

Diversity, productivity and biomass patterns of epiphytes along successional gradient in the Andean Colombian

Abstract

Our objective was to determine the relationship of different successional stages with the diversity, assimilation rates and net productivity of different growth forms of vascular epiphytes in a humid montane forest in Andean Colombian. Three successional stages were selected according to the site conditions. The 30 trees sampled in the three successional stages 4,610 epiphytic individuals to 54 species. A main finding was that species richness, abundance and biomass increased with stage age. Additionally true epiphytes were the growth form with the greatest richness, abundance and biomass. Regarding photosynthesis rates decreased with stage age and were higher for treelets, shrubs and lower for true epiphytes. According the analysis of the ordering of the epiphytes found by stages shows the existence of a successional trajectory with the presence of representative species of each stage. This research can contribute as a basis to the knowledge of epiphytes, with the purpose of enriching and supporting management measures for these species.

Keywords: orchids, bromeliads, neotropical forest, vascular plant, environmental factors

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Introduction

Vascular epiphytes represent a great richness of species in most tropical forests, and their diversity is associated with the state of development of the ecosystem.^{1,2} This group of epiphyte plants contribute greatly to global plant diversity, because they represent between 8% and 10% of all known vascular plant species, where 80% of all vascular epiphytes are concentrated in the families' Orchidaceae, Bromeliaceae, Polypodiaceae and Araceae.^{3,4} The importance of these plants in the ecosystems is notable, because epiphytes can considerably increase the retention of atmospheric water in tropical forests,⁵ in addition to playing a predominant role in the contribution of biomass and the nutrient recycling in upland forests.⁶

Information on the diversity of epiphytes in forests under different successional stages is still insufficient according to their response capabilities to environmental changes.^{1,5-10} Diversity patterns are determined by environmental factors, which limit or favor their diversity. An factors is atmospheric humidity, where environments in conditions of high humidity present, for example, a greater richness and abundance of epiphytes.³ Consequently, epiphytes reach their greatest diversity and abundance in tropical humid montane forests, where moderate temperatures together with constant high humidity favor growth and the accumulation of organic matter.^{6,11,12}

The degree of forest succession affects climatic factors such as light, humidity, temperature and evapotranspiration, affecting forest dynamics, and but also epiphytic species and their growth forms.¹³ Total biomass is expected to be lower in the early successional stage than in the intermediate and late successional stages, because species that grow on thicker branches and in the wetter part of the canopy are more affected by disturbance.^{14,15} On the other hand, successional changes are reported in terms of epiphyte diversity as the primary branches grow in diameter and age.⁵ According to the responses of epiphytes found in trees, more stable forests are expected to promote a greater diversity of epiphytes - notable in orchids species, which are sensitive to human disturbance.^{16,17}

In general epiphytes show a relatively moderate maximum fixation rate in favorable conditions. In conditions with environmental limitations the maximum fixation rate is maintained for short periods, evidencing that photosynthesis rates in drought conditions decrease and the exchange of CO₂ between the atmosphere and the plant is practically suspended.¹⁸ The C3 photosynthetic pathway is the most typical of epiphytes that inhabit the canopies of cloud forests and cold micro-sites, shady and humid.¹⁹ However, in response to less favorable or unfavorable conditions of relative humidity, water availability, air temperature, amount of light and photoperiod, epiphytes species present variable photosynthetic metabolism (facultative or intermediate). In favorable conditions the plant has a C3 metabolism and in less favorable conditions it changes to a CAM metabolism, a variation that can occur in very short periods of time.^{18,20}

Leaf characteristics such as size, shape, mass, inclination, chlorophyll content, nitrogen content and photosynthetic capacity, among others, vary along gradients of altitude, light and under different micro-environmental conditions, so that the plant maximizes carbon gain.²¹ However, it has been shown that two factors are the most determining limitations in carbon gain and annual primary productivity, these are light and water availability, with leaves exposed to the sun presenting higher productivity values.¹⁸ Furthermore, the leaves of epiphytic plants have evolved to optimize and improve photosynthesis through a strategy based on leaf area and carbon acquisition through increasing leaf area per unit of biomass to regulate light capture and tissue development.²²

The eastern Andes of Colombia include diverse ecosystems, among which the cloud forest stands out, which represent the greatest favorability for epiphytes. Given the rapid advance of deforestation in the forest covers of these Andean ecosystems and the insufficient information on the behavior of epiphytic plants under different successional stages, it is necessary to understand how they are related. This research aims to explore the relationship of different successional stages with the diversity, assimilation rates and productivity of the different growth forms of vascular epiphytes in a tropical humid montane forest of Andean Colombian.

Material and methods

Study area

The study was carried out in a humid montane forest at Hacienda Los Llanitos, Zaque village of Gachetá municipality (Cund. state) (Figure 1). It is part of the Regional Protective Forest Reserve system,

east of the Colombian Andes. The forest study is located at an altitude of 2800 m., with an average slope and regular temperature of 12°C. The study area is part of the Orinoco basin, with a very pronounced rainy season (mono-model), with a period of maximum rainfall between June and July, followed by lower rainfall between the end and beginning of the year.²³

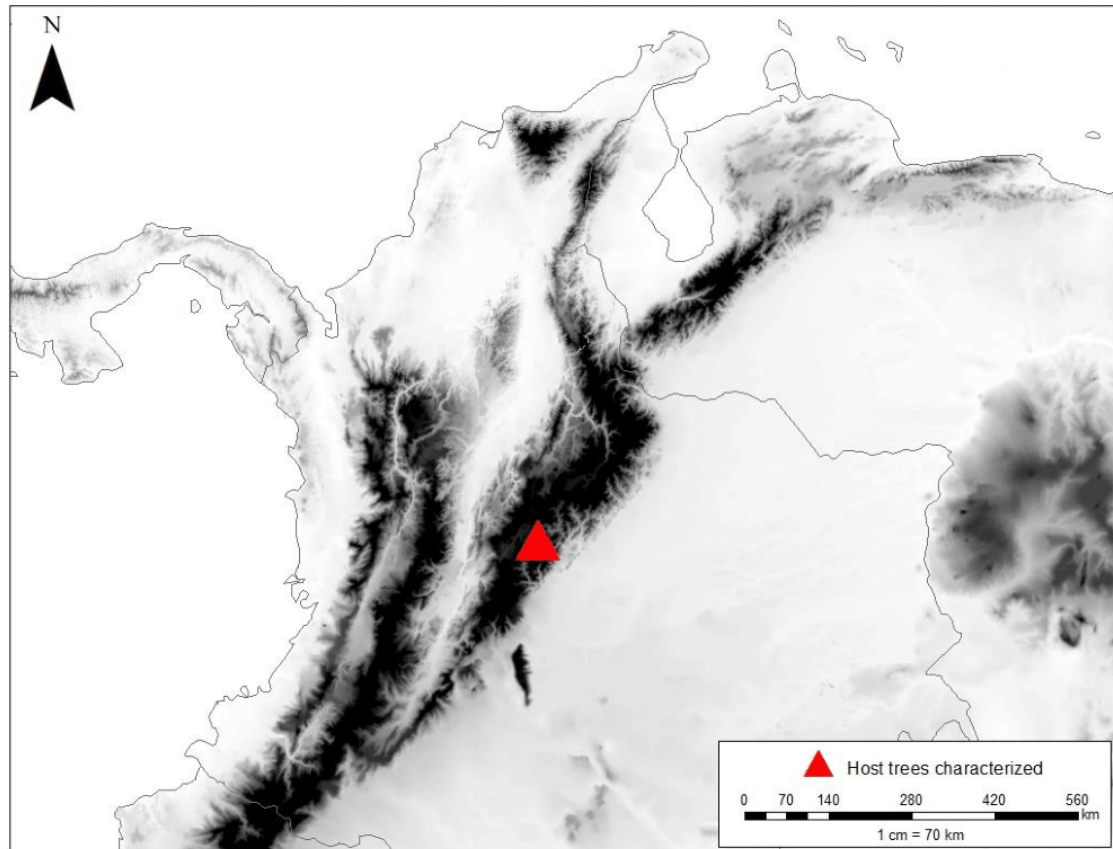


Figure 1 Location of host trees characterized in successional stages in a humid montane forest of Gachetá municipality, Andean Colombian.

Successional stages

- (i) Initial stage, corresponding to a clearing of natural regeneration two years of formation, caused by the natural fall of between five and six mature trees.
- (ii) Intermediate stage, corresponding to patches originally used as grasslands that have been under natural regeneration for the last 30 years.
- (iii) late stage, corresponding to mature forest that has not suffered disturbance or if it did it was more than 50 years ago.²⁴

Epiphytes species classification

- (i) True epiphytes, herbaceous plants with a simple root system attached to the tree (e.g. Orchids).
- (ii) Rosettes, herbaceous plants that grow in compact rosettes attached to trees by short rhizomes (e.g. Bromeliads).
- (iii) Nomadic, herbaceous plants that climb a tree, the roots are usually large and adventitious.
- (iv) Climbing and tree lets plants, woody plants, with roots that generally grow down and around the branches or stem of the host.²⁵

Host selection

We characterize 10 host trees per succession stage, following the RRED methodology.^{26–29} Characteristics related to the size of the host were taken into account- e.g. Diameter at Breast Height DBH,²⁶ the rough cortex,³⁰ and, the possibility of access to the upper canopy strata. The emergent host trees, with accessibility to the crown, had a DBH > 30cm,²⁸ which were accessed with canopy ascent techniques. Each tree was marked, and, its DBH and total height were measured.³¹ The host trees were determined - it was not taken into account for their selection because it could cause some bias in the sampling effort and species richness.²⁹

Diversity

When possible, the number of individuals per species was quantified, but in trees with profuse growth of epiphytes, counting the number of colonies or groups of each of the species was considered the best option.^{28,32} Epiphytic individuals were defined as all independent stems or very close groups of the same species that were spatially separated and distinguished from other stems or groups. In the case of epiphytes with treelets and nomadic habits, they were counted as separate individuals if their rhizomes and stems were not visibly connected.²² From this characterization, samples of vascular epiphytes for each growth form were collected and preserved.

Biomass

It was determined by randomly collecting between ten and 24 foliar individuals by growth form and successional stage, for a total of 31 treelets, 20 nomadic, 36 rosettes and 65 true epiphytic. For the selection of individuals, representativeness was taken into account (richness and abundance of epiphytic species by growth form and successional stage). The samples were taken to the laboratory to dry at 72°C for three days or until there were no variations in the oven dry weight from one day to the next. Biomass in this study is defined as the dry weight of living plants.^{11,25} In addition, the size of the leaf (cm²) was measured for these individuals using a photograph that was processed in the ImageJ program.

Photosynthesis

It was carried out from the characterization of the species in each successional stage, selecting four to 12 individuals of each of the growth forms of the epiphytes between the trunk stratum and lower canopy of the hosts.³³ Photosynthesis was measured from the exchange of CO₂, with the use of a portable photosynthesis equipment.³⁴ The photosynthesis rate was determined *in situ* in two field phases,

- (i) first phase in December 2018 with a portable photosynthesis system LI-6400 (LI-COR) at a light level in the chamber of 300 μmol m⁻² s⁻¹; and,
- (ii) second phase in October 2019 with a LI-6800 portable photosynthesis system (LI-COR) at a light level in the chamber of 500 μmol m⁻² s⁻¹. Assimilation measurements were made on mature, healthy and uniform leaves from the mid-stem region of the individuals between 9,30 and 11,30 hours to ensure a measurement not affected by the daily cycles of plant activity.^{35,36}

Data analysis

An analysis of variance (ANOVA) was applied to determine the

Table 1 Diversity of epiphytic species recorded in the 30 trees sampled in the three successional stages

Growth form	Epiphytic species	Successional stage			
		Initial	Intermediate	Late	Total
Treelets shrubb	<i>Bomarea cf. setacea</i> (Ruiz & Pav.) Herb.	25			25
	<i>Cavendishia bracteata</i> (Ruiz & Pav. ex J.St.Hil.) Hoerold	13	22	157	192
	<i>Dioscorea coriacea</i> Humb. & Bonpl. ex Willd.	19	4	23	46
	<i>Glossoloma ichthyoderma</i> (Hanst.) J.L. Clark			27	27
	<i>Passiflora biflora</i> Lam.		5	3	8
	<i>Peperomia</i> sp.			7	7
	<i>Smilax tomentosa</i> Kunth		3	4	7
	<i>Thibaudia grantii</i> A.C. Sm.		2	12	14
	<i>Anthurium bogotense</i> Schott		6	42	48
	<i>Anthurium cf. longigeniculatum</i> Engl.		2	8	10
Nomades	<i>Anthurium myosuroides</i> (Kunth) Schott		2	28	30
	<i>Anthurium oblongo-cordatum</i> Engl.		7	3	10
	<i>Philodendron</i> sp.		7	19	26
	<i>Greigia</i> sp.		10	3	13
Rosettes	<i>Guzmania gloriosa</i> (André) André ex Mez		3	10	13
	<i>Racinaea riocreuxii</i> (André) M.A. Spencer & L.B. Sm.	10	3	78	91
	<i>Racinaea ropalocarpa</i> (André) M.A.Spencer & L.B.Sm.	13	56	118	187
	<i>Racinaea</i> sp.	5	36	27	68
	<i>Racinaea subalata</i> (André) M.A.Spencer & L.B.Sm.		3	43	46
	<i>Tillandsia biflora</i> Ruiz & Pav.	18	10	7	35
	<i>Tillandsia compacta</i> Griseb.		24	167	191
	<i>Tillandsia restrepoana</i> André	2	1	12	15
	<i>Tillandsia turneri</i> Baker	2			2

differences in the richness of epiphytic species between successional stages. To determine differences in species richness between growth forms (without normal distribution), the non-parametric Kruskal-Wallis test was used. Beta diversity, an abundance matrix of the different species was applied and subsequently an ecological management analysis, using the non-metric multidimensional scaling method (MDS), using the Bray-Curtis similarity index and applying the metaMDS function (McCune & Grace 2002) of "R" program Vegan package, version 2.13.1.³⁷

The total biomass per host tree characterized in each of the three successional stages was estimated. To determine the differences in the biomass of epiphytes between successional stages and between growth forms, the non-parametric Kruskal-Wallis test was used.

An analysis of variance (ANOVA) was applied to determine the differences in photosynthesis rates between successional stages. The non-parametric Kruskal-Wallis test was applied to differences in photosynthesis rates between growth forms. To improve additivity and homoscedasticity, the response variable was log transformed - if necessary. From the data obtained on photosynthesis rates (μmol m² s⁻¹) and taking into account the plant size (cm²) of each of the measured plants, photosynthesis was estimated for the entire leaf of each plant measured in its different forms of growth and successional stages.

Results

Diversity

The 30 trees sampled in the three successional stages housed 4,610 epiphytic individuals corresponding to 54 species (Table 1). Epiphytic richness differed significantly between growth forms (Kruskal-Wallis, P < 0.01). Furthermore, the rosettes were significantly different from the treelets shrubs (P < 0.05).

Table 1 Continued...

Growth form	Epiphytic species	Successional stage			
		Initial	Intermediate	Late	Total
True epiphytes	<i>Cyrtochilum flexuosum</i> Kunth			1	1
	<i>Cyrtochilum megalophium</i> (Lindl.) Kraenzl.			2	2
	<i>Cyrtochilum tetracopis</i> (Rchb.f.) Kraenzl.		10		10
	<i>Elleanthus</i> sp.	80	182	483	745
	<i>Epidendrum aff. frutex</i> Rchb.f.		8		8
	<i>Epidendrum cylindraceum</i> Lindl.		40	38	78
	<i>Epidendrum oxypetalum</i> Hágsater & E.Santiago	27	21	25	73
	<i>Epidendrum scutella</i> Lindl.			4	4
	<i>Epidendrum scytocladium</i> Schltr.			27	27
	<i>Epidendrum sisgaense</i> Hágsater		3		3
	<i>Epidendrum subgrupo</i> Mancum		8	35	43
	<i>Fernandezia sanguinea</i> (Lindl.) Garay & Dunst.		5	40	45
	<i>Fernandezia</i> sp.		10	1	11
	<i>Lepanthes dunstervilleorum</i> Foldats		12	42	54
	<i>Lepanthes monoptera</i> Lindl.		35	72	107
	<i>Lepanthes mucronata</i> Lindl.		26	72	98
	<i>Masdevallia strumifera</i> Rchb.f.		132	94	226
	<i>Oncidium ornithorhynchum</i> Kunth		12	13	25
	<i>Pachyphyllum</i> sp.		2		2
	<i>Platystele consobrina</i> Luer		26	104	130
	<i>Platystele oxyglossa</i> (Schltr.) Garay			113	113
	<i>Pleurothallis coriacardia</i> Rchb.f.			190	190
	<i>Pleurothallis killipii</i> Garay		11	186	197
	<i>Pleurothallis lindenii</i> Lindl.	50	155	275	480
	<i>Pleurothallis phalangifera</i> (C.Presl) Rchb.f.			4	4
	<i>Pleurothallis</i> sp.3	37	63	5	105
	<i>Stelis atra</i> Lindl.	42	82	182	306
	<i>Stelis</i> sp.3		3	8	11
	<i>Stelis chamaestelis</i> (Rchb. f.) Garay & Dunst.	52	24	30	106
	<i>Stelis nutans</i> Lindl.		22	135	157
	<i>Trichosalpinx ligulata</i> Luer & Hirtz	22	18	98	138
Total	45 species	417	1116	3077	4610

The abundance of epiphytes by growth form presented significant differences between true epiphytes and the other three growth forms ($P < 0.02$), as well as between rosettes and nomads ($P < 0.03$).

True epiphytes were the growth form that presented the greatest diversity with 31 species and 3,499 individuals, followed by rosettes (ten species, 661 individuals). The treelets shrubs recorded eight species and 326 individuals, and the nomadic shrubs recorded five species and 124 individuals.

Richness between successional stages differed significantly (ANOVA, $P > 0.0001$), where the initial stage was different from the secondary and late stages ($P > 0.005$). The abundance registered significant differences between the successional stages ($P > 0.005$).

In the initial successional stage, epiphytic species were recorded in the base stratum, with greater richness and abundance for the group of true epiphytes (seven species and 310 individuals) and with a total absence of the nomadic group; The intermediate stage recorded the highest richness and abundance of true epiphytes (24 species and 910 individuals), and the lowest treelets and nomadic shrubs (five species each), and the lowest abundance in the nomadic group (24 individuals). In the late stage, the highest richness and abundance was recorded in the true epiphytes (27 species and 2,279 individuals) and the lowest richness in the nomadic ones (five species and 100 individuals) (Figure 2).

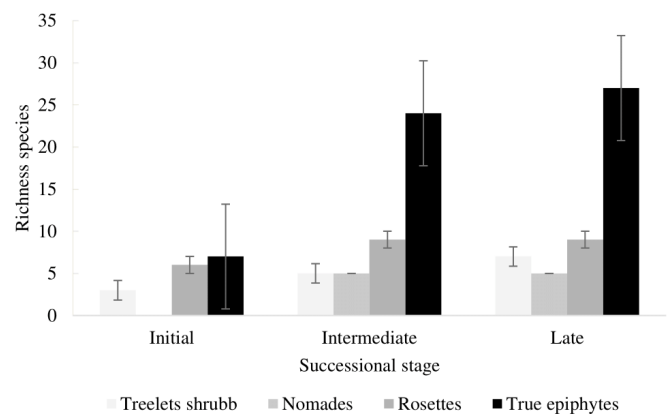


Figure 2 Richness of vascular epiphytes in each growth form reported for each successional stage in a humid montane forest.

The MDS ordination analysis was generated with two dimensions ($R^2 = 0.94$ in a non-linear relationship) under 500 iterations of the original abundance data in the stages, obtaining a stress of 0.197. In the analysis, groupings are observed that represent the different successional stages and the species that are shared between these stages (Figure 3). The greatest closeness occurs between the initial

and intermediate stages due to the rapid advance of the succession in the initial stage, without intervention. Likewise, the late-intermediate stage presents close relationships, suggesting the existence of a successional trajectory with the presence of species representative of advanced stages of the succession (Figure 3).

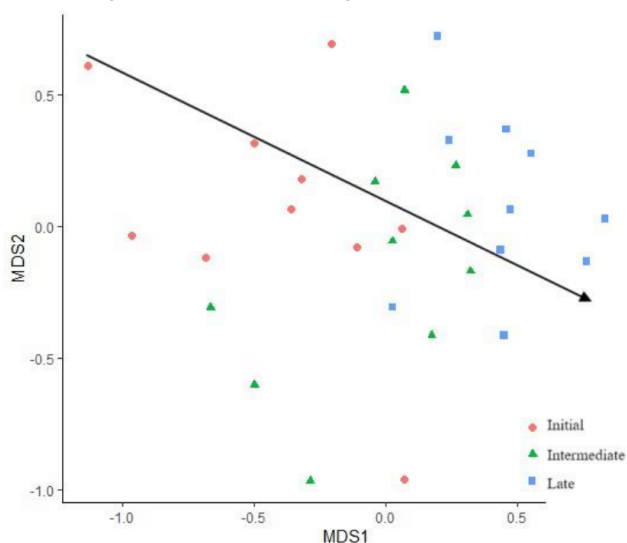


Figure 3 Ordination diagram in MDS for vascular epiphytes present in the three successional stages of a humid montane forest.

Biomass

Biomass did not present significant differences between the three successional stages (Kruskal-Wallis, $P=0.6$). Between growth forms, biomass presented a significant difference ($P < 0.01$), except for nomads and rosettes, which were similar ($P > 0.1$).

The late successional stage presented the highest biomass values per host for all epiphyte growth forms (4,100 gr). The intermediate successional stage presented a biomass value of 1,078 g, with higher values recorded in the rosettes and true epiphytes; the initial stage presented the lowest biomass value per host (480 g), with greater abundance of the growth form of treelets and nomadic shrubs absent (Figure 4).

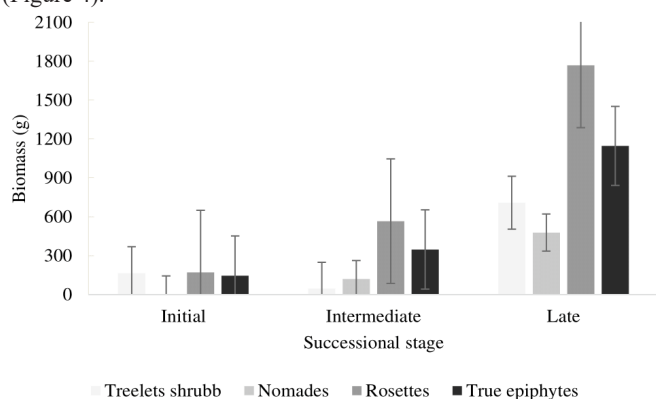


Figure 4 Behavior of biomass per host (g) of epiphytes by growth form through the three successional stages of a humid montane forest.

Rosettes were the growth form with the highest biomass per host (2,503 g) in the three successional stages. Followed by true epiphytes (1,639 g) and treelets shrubs (917 g), with a greater proportion in the initial stage. The values of biomass per host and abundance were lower for the nomads (597 g) in the two stages in which they were recorded.

Photosynthesis

The photosynthesis rates of epiphytes in the initial successional stage presented significant differences compared to the secondary and late stages (ANOVA $P < 0.007$ and $P < 0.005$), while the secondary and late stages presented greater similarity in photosynthesis rates ($P=0.2$). Photosynthesis rates between growth forms were significantly different (Kruskal-Wallis, $P < 0.0009$), where treelets shrubs presented differences compared to true epiphytes ($P < 0.02$), rosettes ($P < 0.03$) and nomads ($P < 0.01$); while nomads, rosettes and true epiphytes were similar in terms of photosynthesis ($P > 0.1$).

Photosynthesis presented the highest average values for the growth form of treelets shrubs in the three successional stages (Figure 5), with a higher value in the initial stage ($5.24 \mu\text{mol m}^{-2} \text{s}^{-1}$) and a lower value in the late stage ($1.92 \mu\text{mol m}^{-2} \text{s}^{-1}$); The nomads follow, with similar values in the intermediate ($1.99 \mu\text{mol m}^{-2} \text{s}^{-1}$) and late ($1.87 \mu\text{mol m}^{-2} \text{s}^{-1}$) stages (absence of this growth form in the initial stage). True epiphytes presented the highest value in the initial stage ($3.68 \mu\text{mol m}^{-2} \text{s}^{-1}$) and the lowest in the late stage ($0.92 \mu\text{mol m}^{-2} \text{s}^{-1}$). The rosettes presented similar values in the three successional stages, with higher values in the intermediate and late stage ($1.32 \mu\text{mol m}^{-2} \text{s}^{-1}$, $1.31 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively) and lower in the initial stage ($1.14 \mu\text{mol m}^{-2} \text{s}^{-1}$).

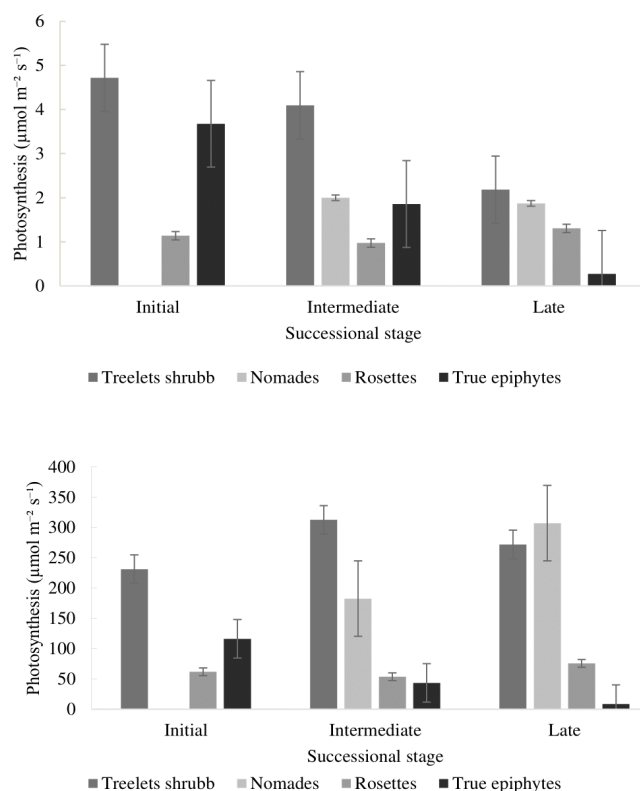


Figure 5 Photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of epiphytes by means of growth form (Top) and plant size (Bottom) of the four growth forms in the three successional stages of a humid montane forest controlled by the quantity of incoming photosynthetic radiation.

The average values of photosynthesis - according to the size of the plant, were higher in the late successional stage for the nomadic growth form ($306.9 \mu\text{mol m}^{-2} \text{s}^{-1}$; Figure 5), followed by the treelets shrubs ($287.3 \mu\text{mol m}^{-2} \text{s}^{-1}$), which presented high values in the other two successional stages; the rosettes presented a higher value in the intermediate stage ($112.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) and a lower value in the initial stage ($61.5 \mu\text{mol m}^{-2} \text{s}^{-1}$). True epiphytes recorded the highest value

in the initial stage ($116 \mu\text{mol m}^{-2} \text{s}^{-1}$) and the lowest in the late stage ($43.1 \mu\text{mol m}^{-2} \text{s}^{-1}$).

Discussion

Diversity

A greater richness, abundance and biomass of epiphytic species was found in the late successional stage compared to the intermediate and initial stages (Figure 2), which suggests a relationship between the abundance of epiphytes and the size of the host tree.³⁸ Older forests have larger surface areas in the trunk and branches, representing a greater supply of habitats and space available for the reception of seeds, colonization and development of biomass.³⁹

The true epiphytes represented the group with the greatest richness and abundance in the three successional stages characterized. These results corroborate what was expected for a family that contains two thirds of the vascular epiphytes in the world and the Neotropics, standing out for their morphological, physiological and distribution adaptations.^{3,40}

It seems that the nomads were the group most affected by the natural disturbance, where no individuals were recorded in the initial successional stage, probably because it is a group that grows only in humid environments.¹ True epiphytes presented the greatest richness in the initial successional stage, but it was affected by the conditions of said stage, given the decrease in richness in relation to the intermediate and late stages. This result suggests that true epiphytes differ widely in their responses to environmental conditions and the heterogeneity that prevails in the different stages and vertical strata of the forest, corroborating what was recorded by Alzate et al.⁴¹

The results of our research correlate with the observations of Benzing,⁴⁰ recording a greater general richness and abundance of epiphytes in the middle part of the tree and the central parts of its crown (trunk, low canopy and middle canopy), which could be related to the fact that these strata are characterized by environmental conditions relatively constant (e.g., humidity, light, temperature) throughout the year.⁴² While the outside of the canopy (external canopy) showed a decrease in richness and abundance, possibly because it was the most exposed area of the canopy.

The ordination analysis suggests a succession trajectory of vascular epiphytes according to composition and abundance. This trajectory suggests a pattern in which pioneer species colonize and dominate early successional phases and are then replaced by later successional phase species. The species that dominated the initial stage have functional characteristics that allow them to resist the strong environmental conditions of drought that characterize the first phases of forest succession.

Another pattern that is evident is related to the availability of substrates for the different growth forms of vascular epiphytes. The composition of true epiphytes and rosettes is largely independent of the degree of development of the initial stages; In contrast, most nomads and treelets shrubs depend on both soil and trunks to establish themselves. Therefore, for nomads and treelets shrubs, substrate availability limits establishment and growth in initial stages that become mature forests, leading to the replacement of species as the predominant successional pattern in successions.²⁵

Biomass

The highest biomass in the growth forms was recorded in the late successional stage compared to the intermediate and initial stage (Figure 4). In the three successional stages, a predominance of rosettes

is observed.⁶ They highlight the development of epiphytic biomass in the cloud forests of Colombia, which may be the result of various factors such as frequent low temperatures, high and permanent humidity, low wind speeds, long-lived trees, orientation of the slopes and high density of tree trunks, among others.

Plant size is one of the variables that can provide information about the use and release of resources to the ecosystem. Our results highlight a greater contribution to the biomass of nomads in the intermediate successional stage, associated with their high weight and size -despite contributing a smaller number of individuals and species. For this reason, measuring the biomass of life forms on host trees will facilitate understanding of epiphyte community structure, and the function and possible contribution of epiphytes to the ecosystem.²⁸

Photosynthesis

The initial successional stage presents the highest average values of photosynthesis compared to the other two stages sampled. Our results suggest greater variation in photosynthesis values between stages for treelets shrubs and orchids, and less variation in average photosynthesis values in the rosette growth form. The rosettes appear to have no noticeable fluctuations in the three stages of succession. The nomads - although they were not recorded in the initial stage, were the second group with the highest average values of photosynthesis for the intermediate and late stages, while the true epiphytes presented the lowest average values of photosynthesis in the late stage. Now, although the growth form of treelets shrubs did not contribute to a greater extent to the richness and abundance of epiphytes in the three stages, the contribution to the biomass of the epiphyte community due to its high weight and size, contributes significantly to the photosynthesis rates and the functioning of the epiphytic community in montane forests,²⁵ being the growth form that presented the highest average values of photosynthesis in the three stages of succession.

In the rosettes, although they generally have a greater photosynthetic capacity,²² a lower rate of photosynthesis is evident in the initial successional stage. Schmidt et al.,⁴³ suggests that it may be determined by the size of the plant, which in this successional stage is smaller. Our data corroborate these suggestions as recorded in the low biomass data for the initial stage. Surely this is because the resulting and more abundant water supply in larger plants may be the immediate cause of the differences observed and related among others to the morphology of the leaf (increase in stomatal density, decrease in trichome density) and leaf physiology (increase in net CO_2 absorption rates, more conservative stomatal behavior, greater residual transpiration, among others). In addition, it is known that young rosette seedlings have a lower tolerance to desiccation than adults; they can withstand at least 65% water deficit without loss of function.⁴⁴

Bromeliads use the C3 photosynthetic pathway, which implies a strong carbon gain, but at the same time imposes high humidity demands, so that in cloud forests this photosynthetic pathway is favored.⁴⁵ However, the forest in our study area is limited in terms of light availability, due to the high and constant cloudiness that occurs, which is why the bromeliads presented low photosynthesis rates. Therefore, these shade-tolerant plants do not actually need shade, but rather require the high humidity of the understory or lower strata of the canopy.^{45,46} In this way, we find species growing both in shaded places and in places with high light exposure. This evidence supports that the great diversification of rosette species is associated with the occupation of an enormous variety of epiphytic niches, from shade-tolerant forms in tropical forests, to light-demanding species that occupy more exposed niches in the forest canopy to drought-tolerant species.⁴⁵

Our photosynthesis data suggest that productivity is highest in the late successional stage for treelets and nomadic shrub growth forms taking into account plant size. Probably due to the contribution of the leaves, which was evidenced by the variable size of the nomadic and treelets plants.²⁵ The physiological behavior of epiphytes is commonly influenced by several factors, such as plant size, because photosynthetic capacity is a function of this variable^{22,43} and environmental conditions.⁴⁷ Our data indicate that - as a group, true epiphytes show low photosynthetic capacities due to limiting environmental conditions and their low leaf area.^{34,43}

Final considerations and recommendations

In Colombia, Resolution No. 213 of 1977 of National Institute of Renewable Natural Resources (INDERENA - today Ministry of Environment and Sustainable Development), declared all species of the Orchidaceae and Bromeliaceae families protected plants, for which it established their ban throughout the national territory. The resolution has implied that for the development or execution of projects, works or activities that require permits or environmental authorization that involve the intervention of closed wild flora species, the competent environmental authority establishes the measures that exist to guarantee the conservation of prohibited species (e.g. ANLA - National Environmental Licensing Authority, and/or, CAR - Regional Autonomous Corporation). These measures may correspond, to the rescue of individuals prior to the intervention of the ecosystems that house them and subsequent transfer and relocation to an ideally equivalent ecosystem. Although these measures have been implemented for several years (approx. 12 years), to date the studies that allow us to know the efficiency of the measures are scarce, therefore, our study suggests:

- i) Carry out research in ecosystems with different conditions (biogeographic districts or life zones) that allow us to understand the ecological and physiological behavior of these plants in different successional stages, in order to investigate which of them and to what degree a relationship exists or association of successional stages and epiphytic species, and thus determine how the characteristics of the stages influence the behavior of the species.
- ii) Evaluate the effect of the transfer in ecological and physiological terms of species in ecosystems with ecosystem equivalence, in order to understand the plasticity or the degree with which said species perform in different successional stages.

In the execution of the measures in Colombia, we recommend:

- i) Carry out a diagnosis of the association of the epiphytic species with the successional stages of the ecosystem to be intervened, in order to determine the characteristics or functional minimums that the species require for their development in the relocation ecosystems (ecosystem equivalence).
- ii) Select the relocation sites contemplating the presence of successional stages with the minimum functional requirements by the species in accordance with their characteristics, in terms of their ecological and physiological plasticity; in order to achieve effectiveness of the measure, it is that is, its establishment, conservation of the genetic pool and fulfillment of ecosystem functions.
- iii) Evaluate theoretically and cartographically the specific sites within the patches of each ecosystem or land cover of relocation, in order to identify those that allow the development of the species, taking into account, among others, factors such as the edge effect

or size of the patches, which condition relevant characteristics for the development and establishment of the species such as light, humidity, precipitation, wind, among others, which will depend on the species object of the relocation measure.

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Conflicts of interest

The authors declare that there are no conflicts of interest.

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