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Surviving in a new host: Eight years of monitoring translocated aroids, bromeliads, and orchids in the Andean forests in Colombia

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Vascular epiphytes are extraordinarily diverse in the tropical Andean region. Compared to trees and terrestrial herbs, epiphytes are more vulnerable to forest alteration due to their structural dependence on trees and environmental requirements. Based on experimental approaches for ecological purposes, monitoring air pollutants, and seeking propagation alternatives, the rescue and translocation of vascular epiphytes (mainly bromeliads and orchids) from a threatened forest to a safer forest has been recently conducted in Colombia. Preliminary assessments indicate that epiphytes benefit from such well-planned measures, and their mortality and survival might be associated with extrinsic and intrinsic factors, which remain to be understood. We evaluated the survival of 16 vascular epiphyte species after translocation into a secondary forest in Antioquia (Colombia) for 8 years. We assessed the role of intrinsic (foliar area, number of leaves, initial pseudobulbs, stems or rosettes, functional group, and epiphyte species) and extrinsic factors (host tree species, bark water-holding capacity, type of substrate, location on the host tree, nutrients, and hormone addition) and the effect of climatic variables on plant survival. The overall mortality rate in this study ranked 1–7% per year, and survival decreased annually, reaching 44% by the end of the 8th year. Host tree species and intrinsic factors such as the functional group and epiphyte species significantly affected the probability of survival. Bromeliads, in particular, exhibited high mortality, which their monocarpic growth form could explain. Another group of species showing high mortality were the miniature orchids, *Masdevalia amanda* and *M. platyglossa*, and are associated with short life cycles. Five host tree species appear to affect the survival of translocated epiphytes; however, the factors or characteristics involved remain unclear. A higher seasonality of precipitation was related to the percentage of overall mortality. This result indicates that extreme precipitation events or drought reduce epiphyte longevity. In conclusion, our study suggests that a wide range of epiphytes may be successfully translocated to secondary forests in the Colombian Andes and demonstrates that the effective introduction of epiphyte assemblages may be useful for ecological restoration efforts in Andean forests.

KEYWORDS

Andean forests, aroids, bromeliads, conservation actions, mortality rate, orchids, survival rate

1. Introduction

Vascular epiphytes are extraordinarily diverse in the tropical Andean region, reaching up to 50% of vascular plant species diversity at a local scale (Gentry and Dodson, 1987a,b). Compared to trees and terrestrial herbs, epiphytes are more vulnerable to forest alteration due to their environmental requirements such as higher humidity and substrate accumulation (Nadkarni, 2000; Köster et al., 2013; Barrancos et al., 2020). Seeds and spores of epiphytes arrive and colonize host trees, increasing species biomass and abundance in a well-established forest (Benavides et al., 2006). During the last few decades, land-use change has dramatically impacted tropical ecosystems, resulting in degraded landscapes with fragmented forests in asymmetric conservation states and submerged in a mosaic of agricultural and livestock patches. This condition affects the dispersion and natural regeneration processes of overall plant communities. It reduces dispersal opportunities for epiphytes, which require well-established and interconnected tree communities (Köster et al., 2009, 2013). However, fragmented forests can recover ecological attributes obtained by the epiphyte assemblage by introducing and maintaining populations of different species (Duarte and Gandolfi, 2013, 2017).

Andean forests in Colombia are home to one of the most extraordinary, highly endemic, and globally threatened diversities of epiphytes. Research on this enormous epiphytic species diversity has significantly progressed in Colombia. However, protecting this unique diversity is restricted to natural reserves and complemented by rescues and translocations of plants growing in forests, which will be destroyed to establish new infrastructure, agriculture, and livestock. Rescues and translocations of plants from forests threatened by extractive activities and land-use change are an alternative for saving epiphytes in Colombia, Brazil, and Peru (Ávila et al., 2017; Fernandez Barrancos et al., 2017). However, increasing pressure from the infrastructure sector requires a deep understanding of the factors associated with epiphyte survival after translocation.

Based on experimental approaches for ecological purposes, monitoring air pollutants, and seeking propagation alternatives, rescue, and translocation of vascular epiphytes (mainly bromeliads and orchids) from a threatened forest to a safer forest have been recently conducted (Malm, 1998; Callaway et al., 2002; Rapp and Silman, 2014). Surveys after 3 years of monitoring indicated that epiphyte survival was associated with both intrinsic and extrinsic factors, such as functional traits and spatial distribution (niche partition; Zotz, 2000; Petter et al., 2015; Duarte and Gandolfi, 2017; Izuddin et al., 2018; Agudelo et al., 2019; Domene, 2019; Faleiro et al., 2020). Studies have also indicated that an epiphyte spatial distribution on the host tree might respond to a niche partition (Wolf, 2005; Reyes-García et al., 2008; Petter et al., 2015; Agudelo et al., 2019). Deep knowledge of factors associated with the establishment and survival of epiphytes after translocation will contribute to maintaining epiphytes, which otherwise might move toward local or even global extinction scenarios.

This study provides the most comprehensive monitoring of translocated vascular epiphytes in Andean forests in Colombia. We evaluated the survival of 16 vascular epiphyte species after translocation into a secondary forest in Antioquia (Colombia) for 8 years. We assessed the role of intrinsic (foliar area, number of leaves, initial pseudobulbs, stems or rosettes, functional group, and epiphyte species) and extrinsic factors (host tree species, bark water-holding capacity, type of substrate, location on the host tree, nutrients, and hormone addition) and the effect of bioclimatic variables on plant survival.

2. Material and methods

Research activities were conducted in northwestern Colombia at 2,300 m in the municipality of Medellin (75° 30′8.04"W, 6°16′54.39"N). The area has an average temperature of 15°C, varying from 5 to 25°C, annual precipitation of 2,000 mm/year, and relative humidity of 89% (SIATA, 2011). The area corresponds to fragmented forests scattered and extensive coverage of cypress pine plantations (*Cupressus lusitanica*). These plantations offer conditions for well-established bryophyte mats on the ground and vascular epiphytes to grow profusely (Morales-Morales et al., 2015; Carmona Higuita et al., 2017).

We collected healthy epiphyte individuals of 16 species corresponding to aroids, bromeliads, and orchids from cypress plantation grounds in November 2013 (Table 1). We assigned functional groups to each species, according to Agudelo et al. (2018, Table 1). Orchids were selected rhizomatous plants with pseudobulbs or stems (corresponding to functional group 7) and ramicuals (FG 3). The bromeliads (FG 4) in this study exhibit sympodial growth; ramets mature by producing a terminal inflorescence, and after flowering, the rosette dies and produces one or two offshoots (rosettes). Aroids, nomadic vines, correspond to functional group 6. We sought initial size conditions to be homogenous among species (Table 1). For aroids, we obtained stem fragments of at least four internodes. Between 33 and 42 individuals per species were attached to the trunk of 70 selected host trees. Host trees were selected adjacent to the nearest tree with a diameter at breast height (DBH) >9 cm, with a straight trunk, and a height of the first branch >4 m. Epiphyte individuals were positioned every 0.5 m (starting at 0.5 m) until reaching 4 m along host trees. The designation of the position and host tree for each individual was randomly selected, except for nomadic vines (aroids), which we located at the base of host trees. Relocated individuals in 35 trees of the 70 trees were irrigated with water during the first 2 months (November and December 2013) and fertilized with phosphorus (Master® 13-40-13), and a synthetic plant hormone from the auxin group, which stimulates root production (Superthrive®), was added. During the same period, watering with sprinklers was conducted after more than 72 h without rain. Half of the individuals of each species were attached to host trees with a substrate made of fique (Sisal) fiber (*Furcraea andina)* or coconut mesocarps fiber (*Cocos nucifera*). We designed a pocket with the fique fiber and added ~40 g of peat. The second substrate consisted of coconut fibers and mesocarp fragments of an average granulometry between 2.5 and 10 mm. We fastened both substrates with strips of cotton and lycra. We registered each individual's initial number of leaves, pseudobulbs, rosettes, or stems. Annually, we registered the survival and the number of leaves until 2021.

A total of five fully expanded and healthy leaves were photographed *in situ* or sampled from three individuals. When it was impossible to get five leaves per individual, we collected additional individuals until we obtained a minimum of 15 leaves per species. We calculated the area from the foliar area mean quantile and multiplied it by the number of leaves registered each year. We considered an individual alive when photosynthetic tissue (green) was evident, and meristems or lateral shoots were present. We reported the formation of flowers or fruits and dry peduncles as evidence of flower formation. Pseudobulbs were recorded at the beginning, but later measurements were not considered due to a high error in the observations because they were hidden by the substrate.

We identified the host tree species, and we determined their maximum water-holding capacity (WHC) at saturation per area. WHC was calculated based on three to five random samples (of ~2 cm^2) that were chiseled from the bark at 1.3 m above ground (three tree species presented only one individual in the area). At the laboratory, each bark sample was cleaned; area and thickness were

TABLE 1 Species functional group [*sensu* Agudelo et al., 2019], initial number of leaves or/and pseudobulbs (p), stems (s) or rosette (r), survival probability z-score, and percentage of mortality at the end of the 8th year*.

Functional group	Family/species	The initial number of leaves ± SD	The initial number of pseudobulbs (p), stems (s), or rosette (r)	Foliar area cm^2 ± SD	Survival probability z-score	Mortality%
	Orchidaceae					
FG 3	*Masdevalia amanda* Rchb.	6.10 ± 4.79		2.02 ± 0.74		46
	Masdevallia platyglossa Rchb.	13.00 ± 8.85		1.04 ± 0.42	-3.36^{***}	47
	Pleurothallis lindenii Lindl.	4.35 ± 1.73		25.17 ± 12.95	-7.41^{***}	12
	Stelis crassilabia Schltr.	7.07 ± 4.40		16.28 ± 13.18	−7.285	15
FG 7	*Cyrtochilum divaricatum* (Lindl.) Dalström	5.38 ± 2.47	2.60 ± 2.47 (p)	17.32 ± 17.72	-5.47^{**}	28
	Dichaea moritzii Rchb. f.	11.73 ± 6.50	4.38 ± 2.92 (s)	5.44 ± 2.08	-6.05^{***}	22
	Maxillaria brevifolia (Lindl.) Rchb. f.	15.63 ± 9.41	4.00 ± 5.46 (s)	1.44 ± 0.88	-2.60^{**}	35
	Odontoglossum sceptrum Rchb. & Warsz.	4.54 + 2.11	2.54 + 2.11 (s)	32.58 ± 19.62	-6.36^{***}	19
	Oncidium cultratum Lindl.	4.49 ± 2.94	2.70 ± 1.08 (p)	8.21 ± 9.36	-5.20^{***}	24
	Bromeliaceae					
FG 4	*Racinaea subalata* (André) M. A. Spencer & L. B. Sm.	10.54 ± 5.18	2.43 ± 0.65 (r)	28.39 ± 14.78		46
	Racinaea penlandii (L. B. Sm.) M. A. Spencer & L.B. Sm.	17.71 ± 11.54	2.18 ± 0.40 (r)	11.37 ± 11.37		44
	Racinaea sp.	9.60 ± 4.56	2.20 ± 0.42 (r)	92.52 ± 19.34		50
	Tillandsia archeri L. B. Sm.	13.63 ± 8.33	2.40 ± 0.84 (r)	36.05 ± 23.50		59
	Tillandsia tetrantha Ruiz & Pav.	13.63 ± 7.97	1.50 ± 0.71 (r)	34.64 ± 13.71		39
	Araceae					
FG 6	*Anthurium nigrescens* Engl.	1.33 ± 1.41		101.97 ±102.46		48
	Philodendron danielii Croat & Oberle	0.79 ± 1.12		102.30 ± 50.45	-6.83^{***}	6

Probability < 0 "***", p < 0.001 "**", p < 0.01 "*".

measured and oven-dried at 60°C for 48 h; their dry weight was determined. Maximum water-holding capacity was determined after soaking the samples in water for 24 h. Excess water was shaken off in a consistent manner, and the samples were weighed again (Einzmann et al., 2015).

Given that epiphyte species seem to be most affected by drought events, four bioclimatic variables related to precipitation dynamics were calculated: annual precipitation amount, precipitation amount of the driest month, precipitation seasonality, and mean monthly precipitation amount of the driest quarter (Karger et al., 2017). These variables were derived from diary precipitation data between 2014 and 2021, obtained from a meteorological station [Santa Helena (27010810)] located at Santa Elena rural township from Medellin (latitude: 6.1969, longitude: 75.5167, elevation: 2550 m asl). This meteorological station belongs to the meteorological monitoring network of the "Colombian Institute of Hydrology, Meteorology, and Environmental Studies" (Instituto de Hidrología, Meteorología y Estudios Ambientaes de Colombia, IDEAM). First, we evaluated variable collinearity among bioclimatic variables and plant survival annual probability and species functional group mortality using the Pearson test. This test allows us to check the dependence among variables, and then, correlated variables were removed. To assess the effect of precipitation bioclimatic variables on plant survival, we performed a multiple linear regression. These analyses were performed using *the stats* R package.

To estimate the probability of survival over time, we used the formula Surv (time, status) ∼1 and the survfit() function to produce the Kaplan–Meier curve. We used the Cox proportional hazards (CoxPH) model to evaluate overall multifactor survival; we ran three models: (a) epiphyte functional groups, substrate, addition or not of fertilization, and height above the host tree; (b) tree species and media WHC; and (c) epiphyte species. The models were constructed using language R (R Development Core Team, 2021) and package survival version 3.2-13 (Therneau and Grambsch, 2000; Therneau, 2022).

3. Results

The initial number of leaves varied between the species at the beginning of the experiment (Table 1). Aroids, *Anthurium* and *Philodendron*, presented 1.1 ± 1.3 leaves (functional group 6). Orchids, rhizomatous with ramicaul stems (FG 3), presented 7.58 ± 6.34 leaves. Rhizomatous plants with pseudobulbs or stems (FG 7) presented 8.28 ± 7.02 leaves, 2.6 ± 2 pseudobulbs, and 4.1 ± 4.5 stems. Bromeliads (FG 4) initially presented 2.3 ± 0.54 rosettes and 13.75 ± 8.46 leaves (Table 1). *Masdevallia platiglossa* showed the mean smallest leaf area (1.02 ± 0.42 cm^2), in contrast to *Philodendron danielii*, the species with the highest mean leaf area (102.29 ± 50.45 cm^2). However, there were no significant differences in the leaf area between species ($F = 1.67$, $P = 0.058$, Table 1). In general, the total leaf area was stable over the years for all species, with the exception of *Philodendron danielii*, which formed new leaves every year (Figure 1).

The host tree's structure was relatively homogeneous (total host tree height 8.2 ± 1.7 m, first branch height 5.2 ± 1.09 m, and DBH 11.2 ± 2.3 cm), and the distance between host trees was, on average, 5.5 ± 4.2 m. Epiphytes were attached to 12 host tree species; *Clusia ducu* was the most abundant species, with 48% of host trees, followed by *Sciodaphyllum trianae* with 10%. Across host species, the maximum water-holding capacity (WHC) content ranged from 21 to 496 mg cm^2, and the statistical result suggests that there is no significant difference between the study tree species bark WHC records ($F = 1.714$, $p = 0.153$, Table 2 supported by Figure 2); however, there was substantial variability in bark WHC within and between tree species (Table 2). The bark thickness ranged, on average, from 1.25 to 3.11 mm (Table 2). Although the measurement of bark WHC has been based on the area, samples chiseled from the bark presented a thickness, giving a volume to the water retention capacity. We checked whether thickness affects water retention capacity in the samples; however, it was not significant ($p > 0.167$; Supplementary material 2).

By the end of the 8th year, 44% of epiphytes survived. Bromeliads, functional group 4, presented the highest mortality, with ∼ 47% of the plants dying at the end of the 8th year (Figure 3C, Table 1). *Tillandsia archerii* was the species with the highest mortality, with 59%. Orchids presented ∼28% of mortality at the end of the 8th year *with Masdevallia* (FG 3), and miniature orchids with ramicuals presented the highest mortality (46–47%). *Pleurothallis lindenii*, with 11%, was the orchid with the lowest net mortality. *Anthurium nigrescens (*FG 6*)* presented high mortality (48%). By contrast, *Philodendron danielii* showed low mortality, with just two plants perishing during the study. Individuals that appeared dead during monitoring (dry and without evidence of photosynthetic tissue) exhibited evidence of survival as the formation of new leaves and living tissue during subsequent monitoring. This phenomenon was observed among 10–16 plants annually, being more frequent in orchids (FG 3, 30%), followed by aroids (24%), and uncommon in bromeliads (3%). All orchid and bromeliad species formed flowers and fruits during the study; 51% (327 individuals) and 31% (195) of the individuals were flowered and fructified, respectively. *Philodendron danielii* was observed initiating flowers in November 2021.

The mortality events, dead plants, fluctuated over the years. A total of 4 years presented mortalities ranging over 5% (37–44 dead plants; 2015, 2017, 2018, and 2019; Supplementary material 1). The annual precipitation amount in the last 8 years was 2,653.37 ± 498.51 mm year^{-1}, where the least rainy years were 2014 and 2015; the precipitation amount of the driest month was 110.5 ± 51.36 mm year^{-1}, the precipitation seasonality was 0.44 ± 0.06 mm year^{-1}, and the mean monthly precipitation amount of the driest quarter was 3.91 ± 1.23 mm year^{-1} (Supplementary material 1). Regarding correlations between bioclimatic variables and survival dynamics, it was found that only precipitation seasonality showed a significant negative effect on the cumulative number of annual dead plants ($r = 0.512$; $p < 0.05$; Figure 4).

In CoxPH, (a) model, type of substrate, location on the host tree, nutrients, and hormone addition showed no significant effect on the probability of survival ($p > 0.01$). By contrast, FG 4, bromeliads, had a significant effect on the probability of survival (Figure 3A). In model (b), five host tree species, and in model (c), nine epiphyte species showed a significant effect on the probability of survival (Tables 1, 2, Figures 3B, C, respectively).

4. Discussion

The overall mortality rate in this study ranked between 1 and 7% per year (Supplementary material 1), which is expected for annual epiphyte mortality (Matelson et al., 1993; Sarmento Cabral et al., 2015; Zuleta et al., 2016). In the Andes, non-mechanical factors, such as desiccation, accounted for a mortality rate of 1.9% per year, and mechanical factors, such as falling branches, accounted for a mortality rate of 5.6% per year (Zuleta et al., 2016). Our study had one of the highest first-year survival rates in the region, in particular for bromeliads and orchids (96 and 98%, respectively, Supplementary material 1). However, this high survival rate, which was within the expected range, did not prevent survival from declining in subsequent years. Enrichments and translocations of the same plant families conducted in forests in Brazil, Costa Rica, and Peru reported lower survivals of 60 and 80% for orchids and bromeliads, respectively (Duarte and Gandolfi, 2017). The particular conditions of the locality, such as high humidity and lower seasonality of precipitation, as well as irrigation during non-rainy periods during this first year, could have favored the survival of the species in this study.

In our study, species and functional groups responded differently over the 8 years of monitoring. Bromeliads (FG 4), in particular, exhibited high mortality, which could be explained by their monocarpic growth form; the plant dies after the fruit is developed. Although under natural conditions, new rosettes would form, and our observations indicated that a large number of the bromeliads detached or turned over, drying out on site, suggesting that no

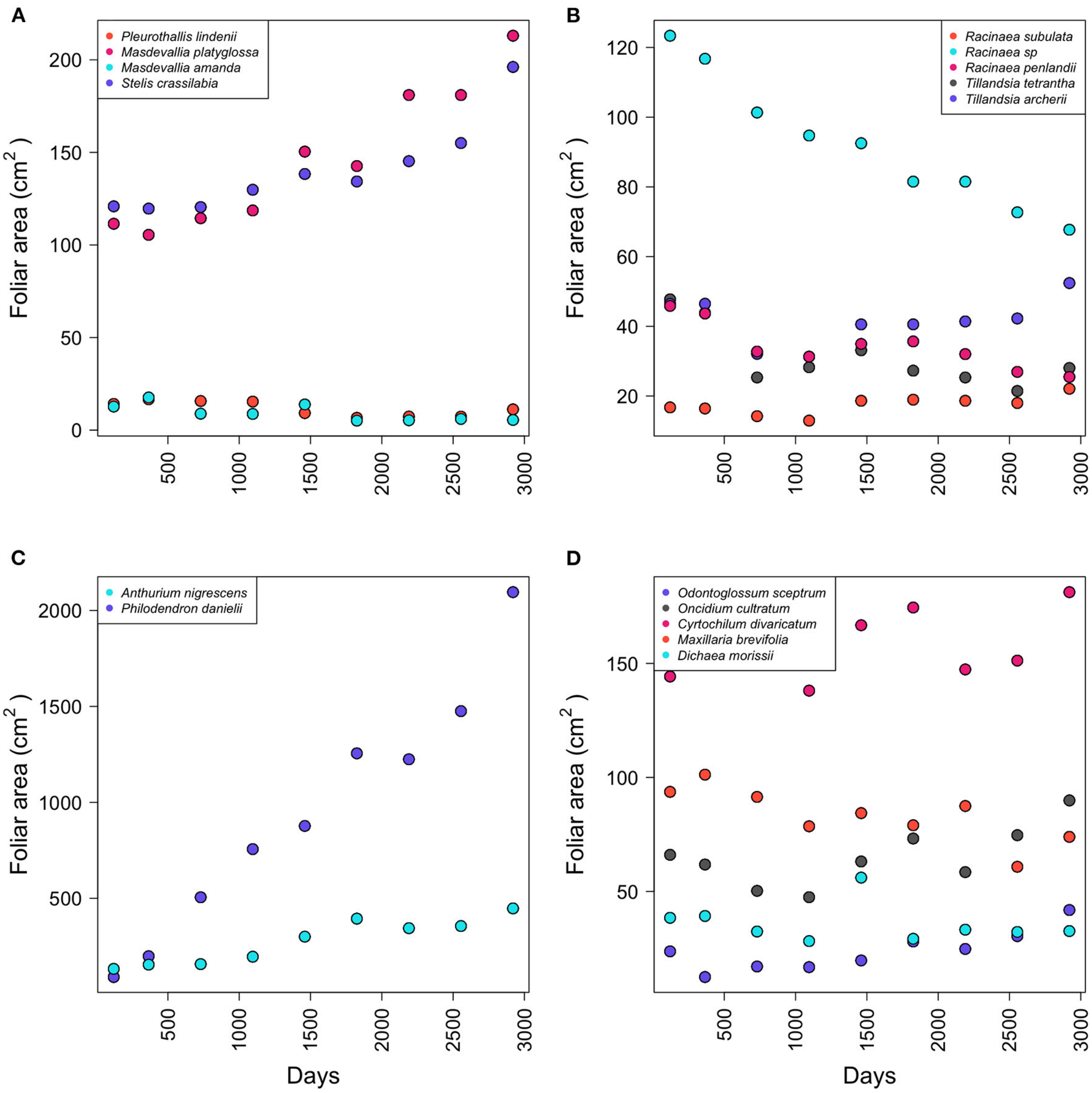

FIGURE 1
Total leaf area by species according to functional group. Epiphytic species correspond to the following functional groups (FG): **(A)** FG3, **(B)** FG4, **(C)** FG6, and **(D)** FG7.

supporting roots were formed, which would limit the establishment of adult plants. Another group of species showing high mortality was the miniature orchids with ramicuals of the FG 3, *Masdevalia amanda*, and *M. platyglossa*. These are associated with short life cycles. However, the presence of seedbeds a few centimeters from the mother plant after 3 years was a remarkable finding for these species. The other species of orchids, FG 3, had longer life cycles and persisted with a stable proportion. The orchids of FG 7, rhizomatous plants with pseudobulbs or stems, presented homogeneous survival percentages below 35% as storage organs for water and nutrients; stems and pseudobulbs play an important role in the survival of orchids. Araceae presented a high contrast between the two species, showing different responses to vegetative reproduction, while *Anthurium nigrescens* presented one of the highest percentages of mortality, which was concentrated in the early years. *Philodendron danielii* showed favorable survival over the years. The ability to reiterate over extended periods of time was surprising; the resilience of many individuals who seemed to be dead for months and had the capacity to reiterate was observed in species of aroids and orchids, which evidences the capacity to reiterate and propagate clonally, as observed in other studies (Lasso et al., 2009; Benavides, 2010), and draws our attention to mortality studies over short periods or isolated observations.

Differences in survival between epiphyte species and functional groups indicate that attention should be paid to the differences required by each species, and therefore, epiphyte adaptations and lifespan must facilitate sexual and asexual reproductive processes that are effective in short periods of time (Zuleta et al., 2016). Although we did not focus on flowering and fruiting, numerous individuals flowered and fructified during this study, indicating the importance of the availability of pollinators in the translocated sites (Phillips et al., 2020). Therefore, it is more likely that epiphyte

TABLE 2 Descriptors of host tree species and the survival probability z-score*.

Tree host species	Average maximum water-holding capacity mg/cm^2 ± desvest	Bark thickness mm	Survival probability z-score
Myrcia cf. *Popayanensis Hieron.*[a]	21.71 ± NA	1.25	
Clethra fagifolia Kunth	98.73 ± 28.01	2.20	−2.739**
Alchornea acutifolia Müll. Arg.[a]	101.11 ± NA	1.59	
Ilex laurina Kunth	110.61 ± 42.42	2.41	
Sciodaphyllum trianae Planch. & Linden ex Marchal	115.70 ± 97.10	1.58	−3.084* * *
Ladenbergia macrocarpa (Vahl) Klotzsch	153.61 ± 61.74	3.02	
Clusia ducu Benth	173.51 ± 78.72	2.39	
Vismia guianensis (Aubl.) Choisy.	198.93 ± 98.84	1.61	−3.525* * *
Persea chrysophylla L. E. Kopp; k	265.23 ± 126.31	3.11	−4.058* * *
Myrcia cf. *Fallax* (Rich.) DC.[a]	267.92 ± NA	2.73	
Chrysochlamys myrcioides Planch. & Triana	296.28 ± 196.05	1.87	
Eschweilera antioquensis Dugand & Daniel	170.91 ± 104.91	1.16	−3.314**

Probability < 0 "***", $p < 0.001$ "**", $p < 0.01$ "*".

[a] Only a single data per species.

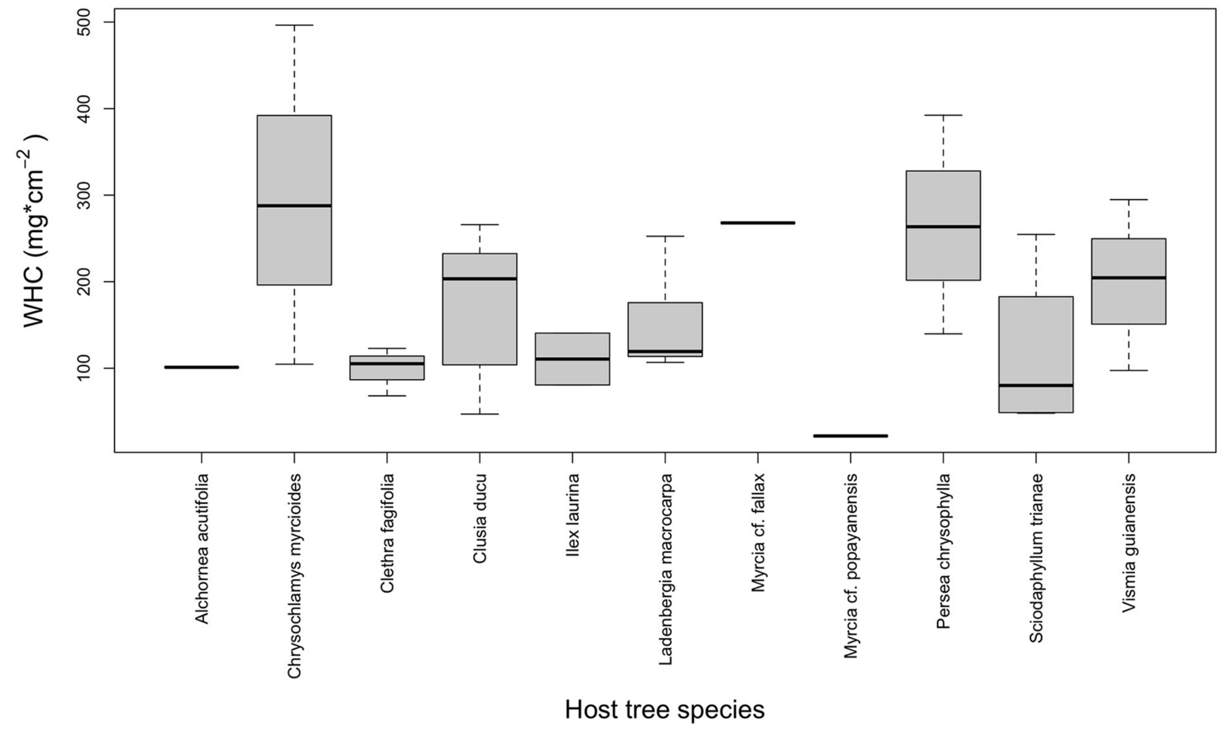

FIGURE 2
Boxplot of water-holding capacity content (WHC) among host tree species.

species producing seeds will increase populations within the forests (Duarte and Gandolfi, 2017). It is also recommendable to explore the viability of these seeds and their established processes to improve conservation outcomes. An unexpected result was the differential effect of survival according to host tree species; five species showed an effect on survival. However, it needs to be made clear which factors or characteristics of tree species affect survival; for example, there is no relationship between structural characteristics that were relatively homogeneous. Species-controlled experiments will be necessary to understand the mechanisms that might be favoring survival in certain species. Moreover, overall annual mortality was not related to other climatic variables associated with precipitation. However, a higher seasonality of precipitation was related to the percentage of overall mortality. This indicates that although epiphytic species are adapted to minimum levels of annual precipitation, they are more affected by extreme precipitation events or drought, indicating that the survival

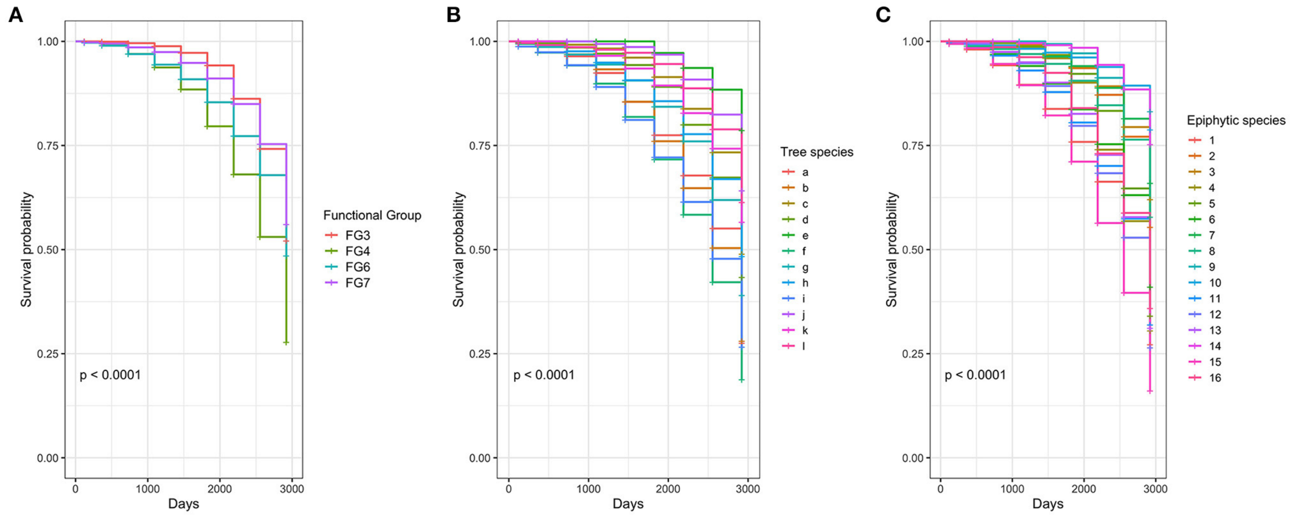

FIGURE 3
Survival probability according to **(A)** functional groups, **(B)** host tree species, and **(C)** epiphytic species. Letters in **(B)** are related to a, *Alchornea acutifolia* Müll. Arg.; b, *Chrysochlamys myrcioides* Planch. and Triana; c, *Clethra fagifolia* Kunth; d, *Clusia ducu* Benth.; e, *Eschweilera antioquensis* Dugand and Daniel; f, *Ilex laurina* Kunth; g, *Ladenbergia macrocarpa* (Vahl) Klotzsch; h, *Myrcia* cf. *fallax* (Rich.) DC.; i, *Myrcia* cf. *popayanensis* Hieron.; j, *Persea chrysophylla* L.E. Kopp; k, *Sciodaphyllum trianae* Planch. and Linden ex Marchal; l, *Vismia guianensis* (Aubl.) Choisy. Numbers in **(C)** correspond to 1, *Anthurium nigrescens*; 2, *Cyrtochilum divaricatum*; 3, *Dichaea morissii*; 4, *Masdevallia amanda*; 5, *Masdevallia platyglossa*; 6, *Maxillaria brevifolia*; 7, *Odontoglossum sceptrum*; 8, *Oncidium cultratum*; 9, *Philodendron danielii*; 10, *Pleurothallis lindenii*; 11, *Racinaea penlandii*; 12, *Racinaea* sp; 13, *Racinaea subulata*; 14, *Stelis crassilabia*; 15, *Tillandsia archerii*; and 16, *Tillandsia tetrantha*.

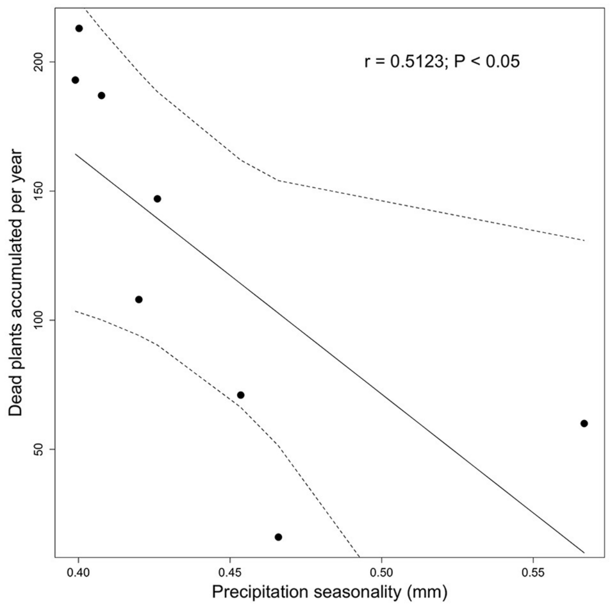

FIGURE 4
Precipitation seasonality vs. dead plants accumulated per year.

probability would be more favored by years with more homogeneous precipitation. This may be essential in order for epiphytes to continue surviving in a rapidly changing climate, as demonstrated by Nadkarni and Solano (2002), who found that increased climatic condition variability may reduce epiphyte assemblage longevity.

Epiphytes have shown a relationship with substrates that allow them to retain water (Dematte and Dematte, 1996; Ghosal et al., 1999). However, differences were not registered after using both substrates (one made of fique fiber and the other made of coconut mesocarp fibers) on individuals from the same species. Natural fibers used have effectively substituted substrates needed for the establishment, which under natural conditions might take years to accumulate (Nadkarni, 2000; Cobb et al., 2001). It is highly recommendable to evaluate the effectiveness of artificial substrates in further studies. Moreover, bark water-holding capacity varied widely among species, and we did not find a direct relationship with survival. In this study, we used plant-associated substrates that can minimize the direct effect of the bark. A similar effect may be occurring in cloud forests, like our site study, where it is common for soil and bryophytes to accumulate massively on top of branches and trunks, forming an interface between the bark and the plants. However, the effect of the bark water retention capacity could be more significant in other ecosystems, such as dry forests or lowland tropical forests with a low presence of fog. In addition, it is important to note that in this study, we only took a measure of the bark water-holding capacity at breast height (1.3 m), but the bark water-holding capacity can vary vertically, and it also depends on the age of the individual and the site conditions (Klamerus-Iwan et al., 2020).

Considering that microclimatic conditions in the first layers of a secondary forest are not expected to vary (Jucker et al., 2018), there was no effect on epiphyte survival within the first 4 m from the base of the host tree, where temperature and humidity facilitate their establishment. Selected host trees did not present branches or bifurcations below the first 4 m from their bases, and therefore, all individuals were positioned on the trunk. However, it is well-documented that branches of the host tree provide higher stability and an opportunity for natural accumulation and retention of substrate for epiphytes (Ingram and Nadkarni, 1993; Zuleta et al., 2016). In our experience, individuals weakly attached to the trunk are more likely to undergo death during the first 6 months after translocation. Therefore, we highly recommend firmly attaching (without movement) individuals to the trunk for at least 6 months, a time in which the majority of them will develop new roots. Moreover, establishing new plants from seedlings or juvenile stages directly in the host tree could guarantee a better long-term establishment of epiphytes, especially for bromeliads (FG 4), allowing the development of holdfast roots, characteristic of these species.

Overall survival of 44% of translocated individuals represents a medium survival percentage. This result indicates that translocation may be an effective conservation action for maintaining individual epiphytes of the selected species in secondary and fragmented forests. Translocation can be a cost-effective measure considering proximity and accessibility to the selected secondary forest and people involved (translocation of 629 epiphytic individuals on 70 host trees took four people and 10 working days). The average cost for the translocation in 2013 for each individual was estimated to be 2.5 dollars (COP 3700), not including technical or professional expenses. As implemented in sites prone to be deforested, this action is an ultimate measure of giving a second chance to these species. Achieving an effective ecological restoration of the epiphyte community requires a deep understanding of the biological aspects of the species as well as their responses to translocation protocols. Colombia's National Development Plan (2018–2022) aims to better leverage natural resources in service to the energy industry, which may increase pressures on the epiphytes assemblages that rely on these same natural areas. However, this context also represents an exciting and promising opportunity to engage local environmental authorities and communities toward biodiversity protection. As local environmental authorities and communities rely on their environments, it is more likely that community-based conservation approaches (engaging local communities in the protection of biodiversity actions) can contribute to protecting forests and their associated epiphyte assemblages. Based on our results, these forests can recover ecological attributes obtained by the epiphyte assemblages by introducing and effectively maintaining populations of different species.

According to the Ministry of Environment and Sustainable Development of Colombia, compensation processes for environmental damage caused to epiphytes (including lichens, bryophytes, orchids, and bromeliads) have mainly focused on strategies of translocation of a determined percentage of individuals to nearby forests and to host trees with similar structural conditions. Details of these processes, such as methods used for plant selection, nursery conditions (or step houses), types of ties used, and type of fertilization, remain to be described. Therefore, documentation and publication of these processes, including successes and failures, are urgently needed. Although compensation is not restricted to reintroduction processes, most compensation processes have focused on it in Colombia. Other measures may include research to generate better management, addressing fundamental questions on epiphyte ecology, adaptation to climate change, and mitigation of species loss. Evaluation of strategies that include propagation from seeds using *in vitro* protocols or nurseries must be included to enhance management and translocation success (Phillips et al., 2020).

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

AB designed the study, monitored each year, and wrote the manuscript. JC-C proved and analyzed the data. All authors jointly discussed and agreed to the final version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2023.834669/full#supplementary-material

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