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REVIEW

Vascular epiphytes in Argentinian Yungas: distribution, diversity, and ecology

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Abstract
Vascular epiphytes are an important component of the flora of subtropical regions, but they remain understudied compared to tropical regions. Subtropical montane region of Yungas in Argentina has high epiphyte diversity, but information on epiphytes remain in little disseminated sources such as herbariums, theses and publications not available on the web. The objective of this study was to describe the distribution and diversity of epiphytes and to review ecological research on epiphytes in Yungas of northwestern Argentina. Occurrence records of epiphytes were compiled to prepare a floristic list, to describe spatial bias, and latitudinal and altitudinal patterns. There are 168 epiphyte species in Argentinian Yungas, which belong mainly to the families Orchidaceae, Bromeliaceae, and Polypodiaceae. Most species are holoepiphytes and facultative epiphytes (83%), and the rest are trees, herbs, and shrubs that occasionally occur as epiphytes. The species richness of the 14 most abundant epiphyte species in this region peaks at 1500 m, and decreases at higher and lower elevations. Most trees with a diameter at breast height ≥ 10 cm (62.2%) are epiphyte hosts, and epiphytes are most diverse in larger than in smaller native trees of this region. Species richness and cover of epiphytes increased with the diameter at breast height of *Ocotea porphyria*, the most important host tree for epiphytes in this region. It is expected that this study will serve to acknowledge the high diversity of epiphytes in the region and identify gaps in knowledge for new sampling and studies.

Keywords Accidental epiphytes · Altitudinal belts · Bibliographic review · Facultative epiphytes · Holoepiphytes · Species richness

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Resumen
Las epífitas vasculares son un importante componente de la flora de regiones subtropicales, pero permanecen menos estudiadas en comparación con regiones tropicales. La región subtropical montana de Yungas en Argentina tiene una alta diversidad de epífitas, pero la información sobre las mismas permanece en fuentes poco difundidas como herbarios, tesis y publicaciones no disponibles en internet. El objetivo de este estudio fue describir la distribución y diversidad de epífitas y revisar los estudios ecológicos de epífitas en las Yungas del noroeste argentino. Registros de presencia de epífitas fueron compilados para preparar un listado florístico, describir sesgos espaciales y patrones latitudinales y altitudinales. En las Yungas de Argentina habitan 168 especies de epífitas, principalmente de las familias Orchidaceae, Bromeliaceae y Polypodiaceae. El 83% son epífitas verdaderas o facultativas y el resto corresponde a árboles, hierbas y arbustos que ocasionalmente pueden ocurrir como epífitas. La riqueza de las 14 especies de epífitas más abundantes en la región tiene su máximo a los 1500 m de altitud, y disminuye hacia mayores y menores elevaciones. El 62.2% de los árboles con un diámetro a la altura del pecho ≥ 10 cm son hospedadores de epífitas, y estas presentan su mayor diversidad en los árboles nativos de mayor tamaño de la región. La riqueza y cobertura de epífitas incrementaron con el diámetro a la altura del pecho de *Ocotea porphyria*, el árbol hospedador de epífitas más importante en esta región. Se espera que este trabajo sirva para dar a conocer la alta diversidad de epífitas de la región e identificar vacíos de conocimiento para nuevos muestreos y estudios.

Introduction

Vascular epiphytes are plants that inhabit on other plants, without extracting water and nutrients from them (Zotz, 2016). Unlike parasitic plants, vascular epiphytes are autotrophic and only depend on other host plants for support or anchorage (Johansson, 1974; Benzing, 1990). Epiphytes generally inhabit the bark of trees and shrubs, although they can also be found on other types of supports such as rocks, wire fences and urban cables (Johansson, 1974; Benzing, 1990; Caldiz et al., 1993). Due to their habitat conditions, epiphytes are exposed to drought, strong winds, nutrient scarcity and intense irradiation, for which they have morphological and physiological adaptations such as organs for water and nutrient storage (e.g., pseudobulbs, rosette leaves), xeromorphism (e.g., succulence of stems and leaves, CAM metabolism) and poikilohydria (e.g., reviviscent ferns).

Vascular epiphytes are an important group of plants due to their diversity and role in ecosystem processes and in the interactions with other species. They comprise more than 31,000 species distributed in 79 families (including obligate epiphytes, facultative epiphytes, and hemiepiphytes), representing 10% of the total number of vascular plants in the world (Zotz et al., 2021). In some forests, epiphytes can contribute up to one third of the vascular plant diversity and particularly in montane forests they can exceed 50% of the vascular flora (Gentry & Dodson, 1987; Kelly et al., 2004). Epiphytes play an important role in ecosystem processes such as the hydrological cycle through interception of fog and rainfall, water storage and transpiration, and in nutrient cycling through their productivity and litter production (Nadkarni & Matelson, 1991, 1992; Lowman & Nadkarni, 1995; Jarvis, 2000; Stanton et al., 2014). They also represent an important source of nutrients and habitat for birds, mammals, amphibians, reptiles, invertebrates and microorganisms (Brown, 1986; Gradstein et al., 1996; Aguilar-Rodríguez et al., 2019; Kessler et al., 2020).

Compared to other terrestrial plants such as trees and lianas, vascular epiphyte assemblages were less studied. However, in the last decades remarkable progress was made in the knowledge of epiphyte diversity and distribution at global (Zotz, 2013; Zotz et al., 2021), continental (Mendieta-Leiva et al., 2020), regional (Ramos et al., 2019), and even at country level (Ibisch et al., 1996). Recently, large databases were prepared to compile epiphyte data in the Neotropics (Mendieta-Leiva et al., 2020) and in the Atlantic Forest (Ramos et al., 2019). These large databases compile samplings and surveys of epiphytes carried out by several researchers in different countries and regions, and will likely increase the knowledge of epiphytes at larger scales in the tropics, which are characterized by the highest diversity for this group of plants (Cascante-Marín et al., 2013; Zotz, 2016; Mendieta-Leiva et al., 2020). Meanwhile, in ecoregions that lie outside the tropic lines (e.g., Subtropics), and where epiphytes are also an important component of the flora, much less is known about their ecology, diversity, and distribution (Alvarez Arnesi et al., 2018; Ceballos, 2020).

In Argentina, Yungas is a subtropical montane region where vascular epiphytes are a conspicuous component of the forest (Brown, 1990; Lomáscolo et al., 2014). In this ecoregion, diversity and distribution patterns are known for several plant groups such as trees (Morales et al., 1995) and lianas (Malizia et al., 2015), but there are still few studies on epiphytes. Much of the information on the diversity and ecology of epiphytes in Yungas is found in poorly disseminated or difficult to access sources such as thesis, book chapters, floristic surveys, and herbaria (Brown, 1986; Ayarde, 1995; Ceballos, 2019; Ramos et al., 2019). In addition, most of the knowledge of epiphyte ecology and diversity comes from local studies (Ayarde, 1995; Roldán, 1995; Malizia, 2003; Ceballos, 2020), making it difficult to extrapolate results to the regional scale. Compiling diverse sources of information for several localities distributed along the latitudinal gradient of Yungas offers the opportunity to describe ecological patterns for epiphytes in the region (e.g., variation of species richness, altitudinal distribution).

The main objective of this study was to synthesize floristic and ecological information on the vascular epiphytes that inhabit in Yungas of northwestern Argentina. Specific objectives were: (1) To make a species list of vascular epiphytes that inhabit the region, including obligate, facultative, and accidental epiphytes. (2) To review the distribution of epiphyte records in this region. (3) To describe the latitudinal and altitudinal distribution of epiphyte species richness considering the 14 most abundant epiphyte species of Yungas. (4) To analyze the relationships between species richness and cover of epiphytes with the size (i.e., diameter at breast height) of *Ocotea porphyria*, the most important host tree for epiphytes in Yungas. (5) To conduct a literature review on different aspects of epiphyte ecology in the region to describe the state of knowledge and suggest lines of research.

Study area

Yungas or subtropical mountain forests (Cabrera & Willink, 1980) extend in discontinuous mountain ranges from southern Bolivia (Chuquisaca and Tarija departments) to Catamarca in Argentina, passing through the Argentinean provinces of Jujuy, Salta, and Tucumán (Fig. 1; Brown et al., 2001). In Argentina, Yungas extend over an area of 5.2 million ha, of 600 km length, 100 km wide, and with an elevation range from 400 to 3000 m asl (Brown et al., 2002). Three elevation belts are defined in this ecoregion as in most Andean forests: premontane forest from ca. 400–700 m asl, low-montane forest from ca. 700–1500 m asl, and high-montane forest from ca. 1500–3000 m asl (Cabrera, 1976; Brown et al., 2002). The study area has a subtropical climate, with a marked dry season from April to October and occasional frost during the winter (Brown et al., 2001). Mean annual temperature decreases from 21.5 °C to 11.5 °C along the altitudinal gradient, and rainfall ranges from 600 to more than 2000 mm annually (Arias & Bianchi, 1996).

Methods

In order to list vascular epiphyte species from Yungas of northwestern Argentina (objective 1), several sources of information were used (i.e., literature review, field

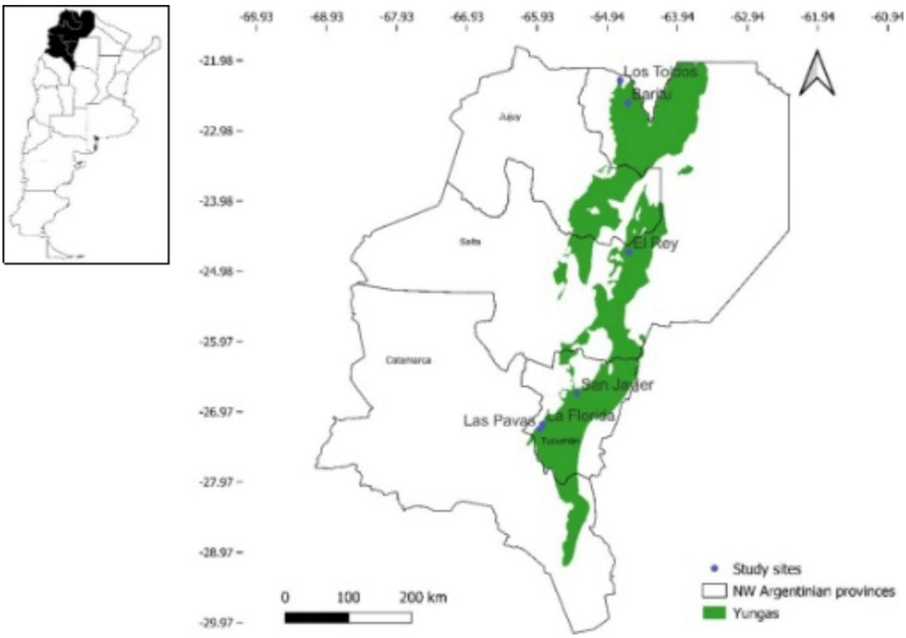

Fig. 1 Subtropical montane forests (Yungas) in NW Argentina showing the sites where ecological studies on epiphytes were performed

sampling, web databases, and expert validation). Fifty-one articles had information on ecology, floristic, distribution, and taxonomy of epiphytes for different localities in the region. A small number of these articles included lists of epiphyte species of some localities of Yungas. Sampling information of epiphytes in 4.8 ha of Yungas forests from Sierra de San Javier (Tucuman, Argentina) was also included (Ceballos, 2019). The list was completed with the assistance of experts in different epiphyte groups (Bromeliaceae, Polypodiaceae, Orchidaceae, Piperaceae) and by consulting the Flora Argentina (http://www.floraargentina.edu.ar/). The list included obligate epiphytes (i.e., those that occur almost exclusively as epiphytes), facultative epiphytes (i.e., those that occur both epiphytically and on the forest floor), and accidental epiphytes (i.e., terrestrial plants that occasionally germinate and grow on other plants).

To describe the distribution of epiphyte records in Yungas (objective 2), data were collected from herbarium collections (i.e. 341 presence records obtained from the package BIEN in R; Maitner et al., 2018; R Development Core Team 2021) and localities cited in the bibliography (68 presence records) (Supplementary Material 1). Only presence records from 62 obligate and facultative epiphyte species with available data were used. Accidental epiphytes were excluded due to sampling bias (i.e., there were only few records in areas that were extensively sampled) and because their actual distribution corresponds to other life forms that are not necessarily epiphytes (i.e., trees, lianas, herbs). Orchidaceae were also excluded because their distribution points were not available, for reasons related to their conservation (i.e., in order to not promote predation). A heatmap of $0.3 \times 0.3°$ squares was used in QGIS (QGIS Development Team, 2021) to identify bias of epiphyte sampling. The heatmap creates a density map by calculating the number of points (epiphyte presence records) per square, allowing an easy identification of areas with high and low number of records. Additionally, elevation data of each presence record was extracted from a digital elevation model in QGIS, in order to describe the altitudinal distribution of epiphytes in this region, considering all 62 species of epiphytes with available data, and only epiphytes from Bromeliaceae and Pterydophyta.

To describe spatial patterns of epiphyte species richness in Yungas (objective 3), species distribution models and geographic information systems were used. Fourteen epiphyte species had enough data (≥ 9 presence records) to model their distribution in this region: *Aechmea distichantha*, *Asplenium argentinum*, *Asplenium monanthes*, *Campyloneurun aglaolepis*, *Microgramma squamulosa*, *Pecluma filicula*, *Peperomia increscens*, *Peperomia collinsii*, *Peperomia lorentzii*, *Peperomia theodori*, *Peperomia tominana*, *Pleopeltis tweediana*, *Tillandsia jucunda* and *Tillandsia tenuifolia*. Bioclimatic variables were downloaded from Chelsa (Karger et al., 2017) and were used to obtain habitat suitability models for each one of the 14 epiphyte species in Maxent (Phillips et al., 2021). Four bioclimatic variables that may be critical for the epiphyte habit were selected: annual mean temperature, annual precipitation, temperature seasonality and precipitation seasonality. Given that models were fitted only with bioclimatic variables, all occurrence records from 1986 to the present were used, according to the period covered by the bioclimatic layers in the Chelsa database (Karger et al. 2017). In addition, occurrence records from a wide period of time were used (1986-present) since most epiphyte species were recorded in protected areas of Yungas that did not experienced significant land-cover changes. Models trained with presence data collected only from Yungas of NW Argentina were used (background area), even though these models probably have lower performance than models from the full species' ranges. For each species, 50 replicates of models were performed selecting at random 75% of occurrences for training and 25% for testing at each run. The models with the greatest AUC (i.e., a measurement of the discriminatory capacity of the habitat suitability models; considering AUC > 0.5) were selected as the final models. Then, the habitat suitability models were reclassified into binary presence-absence maps using the same threshold (10 percentile training presence) for each species in DIVA-GIS (Hijmans et al., 2001). The presence-absence models for each species were summed in QGIS (QGIS Development Team, 2021) to obtain a single map to describe the spatial patterns of the species richness for the 14 most abundant epiphyte species from Yungas. Finally, data was extracted from 300 random points in the species richness map and in a digital elevation model of Yungas, to describe the variation of the species richness with elevation.

Since *Ocotea porphyria* is the most important tree species for epiphytes in Yungas (Lomáscolo, 2014; Ceballos, 2019), the structure of epiphyte assemblages was analyzed in relation with the size of *O. porphyria* trees (objective 4). In secondary and mature forests of Yungas at Sierra de San Javier (Tucumán), epiphytes were surveyed in 259 *Ocotea porphyria* trees with a diameter at breast height (dbh) ≥ 10 cm. In each tree, the richness of epiphytes and the cover of epiphytes were recorded. The cover represented the percentage of the tree surface covered by epiphytes considering the classes: 0 (without epiphytes), 1 (1–5%), (), 2 (6–25%), 3 (26–50%,) and 4 (51–75%). Then, the variation of species richness and cover of epiphytes were analyzed in relation with the dbh of *Ocotea porphyria* trees using generalized linear models in R (R Development Core Team 2021).

A synthesis of the ecology of epiphytes in Yungas (objective 5) was made through a literature review, including types of studies conducted, ecological groups of epiphytes, vertical distribution of epiphytes, description of the most important families, new habitats colonized by epiphytes, epiphyte-tree interactions, and plant-animal interactions. Publications focused on the ecology of epiphytes in the region or that briefly describe ecological data for some species (i.e., taxonomic, floristic studies) were reviewed. After the synthesis of the available information, lines of research on epiphytes that have not yet been addressed in the region were identified.

Results

Species list

There are 168 epiphyte species recorded in Yungas of northwestern Argentina (Supplementary Material 2) that belongs to 71 generas and 28 families. Most of the generas have only one species and 25 generas have two or more species. The generas with more species are *Tillandsia* (26), *Peperomia* (11), *Asplenium* (10), *Pecluma* (7), *Rhipsalis* (6), and *Acianthera*, *Elaphoglossum*, *Epidendrum* and *Pleopeltis* with five species each. There are 93 obligate epiphyte species and 47 facultative epiphytes that can also grow on the forest floor or on rocks. The remaining species (28) are trees, shrubs, lianas, herbs of terrestrial or saxicolous habit that occasionally occur as epiphytes. Seven species are endemic to this region. Fourteen species can be found in transition zones of Yungas with other ecoregions, mainly with Chaco forests.

Distribution of epiphyte records

Sampling bias were observed on the distribution of epiphyte records in Yungas, considering data from herbaria and species lists. Using a heatmap to analyze the latitudinal distribution of epiphyte records, most of them are distributed on certain areas of the south (Tucumán province) and the north (Jujuy and Salta) of Yungas (Fig. 2). The extreme north of Yungas in Argentina, which have the highest biodiversity of the region for trees and lianas (Morales et al., 1995; Malizia et al., 2015), have low number of epiphyte records. The extreme south (Catamarca province) and the middle sector of Yungas have also low number of epiphyte records.

Epiphytes in Yungas have most records between 1300 and 1500 m (Fig. 3a), not only for methodological reasons (i.e., more collections and studies carried out at this elevation) but also because of their high abundance in low montane forests. Regarding to the most abundant families of epiphytes in this region, Bromeliaceae are more frequent in premontane areas (500–700 m) and in low montane forests (1300–1500 m; Fig. 3b), while Pteridophyta (ferns) are more frequent in high montane forests (1700–1900; Fig. 3c). In general, the most important epiphyte families are distributed throughout the whole elevation gradient of Yungas. However, some

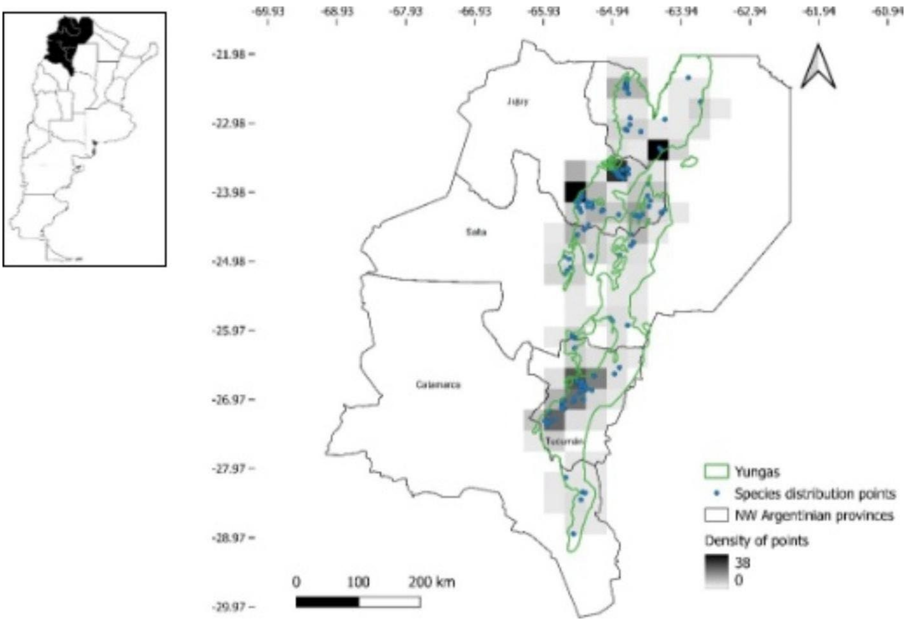

Fig. 2 Heatmap of Yungas of NW Argentina showing the distribution of epiphyte records (points) on 0.3×0.3 degrees squares

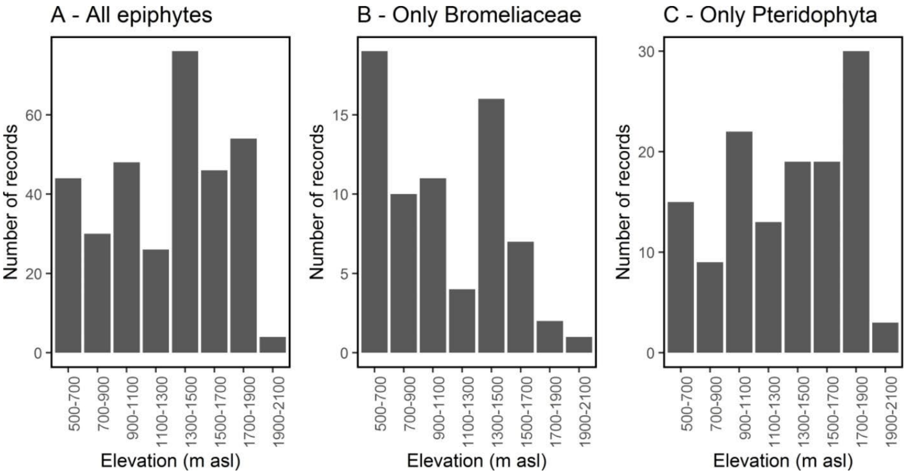

Fig. 3 Number of records of epiphytes from all families (A), only Bromeliaceae (B), and only Pteridophyta (C) in relation to the elevation in Yungas from NW Argentina. Only 62 epiphyte species with available data were included

families are more common in high montane forests, such as Hymenophyllaceae (e.g. Hymenophyllum sp.) and Dryopteridaceae (e.g. Elaphoglossum sp.) (de la Sota, 1977; Guantay & Hernández, 1995).

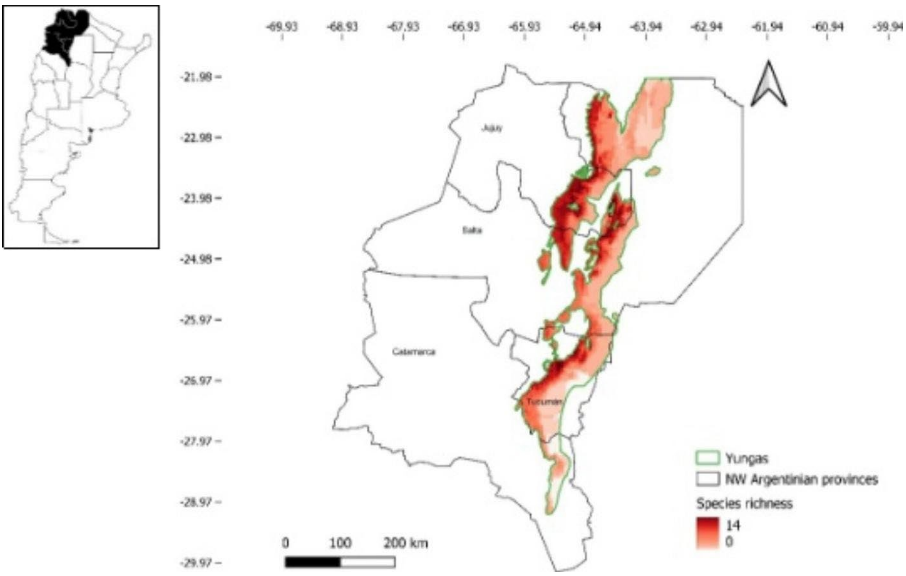

Fig. 4 Distribution of epiphyte species richness in Yungas from NW Argentina considering only the 14 most abundant epiphyte species with enough geographic data to model their distribution (i.e., 9 or more records)

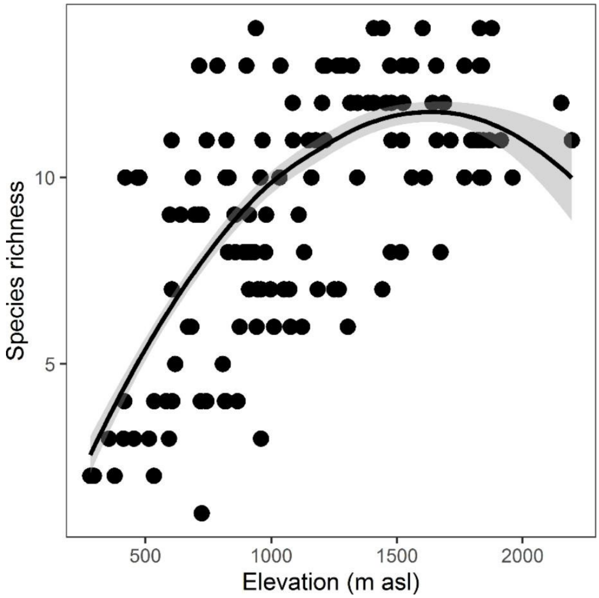

Fig. 5 Variation of epiphyte species richness with elevation in Yungas from NW Argentina. Data were extracted using random points from the map of epiphyte species richness (Fig. 4) and a digital elevation model

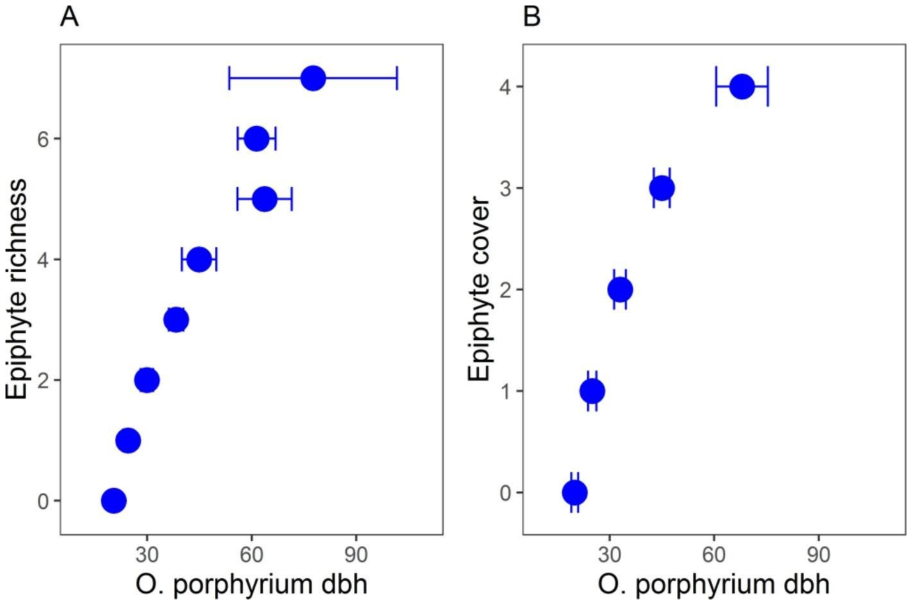

Fig. 6 Increment of species richness (A) and cover (B) of epiphytes in relation to the diameter at breast height (dbh) of the tree *Ocotea porphyria*. Points represent the mean value of species richness and cover of epiphytes, and bars represent standard errors. The cover represents the percentage of the tree surface covered by epiphytes: 0 (without epiphytes), 1 (1–5%), (), 2 (6–25%), 3 (26–50%,) and 4 (51–75%). Data were obtained from 259 trees from Yungas forests of Sierra de San Javier (Tucumán, Argentina)

Distribution of epiphyte species richness

The richness of the 14 most abundant epiphyte species from this region is found mostly on low and high montane forests (Fig. 4). The richness of this abundant species peaks at 1500 m and decreases towards lower and higher elevations (Fig. 5). This pattern is consistent with studies conducted in Andean and tropical forests in which the highest diversity of epiphytes is found between 1000 and 1500 m (Gentry & Dodson, 1987; Wolf & Flamenco, 2003; Krömer et al., 2005).

Ocotea porphyria and epiphytes

In Yungas forests of Sierra de San Javier (Tucumán), epiphyte richness (estimate = 0.049 $t = 13.96$ $p < 0.001$) and cover (estimate = 0.034 $t = 13.89$ $p < 0.001$) increased significantly with the dbh of *Ocotea porphyria* (Fig. 6). Among 259 *Ocotea porphyria* trees surveyed, 74.4% had epiphytes on their bark, including 21 obligate and facultative epiphytes, and 6 occassional epiphytes. Most frequent species on *Ocotea porphyria* trees were *Pleopeltis tweediana*, *Aechmea distichantha* and *Microgramma squamulosa*.

Ecological studies on epiphytes

The first study on epiphyte ecology in Yungas of northwestern Argentina was published in 1963 and consisted of floristic surveys in Myrtaceae forests that included epiphytes (Meyer, 1963). In the last three decades, different aspects of epiphytes ecology such as species richness, composition, abundance, frequency, and interactions with host trees have been studied (Table 1). Ecological studies carried out were relatively few (i.e., 10 in the last 4 decades) and conducted at local scales (i.e., sampling in a single locality or a small area), thus epiphytes were not studied yet at a regional scale. Although different methodologies were used, research in this region had in common that they use plots to study epiphytes (i.e., a delimited forest area where epiphytes and trees were recorded). Generally, all trees within the plots were considered, whether or not they were hosts of epiphytes, based on a given diameter at breast height (dbh) that varied among different studies. Depending on the different research objectives, a single tree or a plot were selected as the sample unit. At lower scales, sample units used in this region to sample epiphytes were tree zones (i.e., following the methodology of Johansson, 1974) or tree branches (Brown, 1986; Ceballos, 2019). Most of the research was carried out in low montane forests of Yungas, while only two studies were performed at other elevations such as premontane forests and high montane forests (Table 1). Even though epiphytes were surveyed in different forests types in this region (i.e., primary and secondary, disturbed or undisturbed, native and invaded), there was a dominance of *Pleopeltis tweediana* and *Peperomia* sp. as the most frequent epiphyte species, and *Ocotea porphyria* as the most important host tree (Table 1).

Table 1 Ecological studied focused on epiphytes that were performed in Yungas forests from northwestern Argentina

Authors	Study area (province)	Forest type	Forest elevation belt	Elevation (m asl)	Sampled área (ha)	Number of plots	Sampled trees (n)	Epiphyte richness	Trees with epiphytes (%)	Most frequent epiphyte species	Most important host tree
Meyer 1963	Las Pavas (Tucumán)	Myrtaceae forest	Low montane forest	900–1300	-	-	-	28	-	-	*Ocotea porphyria*
Brown 1986	El Rey (Salta)	Secondary forest	Premontane forest	700–800	-	1	139	-	62	*Pleopeltis tweediana*	*Allophylus edulis*
		Old secondary forest	Premontane forest	700–800	-	1	64	-	87.5	*Pleopeltis tweediana*	*Scutia buxifolia*
Brown 1990	El Rey (Salta)	Forest of tipa and laurel	Low montane forest	900	1.2	28	92	21	52	*Pleopeltis tweediana*	*Tipuana tipu*
		Myrtaceae forest	Low montane forest	1050	1.1	27	164	30	78	*Peperomia* sp.	*Ocotea porphyria*
Brown & Zunino 1990	Baritú (Salta)	-	Low montane forest	700	0.1	-	500	-	73	-	-
		-	Low montane forest	1000	0.1	-	462	-	57.8	-	-
Ayarde 1995	La Florida (Tucumán)	-	Premontane forest	400	1	1	387	16	83	*Pleopeltis tweediana*	*Blepharocalyx salicifolius y Ocotea porphyria*
Roldán 1995	Las Piedras (Tucumán)	Disturbed forest	Low montane forest	900	0.3	3	147	12	65	*Peperomia* sp.	*Ocotea porphyria*
		Undisturbed forest	Low montane forest	900	0.2	2	77	13	49	*Peperomia* sp.	*Terminalia triflora*
Malizia 2003	Los Toldos (Salta)	Primary forest	High montane forest	1800	1	1	328	18	-	*Pecluma oranense*	*Podocarpus parlatorei*
Ceballos et al. 2016	San Javier (Tucumán)	Old-growth forest	Low montane forest	1000	1.2	3	491	20	44.3	*Peperomia tetraphylla*	*Ocotea porphyria*

Table 1 (continued)

Authors	Study area (province)	Forest type	Forest elevation belt	Elevation (m asl)	Sampled área (ha)	Number of plots	Sampled trees (n)	Epiphyte richness	Trees with epiphytes (%)	Most frequent epiphyte species	Most important host tree
Ceballos 2019, 2020	San Javier (Tucumán)	30-y secondary forest	Low montane forest	721	0.8	2	382	19	41.1	*Pleopeltis tweediana*	*Ocotea porphyria*
		60-y secondary forest	Low montane forest	737	1.6	4	638	26	54.1	*Pleopeltis tweediana*	*Ocotea porphyria*
		Old-growth forest	Low montane forest	909	1.6	4	689	25	61.7	*Peperomia tetraphylla*	*Ocotea porphyria*
		Forest invaded by *Ligustrum lucidum*	Low montane forest	694	0.4	3	265	7	14	*Pleopeltis tweediana*	*Ligustrum lucidum*
		Forest invaded by *Morus alba*	Low montane forest	740	0.4	1	139	13	30	*Pleopeltis tweediana*	*Morus alba*

Ecological groups of epiphytes

Epiphytes of Yungas can be divided into ecological groups according to their shade tolerance, the thickness of the branches on which they live, and successional strategy (Brown, 1990; Ceballos, 2020). For shade tolerance, epiphytes can be classified as:

Shade tolerant species: require high humidity conditions and they wilt under intense light. These species are found in the base of tree trunks or in the lower tree strata. For example, *Asplenium auritum*, *Asplenium praemorsum*, *Malaxis padillana*.

Shade intolerant species: those that are exposed to a greater light intensity and dry conditions, so some have xerophytic characteristics. Brown (1990) classified these species depending on their exposure to moderate or high light intensities. Species exposed to moderate intensities occupy the middle part of the trees and have drought resistance adaptations such as succulent leaves (*Peperomia* sp.), succulent stem (*Rhipsalis* sp.), reviviscence (*Pleopeltis tweediana*, *Pleopeltis minima*), or absition of fronds (*Phlebodium areolatum*). Species exposed to high light intensities are found in the outer crown and have adaptations for rapid moisture absorption (e.g., *Tillandsia didisticha*, *Tillandsia recurvata*, *Tillandsia tricholepis*, *Gomesa viperina* and *Microgramma squamulosa*).

According to the thickness of the branches on which they live, epiphytes are divided in:

Species of coarse support: they are found in suspended soils on thick and inclined branches. These include large bromeliads such as *Aechmea distichantha* and *Vriesea friburgensis*.

Species of fine support: they inhabit the thinnest branches, usually in the outer crown. For example, *Tillandsia tricholepis* and *Tillandsia recurvata*.

Shade tolerance, bark thickness, and tree size are characteristics related to the successional strategy of epiphytes. At the beginning of forest succession, trees are small and their crowns are exposed to a high luminosity, conditions in which epiphyte species such as *Pleopeltis tweediana*, *Tillandsia recurvata* and *Tillandsia tricholepis* (early colonizers) are established. In advanced stages of forest succession, some epiphyte species increase in abundance, such as those that require thicker supports (e.g., *Aechmea distichantha* and *Urera baccifera*) and higher humidity conditions (*Peperomia tetraphylla* and *Peperomia theodori*). However, these ecological groups are not strict because early colonizing species can still be established at later stages of succession. In advanced succession these species continue to be established in areas of trees whose conditions resemble those of early successional stages (e.g., in the outer crown, which is exposed to high intensities of light and has young, thin branches).

Vertical distribution of epiphytes

In Yungas, vertical distribution of epiphytes on trees was classified following the methodology of Yohansson (1974), which is the most common method to study epiphytes and facilitates comparisons among studies. Johansson (1974) proposed that epiphytes have a vertical distribution in five zones following a gradient of humidity and light intensity that vary with tree height. In particular zones or areas of trees, some epiphyte species are more common (Brown, 1990; Woods et al., 2015). In Yungas, the basal part of the trunk up to 1 m usually lack of epiphytes, although occasional epiphytes can be found sometimes (Zone 1 – Johansson, 1974). When the tree is inside the forest, some epiphytes such as *Asplenium auritum*, *Asplenium praemorsum* and *Peperomia* sp. are present in Zone 2 (i.e., the trunk from 1 m up to the first ramification). When the trees are under high light intensity (e.g., trees in borders or isolated trees), *Microgramma squamulosa*, *Pleopeltis tweediana* and *Rhipsalis lumbricoides* are frequent in Zone 2. In the main point of ramification (Zone 3) and tree branches (Zones 4 and 5), diversity of epiphytes increase due to the accumulation of soil and organic matter on these areas. In Zone 3 and on thicker branches (Zone 4), *Aechmea distichantha*, *Vriesea friburgensis*, and accidental epiphytes such as *Urera baccifera* are frequent. On the sides of thicker branches, *Rhipsalis floccosa* and *Phlebodium areolatum* can be found. *Microgramma squamulosa*, *Pleopeltis tweediana* and *Tillandsia* sp. generally cover completely the branches of Zones 4 and 5 under conditions of high radiation. This vertical stratification is common in forest interior, but conditions of humidity and temperature in which epiphyte are exposed vary depending on the arquitecture of tree species and their location (e.g., in disturbed or undisturbed areas, on borders, in the understory or the canopy).

Most important families

Bromeliaceae

Bromeliaceae is one of the most diverse families of epiphytes in Yungas with 31 species, several of which are among the most conspicuous in the ecoregion due to their size and/or abundance. In addition to their epiphytic habit, they can also be found on rocks (e.g., *Tillandsia australis*), on the forest soil (e.g., *Aechmea distichantha*), or in urban wires (e.g., *Tillandsia recurvata*) (Gómez Romero & Novara, 2010; Barberis et al., 2021; Gonzalez & Ceballos 2021). Species composition of Bromeliaceae in Yungas includes species shared with other ecoregions, endemic species such as *Tillandsia jucunda* and *Tillandsia albertiana* (Flora Argentina, 2021; PlanEAr, 2021) and other species widely distributed in the continent such as *Tillandsia usneoides* and *Tillandsia recurvata*. To differentiate functional groups of epiphytic Bromeliaceae in Yungas, species can be divided into: (1) Plants with hanging stems and small leaves, similar to mosses or lichens (*Tillandsia usneoides*), (2) Plants with large, green, and arrosetted leaves (*Aechmea distichantha*, *Vriesea friburgensis*), (3) Plants with narrow, arrosetted leaves (*Tillandsia tenuifolia*, *Tillandsia recurvata*), and (4) Plants with stems completely covered with small, imbricate leaves (*Tillandsia tricholepis*). Even so, several of these species are difficult to identify (particularly those of the genus *Tillandsia*), and in order to differentiate them, it is useful to observe the dried inflorescences that remain on the plants for several months. The most frequent bromeliad epiphytes in Yungas are *Aechmea distichantha*, *Tillandsia recurvata*, *Tillandsia tenuifolia* and *Tillandsia didisticha*.

Ferns and lycophytes

Ferns and lycophytes represent more than a third of the epiphyte richness in Yungas, including 61 species distributed among the families Aspleniaceae, Dryopteridaceae, Hymenophyllaceae, Lycopodiaceae, Nephrolepidaceae, Ophioglossaceae, Polypodiaceae, Psilotaceae, Pteridaceae, Selaginellaceae and Tectariaceae. In addition to their epiphytic habit, most species (42) can grow in a great diversity of environments, mainly on the forest soil (terrestrial plants) or on rocks (saxicolous). Most of the trees in Yungas are cover with epiphytic ferns, generally of the family Polypodiaceae which has 25 species. All fern and lycophyte species are native, with the exception of *Nephrolepis cordifolia*, which is cultivated as ornamental and is the only epiphyte introduced in the Argentine Yungas known so far. The most frequent epiphytic ferns in Yungas are *Microgramma squamulosa* and *Pleopeltis tweediana*.

Orchidaceae

Epiphytic orchids include 39 species in Yungas, making it one of the most biodiverse families in the region. Most are obligate epiphytes, and a few species are terrestrial plants that can occasionally be epiphytes (e.g., *Cyrtopodium paniculatum*, *Aa weddelliana* and *Cyclopogon congestus*). Occasionally, terrestrial orchid species germinate on the soil accumulated at the base of tree trunks. Although Orchidaceae is one of the families with the greatest number of epiphyte species, they are not the most abundant. In addition, many epiphytic orchids are small plants that grow in the canopy among colonies that include other epiphytes species; thus, some orchid species are difficult to observe, which leads to underestimating their richness in ecological sampling. Orchids are characterized by their beautiful flowers, which had led to several species native to the region being cultivated as ornamentals and suffering predation in their natural environments. The most frequent orchid epiphytes in Yungas are *Gomesa bifolia*, *Gomesa viperina* and *Cyclopogon elatus*.

New habitats colonized by epiphytes

Historically, epiphytes were studied in old-growth, primary and well conserved forests, possibly because these forests have the higher diversity of epiphytes (Johansson, 1974; Zotz, 2016). Along with changes in forest cover (e.g., loss of primary forests through deforestation, formation of secondary forests, fragmentation), studies on epiphytes began to focus on new environments with more anthropogenic influence. These studies evaluated the capacity of new environments (e.g., secondary forests, invaded by exotics, disturbed, forest plantations, urban forests) to function as reservoirs of native epiphyte diversity (Cascante-Marin et al., 2009; Boelter et al., 2011; Woods & DeWalt, 2013; Martin et al., 2013; Martins et al., 2020). In Yungas of northwestern Argentina, epiphytes were recently studied in new habitats whose formation was highly influenced by anthropogenic activities, such as secondary forests and urban forests (Ceballos, 2019, 2020; Gonzalez & Ceballos, 2021).

In Yungas, epiphytes established on secondary forests that were previously farmlands, and colonized these forests relatively rapid but under certain conditions (Ceballos, 2020). For example, 30-y secondary forests of Sierra de San Javier (Tucumán) shared 76% of epiphyte species with mature forests, due to their tree composition dominated by native trees and their proximity to propagule sources of epiphytes (Ceballos, 2020). Secondary forests of 60-y had a similar epiphyte species richness and composition with mature forests, which suggest that epiphyte species accumulate with forest age (Ceballos, 2020). These secondary forests are a promising habitat for conservation, but undisturbed mature forests are still the most important habitat for epiphytes in Yungas, due to their old and large trees that bear dense epiphytes assemblages and their high number of colonized trees (Ceballos, 2020). Most common epiphyte species that established early on Yungas secondary forests are *Tillandsia* sp., *Pleopeltis tweediana*, and *Microgramma squamulosa*, but other species such as *Aechmea distichantha* and *Peperomia* sp. establish when secondary forests are older (Brown, 1986; Ceballos, 2019).

In Yungas, secondary forests are frequently invaded by two exotic trees from China, *Ligustrum lucidum* and *Morus alba* (Grau & Aragón, 2000; Montti et al., 2017). Both species invaded abandon agriculture fields, disturbed areas, and formed monotypic secondary forests that have low diversity of native plants (Ceballos et al., 2015; Fernandez et al., 2020). Compared to native forests of similar age from Yungas, these invaded forests had a lower percentage of trees colonized by epiphytes and lower epiphyte diversity (Table 1). This pattern may be related to the simplified structure of invaded forests, and to the characteristics of invasive species, which can reduce the diversity of microhabitat that can be colonized by epiphytes. For example, *Ligustrum lucidum* has a straight trunk, smooth bark, and vertical branches, which could reduce the attachment of epiphytes in the trees (Ceballos, 2020).

Some epiphyte species are found in urban trees, on the bark of both exotic and native tree species (Bhatt et al., 2015; Martins et al., 2020; Gonzales & Ceballos, 2021). In Argentina, epiphytes were studied on urban trees of La Plata and Gran San Miguel de Tucumán, this last city being close to Yungas forests (Caldiz et al., 1993; Gonzales & Ceballos, 2021). In Gran San Miguel de Tucumán, the higher species richness of epiphytes was found in parts of the city that are close to Yungas forests, due to the proximity to propagule sources, the presence of large remnant trees, and the higher humidity and lower temperature in this sector. It was also reported that epiphyte assemblages on urban trees are dominated by species of *Tillandsia* sp. and *Pleopeltis tweediana*, which are typical species of disturbed and early successional forests that have adaptations to tolerate desiccation. In this city, both native and exotic tree species were colonized by epiphytes, but native species had a higher percentage of trees colonized by epiphytes (Gonzales & Ceballos, 2021).

Epiphyte-tree interactions

Although Yungas of Argentina do not have the enormous diversity of tropical Andean forests (Krömer et al., 2005), it has a high percentage of trees covered by epiphytes. In Yungas, including surveys performed in different forest types (primary, secondary, disturbed; Brown, 1990; Roldán, 1995; Ceballos, 2020), 62.2% of trees with a diameter at breast height (dap) ≥ 10 cm are epiphyte hosts. This percentage of colonized trees is an intermediate value compared to other forests where epiphytes were sampled on trees with similar dap (Zotz, 2016). For example, the percentage of colonized trees was 13% in lowland tropical forests in Venezuela (Nieder et al., 2000) and 56–100% in montane forests in China (Zhao et al., 2015).

Trees usually have traits that make them more prone to be colonized by epiphytes (Francisco et al., 2021). In Yungas, larger trees (i.e., both in diameter and height), with rough bark, and horizontal branches are more likely to be covered by epiphytes (Brown, 1990; Malizia, 2003; Ceballos et al., 2016). It is well known that larger trees provide more bark surface, diversity of microhabitats, and are generally long-lived, allowing colonization by epiphyte species with different microclimatic and habitat requirements (Hietz & Hietz-Seifert, 1995; Burns, 2008; Woods et al., 2015). Rough barks have fissures that allow the accumulation of water, nutrients, and organic matter, which are critical for epiphyte establishment and growth (Johansson, 1974; Callaway et al., 2002). Inclined trunks and horizontal branches are generally covered by epiphytes in their dorsal and lateral parts where soil is accumulated, decreasing the chance of epiphyte falling compared to vertical supports (Brown, 1990).

In Yungas, canopy trees such as *Ocotea porphyria*, *Parapiptadenia excelsa*, *Tipuana tipu*, *Podocarpus parlatorei*, *Blepharocalyx salicifolius* and *Terminalia triflora* are the main host tree species for epiphytes (Table 1; Meyer, 1963; Brown, 1990; Malizia, 2003; Ceballos, 2020). Among canopy trees, *Ocotea porphyria* is the most important host tree for epiphytes, possibly because of its size, rough bark and presence of inclined trunk and branches (Meyer, 1963; Brown, 1990; Lomáscolo et al., 2014; Ceballos, 2020). For example, in one *Ocotea porphyria* tree of 20 m height and 1 m dbh, the number of epiphytes recorded was 1125 individuals (Brown, 1990). When the trees of *Ocotea porphyria* are young generally lack of epiphytes, but they accumulate epiphytes as they grow older, probably due to the influence of time for colonization, bark cracking and increase of microhabitat diversity with tree age. Understory tree species usually lack of epiphytes, except the tree *Allophylus edulis*. This is one of the most important epiphyte host of Yungas, due to its squamous bark where seeds and spores of epiphytes are captured (Malizia, 2003).

Myrtaceae tree species such as *Eugenia uniflora*, *Myrcianthes pungens*, and *Myrcianthes pseudo-mato* are less prone to be colonized by epiphytes due to their smooth bark (Brown, 1990; Malizia, 2003; Ceballos et al., 2016). However, under humid conditions (i.e., in forests exceeding 2000–3000 mm of annual precipitation; Meyer, 1963), Myrtaceae trees can host large colonies of epiphytes. Under these conditions, Myrtaceae trees are covered by pendulous epiphytes such as *Tillandsia usneoides* and mosses forming curtains, and also bromeliads mainly on the main branching point (Meyer, 1963; Ceballos, 2019).

Plant-animal interactions

Vascular epiphytes provide a variety of resources to birds, including food (nectar, fruits), nest material, nest sites, and water for consumption and bathing (Nadkarni & Matelson, 1989; Cestari & Pizo, 2008; Boechat et al., 2019). Indirectly, epiphytes serve as micro-habitats for invertebrates and small vertebrates that constitute prey for many bird species (Cestarini & Pizo, 2008). Since epiphytes are important resources for birds, many studies described their interactions in tropical forests and few studies were performed in subtropical forests (Ruiz Contreras, 2019). In Yungas, birds that belong to the families Turdidae and Emberizidae are among the most important seed dispersers of epiphytes (Giannini, 1999). These are generally small, frugivorous or generalist birds that disperse epiphytes seeds using trees as perches (Giannini, 1999; Blendinger et al., 2015). Some epiphyte species that provide fleshy fruits for birds are *Aechmea distichantha*, *Peperomia* sp., *Rhipsalis* sp. and *Pfeiffera ianthothele* (Blendinger et al., 2016; Di Pauli, 2018; Rojas et al., 2019). Compared to other studies that focused on epiphytes and birds, these interactions in Yungas were studied within a large system of interactions between seed dispersal animals and plants (Giannini, 1999; Blendinger et al. 2015; Rojas et al. 2019).

In Yungas, Bromeliaceae was the most studied family considering epiphyte-plant interactions. In protected areas of Yungas, 72.3% of plant consumption of the monkey *Cebus apella* was six species of epiphytic bromelias, being the most consumed species *Aechmea distichantha*, *Tillandsia tenuifolia*, and *Vriesea friburgensis* (Brown, 1986; Brown & Zunino, 1990). *Cebus apella* eats the base of leaves, in sites with a high density of bromelias, mainly during the dry season when fruits are not available (Brown & Zunino, 1990). Some bromeliad species form a tank or phytotelma accumulating water and detritus, which can contain associated organisms (Benzing, 1990; Amadeo et al., 2017). Although many organisms inhabit or depend on these water pools, few of their interactions were studied in Yungas. In peri-urban forest areas of Yungas, *Aedes aegypti* larvae (i.e., the vector of dengue) were found in the water accumulated between the leaves of *Aechmea distichantha* (Stein et al., 2013). This bromeliad form phytotelmas that are important for coleopterans in other subtropical and temperate forests of Argentina (Campos & Fernández, 2011). In other regions, *Aechmea distichantha* provide phytotelmas to aquatic insect larvae communities, flagellate protists, and it is used as habitat or shelter, food supply (herbivores, detritivores, predators), and for nesting (Silva Costa Duarte et al., 2013; Amadeo et al., 2017; Freire et al., 2021).

Research priorities

Since few studies on epiphytes were performed in Yungas of NW Argentina, many research lines can be proposed as priorities in this region. However, research priorities here were defined on methodological issues, which can be improved or being used as an advantage in this region in particular. Methodological issues to be improved are epiphyte sampling, particularly on areas with few records. Methodologies that can be used as an advantage in this region are permanent plots where epiphytes were surveyed for long-term research.

All studies on epiphyte ecology in Yungas were conducted with binoculars from the forest floor, probably underestimating the cover and species richness of epiphytes. In addition, most studies sampled epiphytes on trees ≥ 10 cm dbh, without considering epiphytes inhabiting smaller trees or fallen trees in the understory. Therefore, to increase the completeness of epiphyte sampling in Yungas, it is suggested to record the species that inhabit the understory and incorporate sampling techniques such as climbing trees with ropes (Perry, 1978). However, before carrying out these surveys it is necessary to consider the safety of the technique (i.e., because Yungas forests are on steep slopes) and to evaluate different solutions (e.g., reduce the number of trees sampled but increase the observation time). Using better techniques could lead to increase the number of records of orchids in Yungas, which often have low abundance and are difficult to observe with binoculars. Additionally, new surveys can be carried out in understudied areas, especially in high montane forests and in the northern area of the region where epiphytes possibly have the highest diversity.

Most studies on epiphyte ecology in Yungas consisted on unrepeated sampling in time, thus it is unknown how epiphyte assemblages change over time during succession (Brown, 1986; Ceballos, 2019). In Yungas, temporal dynamic of epiphytes was studied using chronosequences of forests of different age and observations of epiphyte assemblages growing on branches of different sizes (Brown, 1986, 1990; Ceballos, 2020, 2019). Through observations, a study suggested that epiphyte succession in Yungas begins when young and thin branches are colonized by lichens, and later by drought tolerant ferns and atmospheric bromeliads (Brown, 1990). *Aechmea distichantha*, one of the biggest bromeliads of Yungas, establishes when branches are thicker near to the main tree axis (Brown, 1990). This species reproduces sexual and asexual and form colonies that cover the entire branch surface. At this successional stage, the species that establish are accidental epiphytes (e.g. *Urera baccifera*) between *Aechmea distichantha* colonies, and holoepiphytes on the sides of branches such as *Phlebodium areolatum* and *Rhipsalis floccosa* (Brown, 1990). However, using this methodology it is not clear if epiphyte turnover is a true successional process or a facilitation between species (Zotz, 2016). The advantage is that some of these studies were conducted in forest permanent plots where trees were identified and marked with numbered aluminum tags. Thus, epiphyte sampling can be repeated in the permanent plots to evaluate temporal dynamics of epiphytes (i.e., identify new or lost species in an assemblage; Nadkarni, 2000). It is generally unknown for most of the world's forests how epiphyte assemblages change in the long term, and using this methodology in Yungas could generate novel information for this group of plants.

Conclusions

In this study, it was reported a list of epiphyte vascular species and descriptions of their ecology, diversity and distribution in Yungas of northwestern Argentina. Epiphytes in this region include 168 species that colonize most of the tree species in native forests, and also in the most modified environments such as disturbed, invaded, or urban forests. In this region, epiphytes are studied since 1963 and few papers were published on the ecology of this group of plants. These papers focused on descriptions of epiphyte assemblages at local scales and some ecological aspects such as species habit, distribution and interactions. All these studies were compiled to report general patterns of epiphytes in Yungas, such as the distribution of epiphyte records, and latitudinal and altitudinal distribution for the most abundant epiphyte species. It is expected that this study can be useful to give visibility to the important richness of epiphytes of Yungas and to encourage further research on the group in the region.

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Declarations

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