (Aubl.) Cogn	2, 10	4	2	0	6	6	0		II
	<i>Epidendrum compressum</i> Griseb. *	2	-	0	0	0	0	0		II
	<i>Epidendrum coronatum</i> Ruiz & Pav.	2, 7	3	1	2	1	0	0		II
	<i>Epidendrum fimbriatum</i> Kunth	2	3	4	0	4	0	0		II
	<i>Epidendrum flexuosum</i> G.Mey *	3	-	0	0	0	0	0		II
	<i>Epidendrum isomerum</i> Schltr.	2	1	0	0	1	0	0		II

Family	Species	Phorophyte species	Number of phorophytes	Stratum					IUCN Category	CITES Appendix
				I	II	III	IV	V		
Orchidaceae	<i>Epidendrum longicolle</i> Lindl.	2	1	0	0	6	0	0		II
	<i>Epidendrum paniculatum</i> Ruiz & Pav.	2	2	0	0	2	6	0		II
	<i>Epidendrum piliferum</i> Rchb.f. *	2	-	0	0	0	0	0		II
	<i>Epidendrum</i> sp.1	2, 5	6	2	3	20	0	0		II
	<i>Epidendrum</i> sp.2	2, 7, 10	4	3	1	4	0	0		II
	<i>Epidendrum</i> sp.3	7	1	1	0	2	0	0		II
	<i>Epidendrum</i> sp.4 *	3	-	0	0	0	0	0		II
	<i>Epidendrum splendens</i> Schltr. *	3	-	0	0	0	0	0		II
	<i>Epidendrum schizoclinandrium</i> D.E. Benn. & Christenson	1	1	2	0	0	0	0		II
	<i>Epidendrum tessmannii</i> Mansf	2	2	3	0	1	0	0		II
	<i>Erycina pusilla</i> (L.) N.H.Williams & M.W.Chase *	2	-	0	0	0	0	0		II
	<i>Gongora atropurpurea</i> Hook. *	3	-	0	0	0	0	0	VU ^b	II
	<i>Macradenia lutescens</i> R. Br.	2	1	0	0	1	0	0		II
	<i>Masdevallia weberbaueri</i> Schltr. *	8	-	0	0	0	0	0	VU ^b	II
	<i>Maxillaria aff. ochroleuca</i> Lodd. ex Lindl. *	2	-	0	0	0	0	0		II
	<i>Maxillaria graminifolia</i> (Kunth) Rchb. f.	2	2	0	1	0	3	0		II
	<i>Maxillaria reichenheimiana</i> Endres & Rchb.f. *	9	-	0	0	0	0	0		II
	<i>Miltoniopsis roezlii</i> (Rchb.f.) God.-Leb.	2, 5	6	11	0	41	0	0		II
	<i>Myoxanthus affinis</i> (Lindl.) Luer	2	1	0	3	0	0	0		II
	<i>Myoxanthus exasperatus</i> (Lindl.) Luer	2	1	0	3	0	0	0		II
<i>Ornithidium mapiriensis</i> (Kraenzl.) L.O. Williams	2	2	0	0	2	7	0		II	
<i>Ornithidium pendulum</i> (Poepp. & Endl.) Cogn.	2	1	0	0	0	4	0		II	
<i>Phragmipedium warscewiczii</i> (Rchb.f.) Christenson *	8	-	0	0	0	0	0		I	



Family	Species	Phorophyte species	Number of phorophytes	Stratum					IUCN Category	CITES Appendix
				I	II	III	IV	V		
Orchidaceae	<i>Platystele</i> sp.1 *	6	-	0	0	0	0	0		II
	<i>Pleurothallis ruscifolia</i> (Jacq.) R. Br.	2	1	0	0	0	3	0		II
	<i>Prosthechea fragrans</i> (Sw.) W.E. Higgins	2, 10	2	1	0	0	6	0		II
	<i>Sobralia candida</i> (Poepp. & Endl.) Rchb. f.	2	2	14	8	0	0	0		II
	<i>Sobralia fimbriata</i> Poepp. & Endl. *	11	-	0	0	0	0	0		II
	<i>Sobralia</i> sp.1	2	1	0	0	0	7	0		II
	<i>Stanhopea candida</i> Barb. Rodr.	2	1	0	0	0	6	0	VU ^b	II
	<i>Stelis capillaris</i> Lindl.	2	1	0	0	4	0	0		II
	<i>Stelis parviflora</i> (Ruiz & Pav.) Pers.	2	4	0	46	0	0	0		II
	<i>Stelis</i> sp.1 *	2	-	0	0	0	0	0		II
	<i>Stenia pallida</i> Lindl. *	2	-	0	0	0	0	0		II
	<i>Sudamerlycaste ciliata</i> (Ruiz & Pav.) Archila *	2	-	0	0	0	0	0		II
	<i>Vanilla odorata</i> C.Presl *	11	-	0	0	0	0	0	EN ^a	II
	<i>Vanilla palmarum</i> (Salzm. ex Lindl) Lind.	11	1	0	1	0	0	0		II
<i>Vanilla pompona</i> subsp. <i>grandiflora</i> (Lindl.) Soto Arenas	11, 12	1	0	1	0	0	0	EN ^a	II	
<i>Xylobium variegatum</i> (Ruiz & Pav.) Garay & Dunst. *	3	-	0	0	0	0	0		II	
Piperaceae	<i>Peperomia alata</i> Ruiz & Pav.	2	1	0	0	3	0	0		
	<i>Peperomia circinnata</i> Link	2	5	0	18	69	3	0		
	<i>Peperomia coloniae</i> Trel.	2	3	0	47	43	0	0		
	<i>Peperomia haematolepis</i> Trel.	2	2	0	9	8	0	0		
	<i>Peperomia obtusifolia</i> (L.) A. Dietr.	2, 7	14	0	120	1067	1	0		

Family	Species	Phorophyte species	Number of phorophytes	Stratum					IUCN Category	CITES Appendix
				I	II	III	IV	V		
	<i>Campyloneurum aphanophlebium</i> (Kunze) T. Moore	2	4	0	26	27	0	0		
	<i>Campyloneurum nitidissimum</i> (Mett.) Ching *	2	-	0	0	0	0	0		
	<i>Campyloneurum phyllitidis</i> (L.) C. Presl	3, 7	3	5	0	3	0	0		
	<i>Dicranoglossum desvauxii</i> (Klotzsch) Proctor	2	3	0	7	1	0	0		
	<i>Microgramma dictyophylla</i> (Kunze ex Mett.) de la Sota	2	8	0	28	17	0	0		
	<i>Microgramma nana</i> (Liebm.) T.E. Almeida	2, 4	4	10	6	0	0	0		
	<i>Microgramma percussa</i> (Cav.) de la Sota	2	2	0	0	75	0	0		
<i>Polypodiaceae</i>	<i>Microgramma</i> sp.1 *	2	-	0	0	0	0	0		
	<i>Niphidium anocarpos</i> (Kunze) Lellinger	2	2	0	0	6	0	0		
	<i>Niphidium</i> sp.1	2	1	0	0	6	0	0		
	<i>Pecluma divaricata</i> (E. Fourn.) Mickel & Beitel	2	2	0	3	0	7	0		
	<i>Pecluma plumula</i> (Humb. & Bonpl. ex Willd.) M.G. Price	2, 3, 9,	11	5	6	58	6	0		
	<i>Pecluma</i> sp.1	2	1	0	0	2	0	0		
	<i>Pleopeltis burchellii</i> (Baker) Hickey & Sprunt ex A.R. Sm.	2	1	0	0	0	4	0		
	<i>Serpocaulon caceresii</i> (Sodirol) A.R. Sm. *	2	-	0	0	0	0	0		
	<i>Ananthacorus angustifolius</i> (Sw.) Underw. & Maxon	1, 2	3	1	14	0	0	0		
<i>Pteridaceae</i>	<i>Vittaria costata</i> Kunze	2, 7, 9,	3	0	0	3	16	0		
	<i>Vittaria lineata</i> (L.) Sm.	2	4	0	5	2	0	0		
<i>Urticaceae</i>	<i>Pilea pubescens</i> Liebm.	2	1	0	0	0	11	0		

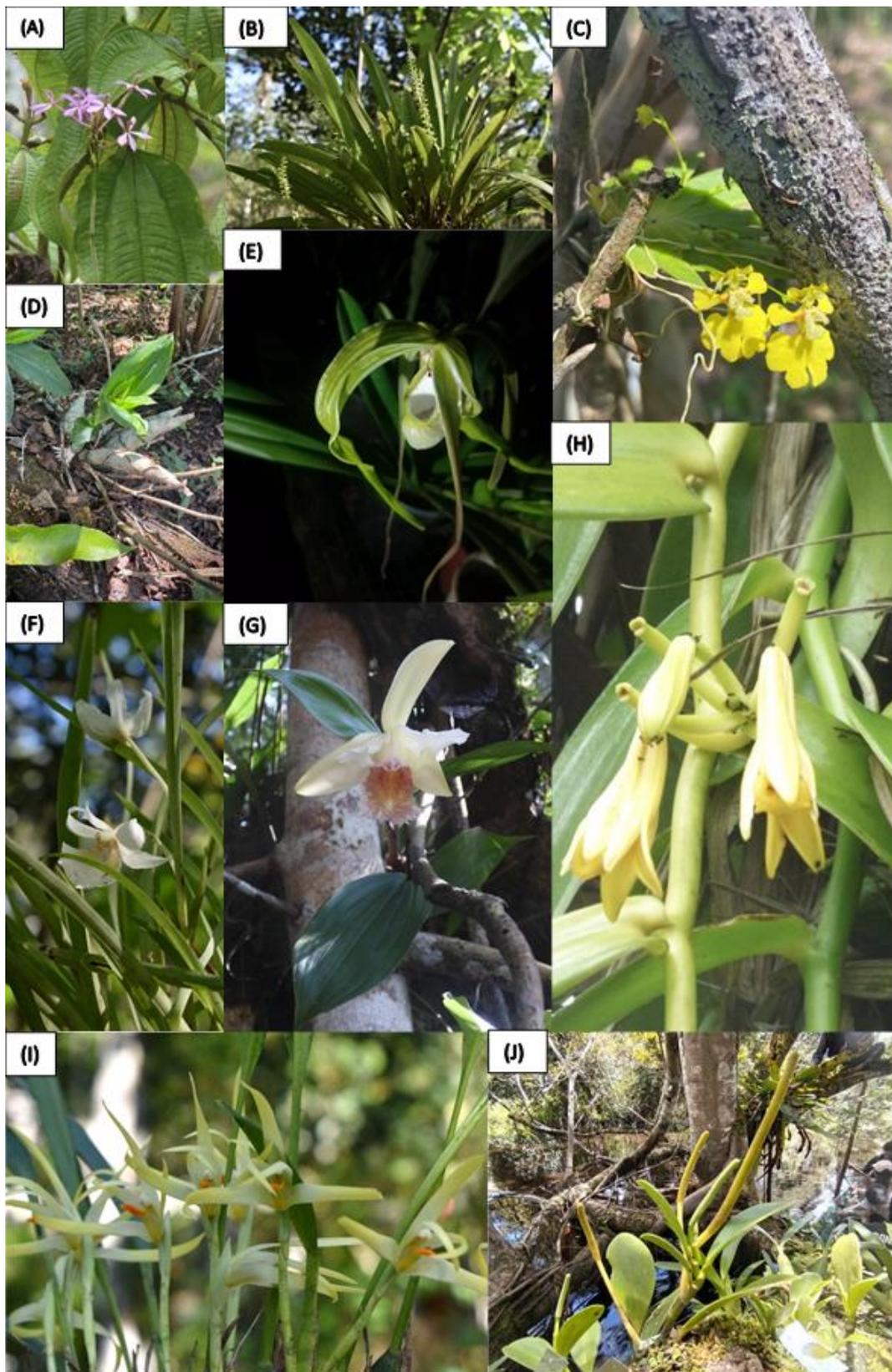


Figure A2. Photographs of some epiphytes from Tingana, San Martin, Peru. (A): *Epidendrum flexuosum* G.Mey.; (B): *Stelis* sp.; (C): *Erycina pusilla*. (L.) N.H.Williams & M.W.Chase; (D): *Catasetum saccatum* Lindl.; (E): *Phragmipedium warscewiczii* (Rchb.f.) Christenson; (F): *Miltoniopsis roezlii* (Rchb.f.) God.-Leb.; (G): *Sobralia fimbriata* Poepp. & Endl.; (H): *Vanilla pompona* subsp. *grandiflora* (Lindl.) Soto Arenas; (I): *Maxillaria* aff. *ochroleuca* Lodd. ex Lindl.; (J): *Peperomia obtusifolia* (L.) A. Dietr.