

Diversifying growth forms in tropical forest restoration: Enrichment with vascular epiphytes



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ABSTRACT

Ecological restoration of forests is largely favored by tree planting, often leaving out other important growth forms. Despite their relevant ecological roles, in restoration plantations, epiphytic richness rarely reaches values found in reference ecosystems. At the same time, epiphytes are wasted when forests are cleared for infrastructure projects, instead of being properly relocated. The goal of this study is to improve the knowledge for epiphytic relocation and enrichment, in restoration forests. We seek to answer the following questions: (i) Over a one year period, can six species of epiphytes survive, attach to phorophytes and reproduce, after being transplanted to host trees? (ii) Is epiphyte development after transplantation affected by species of phorophytes, bark roughness, canopy cover and position of transplantation? (iii) Is performance of relocated epiphytes species specific? For this purpose, 360 adult individuals of vascular epiphytes (Bromeliaceae, Cactaceae and Orchidaceae) were transplanted onto host trees located in two semi-deciduous seasonal forests in the Atlantic Forest of Sao Paulo, Brazil. Epiphytes achieved high survival rates after one year (55.2–100% of individuals) and all species presented structures for either sexual or asexual reproduction. Their overall development was enhanced when we carried out transplantations at the beginning of wet season and using sisal string to attach epiphytes and palm fiber to cover phorophyte's bark, which were relevant factors attributing to the success of transplantations. Species of phorophyte was not an attributing factor to the successful development of transplanted individuals, which only showed slight responses to conditions they provided. However, responses among epiphytes were species-specific, demonstrating the importance of studying their biology in order to successfully enrich restoration forests.

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1. Introduction

In the process of restoring degraded lands for forest restoration projects, planting tree seedlings is a highly favored method (Ruiz-Jaen and Aide, 2005). Meanwhile, the introduction of non-arboreal growth forms has commonly been disregarded. We expect trees to provide vegetative structures which allow other species to establish, assuring the long-term sustainability of forest systems (Rodrigues et al., 2009). Nevertheless, it is common in forests undergoing restoration, specifically in fragmented landscapes, that the diversity of growth forms comparable to reference ecosystems is not achieved after a few decades, including epiphytes (Kanowski et al., 2003; Garcia et al., 2016; Shoo et al., 2016).

Epiphytes are plants that grow on host trees (hereafter phorophytes), using them only for support. Their relationship with phorophytes may vary from incidental to very intimate (Benzing, 1987). In this study we considered only vascular holo-epiphytes (hereafter epiphytes), which are primarily arboreal with no soil contact (Font Quer, 1953). These plants and the organic matter they accumulate can considerably contribute to the biomass of an ecosystem (Nadkarni et al., 2004). Epiphytes develop relying on water and nutrients from atmosphere (Nadkarni and Solano, 2002), depositions and leachates, without taking them from forest floor, thus having an underlying role in biomass input and mineral cycling (Benzing, 1995). They can also retain water and make it available for fauna to drink, to bath, to forage for small insects (Cestari, 2009) and for anurans to dwell (McCracken and Forstner, 2014) and reproduce (Haddad and Prado, 2005). They can provide distinct microhabitats, microclimates and resources for both invertebrates and vertebrates (Cestari, 2009; DaRocha

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et al., 2016; Fernandez Barrancos et al., 2016). In summary, epiphytes maintain a large array of interactions with other organisms and with inorganic components of an ecosystem (Benzing, 1995).

For their relevance shown above, we expect epiphytes to naturally reach forests undergoing restoration and to contribute to their ecosystem processes. These plants, however, rarely reach desirable diversity in restoration forests in short time, which highlights their need for enrichment into these areas (Garcia et al., 2016; Shoo et al., 2016). Most studies regarding seeding or transplantation of epiphytes aim to understand their distribution in natural ecosystems (Callaway et al., 2002; Winkler et al., 2005; Cascante-Marín et al., 2008; Wagner et al., 2013) or to favor conservation of their biodiversity (Nadkarni and Solano, 2002; Mondragon and Calvo-Irabien, 2006; Toledo-Aceves and Wolf, 2008). Nevertheless, research focusing on outcomes of enriching forests undergoing restoration is still very scarce (Jakovac et al., 2007; Fernandez Barrancos et al., 2016).

The need for knowledge regarding enrichment of forests is even more pressing, since there is epiphytic material available for it, which otherwise would be wasted. Infrastructure projects over the world count on legal clear cutting of tropical forests (Correa et al., 2008; Fearnside, 2015; Li et al., 2015), from where epiphytes could be rescued (McCracken and Forstner, 2014). In addition to that, it is common that, in tropical forests, epiphytes naturally fall from host trees, most part of them in healthy conditions. They would eventually die, if left on the forest floor (Toledo-Aceves et al., 2014) and could be collected instead, as shown in Fernandez Barrancos et al. (2016). Using this material to enrich forests undergoing restoration would be an interesting destination for it, solving two problems at once.

Knowledge on how to best carry out enrichment of epiphytes into restoration forests is still lacking (Shoo et al., 2016). However, studies regarding the biology of epiphytes and their relationship with host trees in natural communities may provide clues. Past observations demonstrate that their distribution is not random (Reyes-García et al., 2008; Einzmann et al., 2015). Studies detected host specificities for epiphytes (Callaway et al., 2002; Otero et al., 2007; Benavides et al., 2011). Others found epiphytes distribution to be related to phorophytes' features such as bark roughness (Callaway et al., 2002; Addo-Fordjour et al., 2009), deciduousness (Andrade and Nobel, 1997; Einzmann et al., 2015), size (Wolf, 2005; Reyes-García et al., 2008) and different tree micro-sites (Andrade and Nobel, 1997; Nadkarni et al., 2004; Sillett and Van Pelt, 2007; Einzmann et al., 2015). Wagner et al. (2015) proposed that the association between epiphytes and their hosts can be even more complex, led by a combination of various factors such as epiphyte's and phorophyte's traits and local conditions. Epiphytes' ability to live may vary depending on the availability of favorable microclimates. In general, species abundance decreases in dryer climates (Gentry and Dodson, 1987), though some epiphytes may be tolerant in times of water scarcity (Reyes-García et al., 2008; Larrea and Werner, 2010).

Based on existing information about epiphytes and their symbiotic relationship with phorophytes, this study aims to answer the following questions: (i) Can six species of epiphytes survive, attach to phorophytes and reproduce one year after being transplanted to host trees, in two different forests undergoing restoration? (ii) Is epiphytic development after transplantation influenced by species of phorophyte, bark roughness, canopy cover and position of transplantation? (iii) Is performance of relocated epiphytes species-specific? By answering these questions, we expect to not only contribute to the knowledge on epiphyte enrichment in restoration forests, but also to propose a form to adequately relocate the epiphytes from forests about to be harvested or cleared.

2. Methods

2.1. Study sites

This study took place in two semi-deciduous seasonal forests undergoing restoration (23 years old and 13 years old respectively). Both forests are surrounded by sugarcane plantations, set amongst highly fragmented landscapes. These forests are located within the Atlantic Forest biome, where very little (approximately 11.4–16%) of the original forest cover remains (Ribeiro et al., 2009). In a reference ecosystem within the same vegetation type as these two forests under restoration, Garcia et al. (2016) found 15 epiphyte species.

The first study site (hereafter IRA) is located in Iracemápolis, São Paulo, Brazil (22°34'37"S, 47°30'31"W). Iracemápolis is a city that underwent a severe water shortage in 1986 and, in an effort to improve the watershed quality, a 50 m wide buffer around the main reservoir of the city was established (Rodrigues et al., 1992). Between 1988 and 1990, seedlings of 140 tree species (120 native and 20 exotic) were planted to restore approximately 80 ha of forest within the zoned buffer (Brancalion et al., 2014). After 23 years, no epiphyte was found in this forest (Garcia et al., 2016).

The city of Iracemápolis is located 599 m a.s.l. and has a Cwa climate (humid subtropical, with a dry winter and hot summer), according to Köppen classification. Annual precipitation is around 1333 mm, ranging from 24 mm in July to 248 mm in January. Mean annual temperature is 20.2 °C, varying from 16.5 °C to 23.0 °C in different months (Alvares et al., 2013).

The second study site (hereafter SBO), located in Santa Bárbara D'Oeste, Sao Paulo, Brazil (22°49'12"S, 47°25'00"W), has a restoration forest planted around a water reservoir. In 1998 and 1999, 34,000 seedlings from 72 different tree species were planted (Mônico, 2012) in 30 ha. Two species of epiphytes were present in the forest after 12 years (Garcia et al., 2016).

Santa Bárbara D'Oeste is located 585 m a.s.l.. The climate is classified as Cfa (humid subtropical, without dry season and with hot summer) according to Köppen classification. SBO receives an annual rainfall of approximately 1278 mm, ranging between 28 mm in July and 239 mm in January. Mean annual temperature is 20.1 °C, varying from 16.4 °C to 23.0 °C throughout different months of the year (Alvares et al., 2013).

2.2. Collection of epiphytes

Six regional species of epiphytes from three different families were collected to enrich restoration forests: *Aechmea bromeliifolia* (Rudge) Baker, *Tillandsia pohliana* Mez (Bromeliaceae), *Lepismium cruciforme* (Vell.) Miq., *Rhipsalis floccosa* Salm-Dyck ex Pfeiff. (Cactaceae), *Catasetum fimbriatum* (C.Morren) Lindl. and *Rodriguezia decora* (Lem.) Rchb.f. (Orchidaceae), all of which are classified as holo-epiphytes (Breier, 2005; Neto et al., 2009). For each experiment, 30 individuals from each species were used. We chose the healthiest specimens we could find.

In February 2011, we collected individuals of *A. bromeliifolia* and *R. decora* from phorophytes at a forest that was about to be cleared, in Santa Bárbara D'Oeste, Sao Paulo, Brazil. In March and April 2011, we collected ramets of *L. cruciforme*, *R. floccosa* and *T. pohliana* and pseudobulbs of *C. fimbriatum* from trees at the University of Sao Paulo campus in Piracicaba, Sao Paulo, Brazil. These ramets were transplanted into IRA. From June to November 2011, individuals transplanted to SBO were collected from the same places mentioned above.

We kept all individuals shaded and irrigated until the moment of transplantation. We weighted and measured all specimens

Table 1

Initial sizes of epiphytes - mean fresh weight and standard errors for *A. bromeliifolia*, *T. pohliana*, *L. cruciforme*, *R. floccosa* and *C. fimbriatum* and mean width and standard errors for *R. decora*, in Iracemápolis (IRA) and Santa Bárbara D'Oeste (SBO), Sao Paulo, Brazil.

Family	Species	Weight or width (IRA)	Weight or width (SBO)
Bromeliaceae	<i>A. bromeliifolia</i>	183.28 ± 39.70 g	490.87 ± 58.64 g
	<i>T. pohliana</i>	21.85 ± 5.16 g	39.49 ± 3.57 g
Cactaceae	<i>L. cruciforme</i>	6.13 ± 0.49 g	3.71 ± 0.30 g
	<i>R. floccosa</i>	4.26 ± 0.20 g	5.63 ± 0.39 g
Orchidaceae	<i>C. fimbriatum</i>	56.12 ± 9.87 g	50.93 ± 3.12 g
	<i>R. decora</i>	1.04 ± 0.08 cm	1.58 ± 0.05 cm

(Table 1). Their existing roots and pseudobulbs or ramets were scribed with a permanent marker, so that we could identify new ones in the future.

2.3. Transplantation of epiphytes

In both study sites, we transplanted one individual from each epiphyte species to 30 host trees, at heights of 1.5–3 m in IRA and up to 2 m in SBO. Within each species of epiphyte, we randomly chose the individuals to be transplanted to every tree. Thus, our experiments were carried out using a nested design (Gotelli and Ellison, 2004). For *A. bromeliifolia*, *C. fimbriatum* and *T. pohliana*, in IRA, we previously organized individuals in groups according to size. Only groups within *A. bromeliifolia* showed differences in development, as reported before, in Duarte and Gandolfi (2013).

At IRA, we chose those 30 phorophytes in the following manner: five individuals from each of the six species, differing in deciduousness and bark roughness according to the reviewed literature (Table 2). In April 2011, epiphytes were tied to the trunk of phorophytes using sisal string.

At SBO, 30 phorophytes from three species (differing in deciduousness) were chosen (Table 2). In November 2012, we transplanted epiphytes to the trunks of five individuals of *S. leucanthum* and *E. speciosa* and four individuals of *B. forficata*, and to the forks of five individuals of the two former and six individuals of the latter. Hereafter, we call 'position of transplantation' the categorical variable with the levels 'fork' and 'trunk'. Differently from

Table 2

Species of host trees differing from each other in deciduousness and bark roughness, in a 23-year-old Semideciduous Seasonal Forest, in Iracemápolis (IRA) and in a 13-year-old Semideciduous Seasonal Forest, in Santa Bárbara D'Oeste (SBO), São Paulo, Brazil. References: (1) Lorenzi (1992); (2) Morellato (1991); (3) Backes (2004); (4) Carvalho (2006); (5) Carvalho (1994).

Family	Species	Deciduousness	Bark roughness
<i>IRA</i>			
Boraginaceae	<i>Cordia ecalyculata</i> Vell.	Evergreen ²	Rough ³
Lauraceae	<i>Nectandra megapotamica</i> (Spreng.) Mez	Evergreen ¹	Smooth ⁴
Rutaceae	<i>Balfouriodendron riedelianum</i> (Engl.) Engl.	Semideciduous ¹	Smooth ⁵
Lythraceae	<i>Lafoensia glyptocarpa</i> Koehne	Semideciduous ¹	Rough ³
Lecythidaceae	<i>Cariniana estrellensis</i> (Raddi) Kuntze	Deciduous ²	Rough ⁵
Fabaceae	<i>Centrolobium tomentosum</i> Guillem. ex Benth.	Deciduous ²	Smooth ⁵
<i>SBO</i>			
Fabaceae	<i>Bauhinia forficata</i> Link	Evergreen ²	
Bignoniaceae	<i>Sparattosperma leucanthum</i> (Vell.) K.Schum	Semideciduous ¹	
Fabaceae	<i>Erythrina speciosa</i> Andrews	Deciduous ¹	

what was done in IRA, we previously covered a part of the host tree surface with palm fiber (to retain humidity) and placed the epiphytes on this fiber cover. Then, we tied them to the phorophytes using sisal string and palm fiber (Fig. 1).

2.4. Observation of epiphytes

After transplantation, epiphytes were observed at three months intervals (IRA: July and October 2011, January and April 2012; SBO: February, May, August and November 2012). During observations we recorded if they were dead or alive, attached or not to the host tree, whether they were in reproductive or vegetative stage and counted the number of new ramets produced (hereafter sprouting).

An individual was considered 'alive' when apical meristems or lateral buds were present. An epiphyte was considered 'dead' when it failed to show viable buds for further development. An epiphyte was 'attached' to the host tree when its roots were fixed to the bark. We considered a plant in 'reproductive stage' when it had flowers or fruit and in 'vegetative state' when reproductive material was not present. Finally, to determine 'sprouting', we counted the number of new ramets; i.e. orchids, number of new pseudobulbs; bromeliads, number of new sprouts and cacti, number of new segments of cladodes.

2.5. Measurement of local conditions

Measurement of local conditions included canopy cover over epiphytes and amount of rainfall. In IRA, from June 2011 to April 2012, canopy cover was measured monthly using a concave spherical densiometer, model C, Forest Densiometers, following the method proposed by Lemmon (1957). In SBO, the same measure-



Fig. 1. Transplantation of epiphytes, using sisal string to attach and palm fiber to retain humidity. Santa Bárbara D'Oeste, São Paulo, Brazil, November 2011.

ments were taken from December 2011 to November 2012. It was important to measure canopy cover at each sample point to confirm phorophyte deciduousness, since these data were taken from the literature. Besides, measurements taken by the spherical densitometer could detect potential influence by other plant forms near host tree on canopy cover.

For IRA, to record monthly rainfall from April 2011 to April 2012, we obtained data from the closest meteorological station accessible, “LEB-ESALQ-USP”, in Piracicaba, São Paulo, Brazil (22°42′30″S, 47°38′30″W, 546 m a.s.l., 20 km from the experimental site). For SBO, we used data from the department of water and sanitation (DAE) meteorological station of Santa Bárbara D’Oeste, São Paulo, Brazil, in which monthly rainfall from November 2011 to November 2012 was recorded.

2.6. Data analyses

To answer question (i), we analyzed both study areas for rates of survival, attachment, flowering/fruitleting (percentage of individuals transplanted that survived, attached to phorophytes and presented reproductive material) and sprouting (total number of sprouts produced divided by the number of individuals transplanted) of each species, one year after transplantation. We performed chi-squared tests to estate if rates of survival, attachment and flowering/fruitleting (of all species together) were different between the two areas and Student’s t-tests to estate if each epiphyte species’ sprouting rates varied according to site. We also plotted percentages of individuals for each species of epiphytes that were alive, attached to a host tree and had reached reproductive stage and the number of sprouts produced, every three months. In the same graph, monthly rainfall was plotted to observe if epiphyte development was related to climate conditions.

We had shown, in a previous work, that initial size of *A. bromeliifolia* individuals, in IRA, was an important factor to explain their development (Duarte and Gandolfi, 2013). For the other species in IRA and for all specimens transplanted to SBO, we carried out correlation analyses (using Spearman’s rank correlation coefficient) to estate if sprouting was related to initial fresh weight (for *A. bromeliifolia*, *T. pohliana*, *L. cruciforme*, *R. floccosa* and *C. fimbriatum*) or pseudobulb width (for *Rodriguezia decora*). To estate if survival, attachment and flowering/fruitleting were related to initial weight or pseudobulb width, we performed logistic regressions.

To answer question (ii), we carried out analyses to verify if epiphytes behaved differently according to the species of host tree and the environmental conditions they provided. We performed several chi-squared tests to assess if the number of (1) individuals alive, (2) individuals that had attached to host tree and (3) individuals that presented reproductive material in any observation, one year after transplantation, differed according to (1) phorophyte species (in each study area), (2) phorophyte bark roughness (only in IRA) and (3) transplantation position (only in SBO). For these analyses, epiphytes were not separated according to species; instead individuals of different species were grouped. We also carried out logistic regressions for each species of epiphytes separately, to verify if mean annual canopy cover over each individual affected its (1) survival, (2) attachment to phorophyte and (3) production of flowers/fruit over the one-year period, in each study area. To verify if sprouting was influenced by the species of phorophyte or its features, we performed four different two-way nested ANOVAs, with number of sprouts produced after one year as the dependent variable and the following pairs of independent variables: (1) epiphytes’ and phorophytes’ species (analyses done for each of the two study sites separately); (2) epiphyte species and bark roughness (only in IRA); and (3) epiphytes species and the combination of phorophyte species and position of transplantation (only in SBO). In IRA, we had to perform a box-cox trans-

formation of sprouting data ($\lambda = -0.1$). In SBO, we excluded an individual of *L. cruciforme* from the analyses as an outlier. Finally, to check if sprouting was related to phorophyte’s deciduousness, for each epiphyte species, we performed correlation analyses (using Spearman’s rank correlation coefficient) between the numbers of sprouts produced within a year and mean annual canopy cover on each sample point.

To answer question (iii), we performed chi-squared tests to determine whether the different numbers of individuals that (1) survived, (2) attached to host trees and (3) produced flowers or fruit at any observation, after one year, varied according to epiphyte species, in each study site. To test if sprouting was different among species of epiphytes, we used the nested ANOVA previously mentioned, with number of sprouts produced in one year as the dependent variable and epiphytes’ and phorophytes’ species as the independent variables.

All of the analyses were carried out using the software R (R Development Core Team, 2012).

3. Results

3.1. Canopy cover

Mean annual canopy cover of IRA was 86.91% (± 0.76 SE), ranging from 83.30% in September 2011 to 91.14% in February 2012. SBO had lower canopy cover; with a mean annual value of 76.94% (± 1.68 SE), ranging from 58.66% in September 2012 to 89.08% in November 2012.

3.2. Overall development of epiphytes over time

One year after transplantations, survival rates among different species ranged from 55.2 to 89.7% (IRA) and from 63.3 to 100% (SBO), attachment rates from 6.9 to 86.2% (IRA) and from 33.3 to 96.7% (SBO) and flowering/fruitleting rates from zero to 55.2% (IRA) and 3.3 to 40.0% (SBO). Sprouting rates varied from zero to 0.97 (IRA) and from 0.17 to 1.70 (SBO) (Table 3). Overall survival and attachment rates were higher in SBO ($P < 0.01$) and sprouting was significantly higher in this site for all species ($P < 0.05$) but *A. bromeliifolia* ($P < 0.1$). Of all of the development measurements considered in this study (survival, attachment, flowering/fruitleting and sprouting), initial size of epiphytes was positively related only to flowering/fruitleting for *C. fimbriatum* ($z = 2.271$, $P < 0.05$), *R. floccosa* ($z = 2.514$, $P < 0.05$) and *L. cruciforme* ($z = 2.261$, $P < 0.05$), in IRA, and for *R. floccosa* ($z = 2.014$, $P < 0.05$), in SBO.

Fig. 2 shows increase of attachment and sprouting during the rainy period and flowering/fruitleting peaking at the beginning of this period, in IRA. In this study area, transplantation was carried out at the end of the rainy season, thus there was a period of drought immediately following transplantation. In 13 months, total precipitation was 1365 mm.

Fig. 3 shows increase in attachment and sprouting right after transplantations, in SBO. Flowering/fruitleting was irregularly distributed over the year. Survival rates did not decrease intensely over the year, except for the species *T. pohliana*. In this area, transplantations were carried out at the beginning of the rainy season. Atypically, in 2012, the dry season (April to September, according to Ivanauskas and Rodrigues, 2000) counted on much rainfall. Total precipitation in the 13 months when the experiment took place was 1441 mm.

3.3. Development of epiphytes under different conditions provided by hosts

We did not find any significant effect of host tree species on epiphytes’ survival ($\chi^2 = 5.814$, d.f. = 5, $P = 0.325$, in IRA and

Table 3

Within each species of epiphytes, percentage of individuals that survived (Survival (%)), attached to phorophyte (Attachment (%)) and produced flowers/fruit (Flow./fru. (%)) and mean number of sprouts produced per individual (with standard errors), during one year study period in IRA (Iracemópolis-SP, Brazil) and SBO (Santa Bárbara D'Oeste-SP, Brazil). Means of sprouts showing different superscript letters are statistically different according to Tukey's test at the 0.05 significance level. Survival, attachment and flowering/fruitering rates showing different superscript letters are statistically different according to chi-squared test at the 0.05 significance level.

Epiphyte	Family	Survival (%)	Attachment (%)	Flow./fru. (%)	Sprouts (mean)
IRA					
<i>A. bromeliifolia</i>	Bromeliaceae	75.9 ^{abc}	20.7 ^{cd}	0 ^b	0.79 ± 0.14 ^{ab}
<i>T. pohliana</i>	Bromeliaceae	69.0 ^{abc}	6.9 ^d	0 ^b	0.00 ^c
<i>L. cruciforme</i>	Cactaceae	62.1 ^{bc}	62.1 ^{ab}	13.8 ^b	0.38 ± 0.10 ^b
<i>R. floccosa</i>	Cactaceae	86.2 ^{ab}	86.2 ^a	55.2 ^a	0.00 ^c
<i>C. fimbriatum</i>	Orchidaceae	89.7 ^a	82.8 ^a	13.8 ^b	0.97 ± 0.08 ^a
<i>R. decora</i>	Orchidaceae	55.2 ^c	41.4 ^{bc}	3.4 ^b	0.72 ± 0.12 ^{ab}
SBO					
<i>A. bromeliifolia</i>	Bromeliaceae	100.0 ^a	93.3 ^a	3.3 ^b	1.33 ± 0.14 ^{ab}
<i>T. pohliana</i>	Bromeliaceae	63.3 ^b	33.3 ^b	40.0 ^a	0.17 ± 0.07 ^c
<i>L. cruciforme</i>	Cactaceae	96.7 ^a	96.7 ^a	3.3 ^b	1.66 ± 0.16 ^a
<i>R. floccosa</i>	Cactaceae	93.3 ^a	96.7 ^a	23.3 ^{ab}	0.33 ± 0.12 ^c
<i>C. fimbriatum</i>	Orchidaceae	93.3 ^a	90.0 ^a	16.7 ^{ab}	1.70 ± 0.13 ^a
<i>R. decora</i>	Orchidaceae	96.7 ^a	96.7 ^a	10.0 ^b	1.13 ± 0.09 ^b

$\chi^2 = 0.909$, d.f. = 2, $P = 0.635$, in SBO), attachment ($\chi^2 = 2.267$, d.f. = 5, $P = 0.811$ in IRA; $\chi^2 = 0.592$, d.f. = 2, $P = 0.744$ in SBO), flowering/fruitering ($\chi^2 = 4.942$, d.f. = 5, $P = 0.423$ in IRA; $\chi^2 = 0.329$, d.f. = 2, $P = 0.848$ in SBO) or sprouting ($F = 0.518$, d.f. = 5, $P = 0.762$, in IRA; $F = 0.607$, d.f. = 5; $P = 0.695$, in SBO). Similarly, bark roughness could not be related to epiphytes' development over the one year period (survival: $\chi^2 = 3.292$, d.f. = 1, $P = 0.070$; attachment: $\chi^2 = 0.368$, d.f. = 1, $P = 0.544$; flowering/fruitering: $\chi^2 = 0.801$, d.f. = 1, $P = 0.371$; sprouting: $F = 0.817$, d.f. = 1, $P = 0.368$, in IRA). Furthermore, position of transplantation was not an underlying factor explaining the development of epiphytes either (survival: $\chi^2 = 1.115$, d.f. = 1, $P = 0.291$; attachment: $\chi^2 = 0.148$, d.f. = 1, $P = 0.700$; flowering/fruitering: $\chi^2 = 1.005$, d.f. = 1, $P = 0.316$; sprouting: $F = 0.031$, d.f. = 1; $P = 0.861$, in SBO) (see [supplementary content, Tables S1 and S2](#)).

Mean annual canopy cover was significantly related to development of epiphytes only in some cases. Specifically only in SBO and for species of *C. fimbriatum*, where canopy cover did enhance attachment ($z = 2.124$, $P < 0.05$) and sprouting ($\rho = 0.466$, $P < 0.01$). In IRA, flowering and fruiting of *R. floccosa* decreased according to annual canopy cover ($z = -2.428$, $P = 0.015$). For the majority of species analyzed, we did not find any influence of canopy cover on attachment, flowering/fruitering and sprouting. Canopy cover was not related to survival of epiphytes in any of the study sites either, at the 0.05 significance level.

3.4. Development of epiphytes according to their species

Species of epiphytes showed significant differences in rates of survival ($\chi^2 = 13.438$, d.f. = 5, $P = 0.020$, in IRA and $\chi^2 = 32.284$, d.f. = 5, $P < 10^{-5}$, in SBO), attachment ($\chi^2 = 61.724$, d.f. = 5, $P < 10^{-11}$ in IRA and $\chi^2 = 72.406$, d.f. = 5, $P < 10^{-13}$ in SBO) and flowering/fruitering ($\chi^2 = 51.803$, d.f. = 5, $P < 10^{-9}$ in IRA; $\chi^2 = 21.909$, d.f. = 5, $P < 10^{-3}$ in SBO) among each other. They also produced significantly different numbers of sprouts ($F = 24.703$, d.f. = 5, $P < 10^{-15}$ in IRA and $F = 31.599$, d.f. = 5, $P < 10^{-15}$ in SBO) ([Table 3](#)).

4. Discussion

Transplants of adult epiphytes were successful in both experimental restoration sites, at least in the short-term. Epiphyte species, in different degrees, could survive, attach to host trees and produce flowers, fruit and sprouts, during the one-year period. Despite the fact that our data cannot assure their long-term permanence in their new environment, we cannot either discard the

possibility that epiphytes could establish their populations. Still, studies with longer observation of epiphytes are fundamental to assess the effectiveness of enrichment, since this growth form's development can greatly vary over time ([Mondragón et al., 2004](#); [Zotz et al., 2005](#)) in different species ([Winkler et al., 2007](#)).

Literature concerning transplants of adult vascular epiphytes into restoration forests is still in its infancy ([Carvalho et al., 2007](#); [Jakovac et al., 2007](#); [Fernandez Barrancos et al., 2016](#)). [Fernandez Barrancos et al. \(2016\)](#) achieved survival rates of 65–95% in nine months of studies, in Costa Rica. However, they only considered one bromeliad species. Transplantations of adult epiphytes to mature fragments of the Atlantic Rainforest showed survival rates of 40% when transplanted in the dry season, and 80% when transplanted in the rainy season ([Nievola and Tamaki, 2009](#)). When considering different families of epiphytes, [Jasper et al. \(2005\)](#) obtained mean survival rates of 67% for Bromeliaceae, 73.6% for Orchidaceae and 80.7% for Cactaceae after ten months. Thus, the results we obtained for forests in the process of restoration did not diverge greatly from those obtained in transplantations to old-growth forests, indicating that the former may be as likely for enrichment as the latter.

Literature regarding the seeding of epiphytes in forests showed very low germination rates, between zero and 33% ([Winkler et al., 2005](#); [Mondragon and Calvo-Irabién, 2006](#); [Goode and Allen, 2009](#)), in contrast to greater germination rates obtained under optimum laboratory conditions ([Mondragon and Calvo-Irabién, 2006](#); [Toledo-Aceves and Wolf, 2008](#); [Goode and Allen, 2009](#)). Subsequently, further studies have proposed to germinate seeds in laboratories and then transplant these plantlets/seedlings into forests, though survival rates have been highly variable, ranging from 9.3 to 82.6% ([Zotz and Vollrath, 2002](#); [Toledo-Aceves and Wolf, 2008](#); [Scheffknecht et al., 2012](#); [Wu et al., 2014](#)). The transplants carried out in our study, using adult individuals were very feasible, compared to labor involved in seeding and transplanting epiphytic plantlets. In addition to that, these adult plants present the advantage of having already overcome a long juvenile period ([Benzing, 2004](#)) and being able to reproduce sooner. Thus, if adult epiphyte individuals are available (e.g. in forest which is about to be cleared/suppressed and epiphytes need relocating), transplanting them to forests undergoing restoration could be a potentially viable option, counting on low costs ([Fernandez Barrancos et al., 2016](#)).

In both of study areas, attachment to host trees peaked during rainy seasons, ([Figs. 2 and 3](#)) i.e. IRA: nine months after transplantation and SBO: right after transplantation. As epiphytes depend on precipitation and nutrient deposition, resources become available

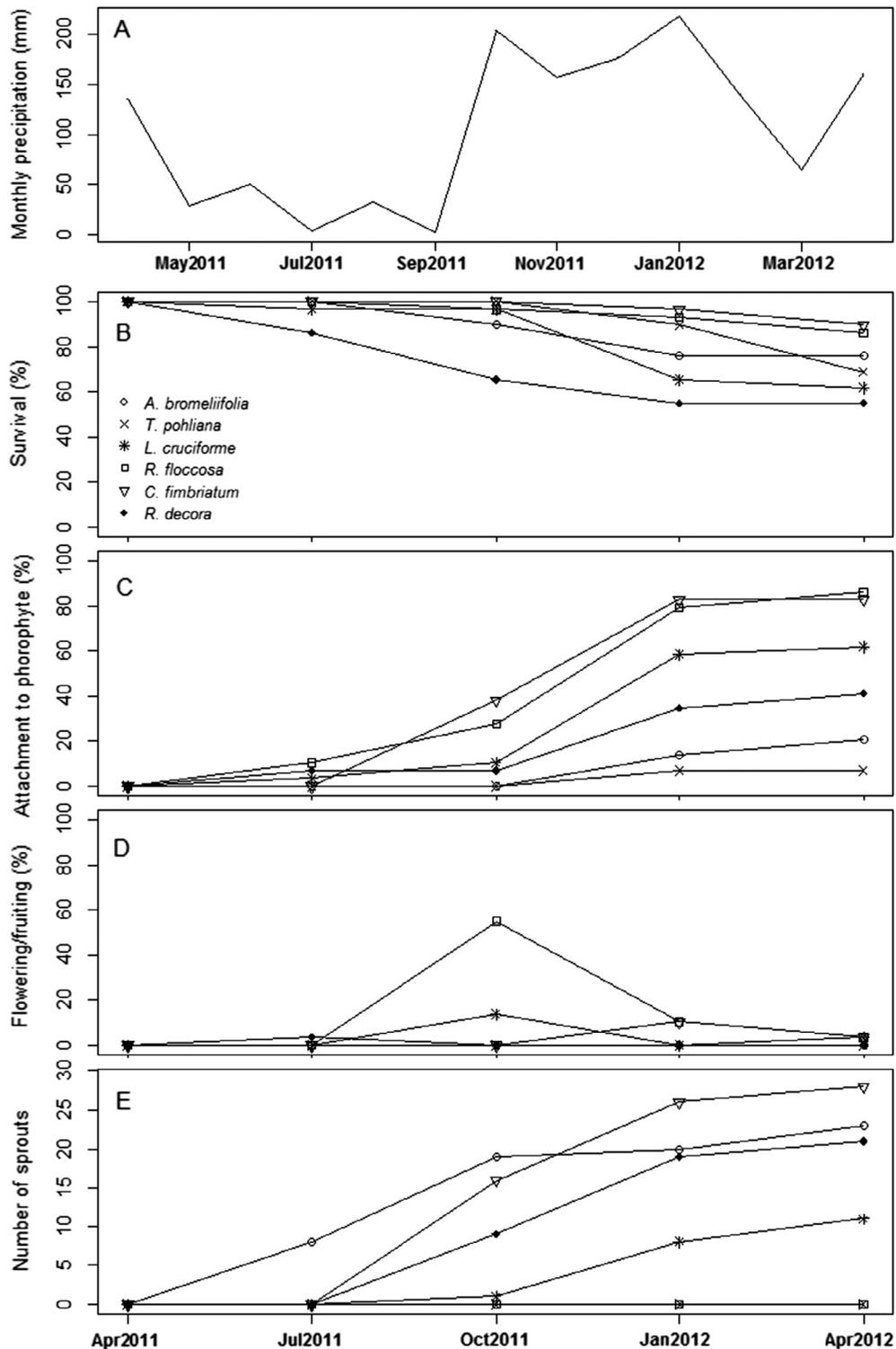


Fig. 2. Monthly precipitation between April 2011 and April 2012 in Itacemápolis-SP, Brazil (A), percentage of epiphytes per species that survived (B), attached to the host tree (C) and produced flowers/fruit (D) and mean number of sprouts produced per individual (E) in each quarterly observation.

for them in pulses and a considerable difference in development can be seen between dry and rainy seasons (Benzing, 2004). Consequently, the material used to tie epiphytes must last until the following rainy season, when plants are more likely to root and attach to trees by themselves. Jasper et al. (2005) found the main reason for epiphyte's mortality was due to their fall from host trees. In our study, sisal string was used as the material to tie epiphytes to their host tree and despite being biodegradable in nature, it was able to

withstand and remain for the year long experiment. Therefore, we recommend the use of this material for transplantation.

Sprouting was higher when long periods of drought were absent (Figs. 2 and 3) since water is one of the most limiting factors for epiphytic growth (Benzing, 2004). Flowering and fruiting peaked at different times. Some species reproduce at the beginning of the rainy season (Liebsch and Mikich, 2009) and others at differing times to prevent competition for pollinators and dispersers

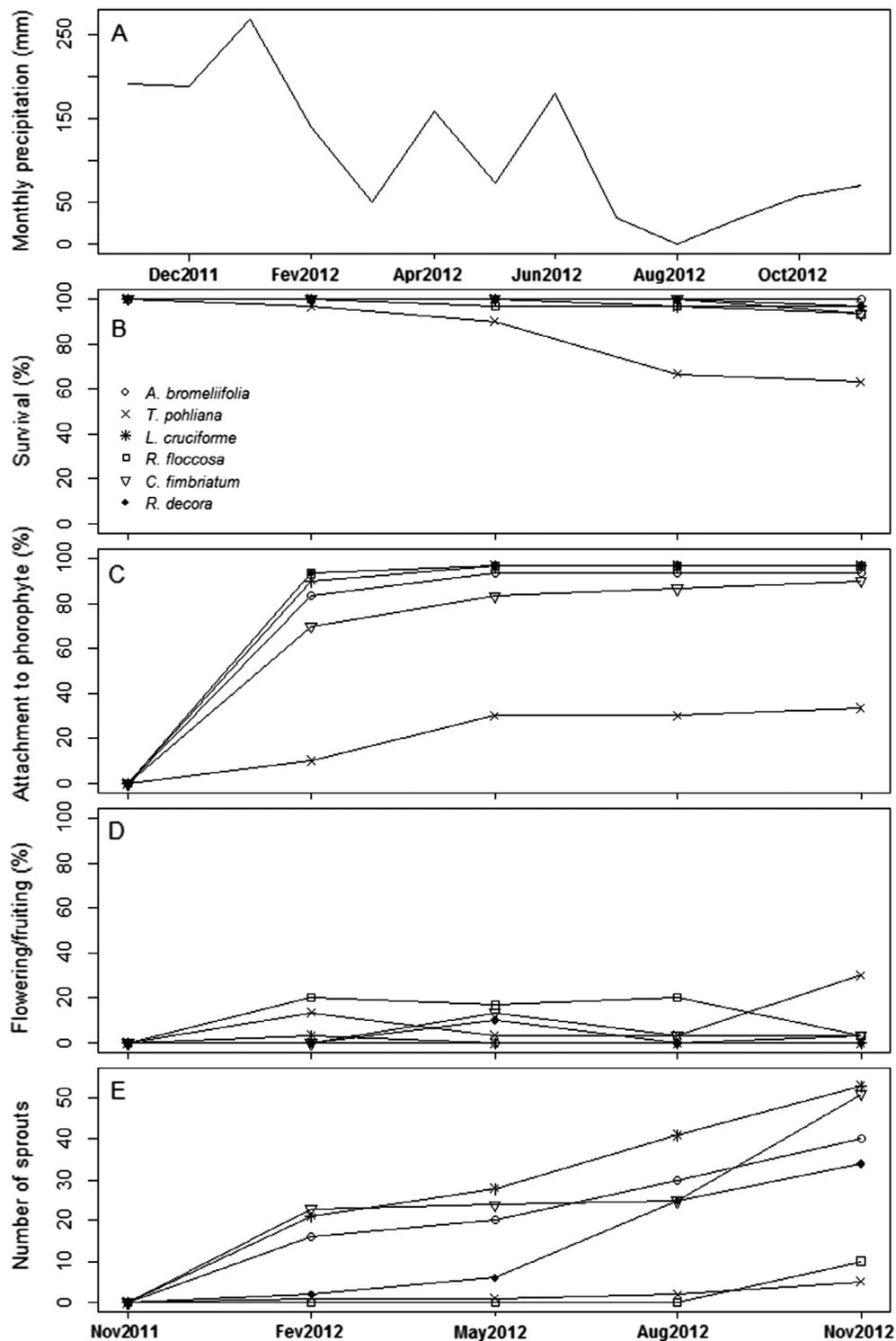


Fig. 3. Monthly precipitation between November 2011 and November 2012 in Santa Bárbara D'Oeste-SP, Brazil (A), percentage of epiphytes per species that survived (B), attached to the host tree (C) and produced flowers/fruit (D) and mean number of sprouts produced per individual (E) in each quarterly observation.

(Ramírez, 2002). It is clear that one year of observations is a short period of time to observe reproduction patterns in epiphytes, as their reproduction cycles are generally slow (Benzing, 2004). In fact, initial stature was related to reproduction, for some species, since it is common for epiphytes to reach a minimum size class before starting to reproduce (Winkler et al., 2007). Nevertheless, for sexual reproduction to be effective (even though autogamy is

common among epiphytes (Benzing, 2004)), some species rely on pollinators (Dulmen, 2001; Tschapka and von Helversen, 2007) and diaspore dispersers (Liebsch and Mikich, 2009). Furthermore, it is essential that seeds can germinate and that seedlings are able to survive, which we did not test. We recognize, in addition to that, that in our experiments epiphytes were transplanted to a very low position on host trees, which could preclude diaspore dispersion.

For further studies, we suggest transplantation to higher positions, since it can favor wind-dispersed species (Mondragon and Calvo-Irabien, 2006).

For most epiphyte species, the SBO study site presented higher values than IRA for survival, attachment and sprouting rates. We may explain this difference by the abundance of precipitation when transplantations took place and by the method of transplantation. The SBO study area only faced water shortage nine months after the beginning of the experiment. Epiphytes tend to suffer greater developmental changes between seasons as opposed to other plants that count on humidity retained in the soil (Benzing, 2004). In forests, rainfall is an important factor to explain abundance of natural epiphyte populations (Deng et al., 2008). Availability of water in the SBO study site was an underlying factor contributing to the survival of epiphytes during the stressful period after transplantation. In addition, the use of palm fiber cover under the epiphytes may have reinforced a greater contact area for these plants' structures to absorb water and nutrients available in the trunks of phorophytes. According to Taiz and Zeiger (2006), for new roots to arise, there must be water and minerals in the adjacent space (i.e. tree trunk surface). Consequently, the use of palm fiber, along with constant precipitation, could have enhanced rooting. Nevertheless, there may be a large array of factors varying between the two forests that were not taken into account in this study and that could be important to explain better epiphyte performance in SBO. For instance, since very few studies have been carried out regarding transplants of epiphytes to sites undergoing restoration (Jakovac et al., 2007; Fernandez Barrancos et al., 2016), little is known about the effects forest age could have on its permeability for enrichment. Environmental conditions specific to each forest could have influenced epiphytes' responses as well.

Host tree species was not related to epiphyte species' performance, as we had found out for *A. bromeliifolia* (Duarte and Gandolfi, 2013). Intraspecific traits may be more divergent than interspecific traits (Hubbell, 2005). Thus, individuals of the same host species will not always necessarily provide the same conditions. Moreover, neighboring trees can influence regions within a forest (Potvin and Dutilleul, 2009) as ecosystem engineers (Wright and Jones, 2006). Thus, an epiphyte does not suffer influences solely from its phorophyte, but also from different trees in a forest.

Bark roughness of phorophytes was not related to epiphyte development either, as we had reported before for *A. bromeliifolia* in IRA (Duarte and Gandolfi, 2013). In forests undergoing restoration, trees may be too young to fully express these features. The older and more mature the trees are, the more likely they are to diversify aspects of their bark and provide distinct micro-habitat environments (Flores-Palacios and Garcia-Franco, 2006; Wagner et al., 2015). In addition to that, by transplanting adult individuals directly to host tree, the initial challenges involved with colonization (fixation and germination of seeds and establishment of plantlet *in situ*) are overcome, a process which bark roughness could strongly influence (Callaway et al., 2002).

Transplantation position (trunk or fork) did not affect epiphyte performance, even though some studies showed that forks are able to accumulate sufficient water and nutrients that can enhance epiphyte development (Andrade and Nobel, 1997; Sillett and Van Pelt, 2007). In our study, the palm fiber used may have masked the effects of the fork, since this fiber can hold humidity and nutrients. Nonetheless, there is the future possibility that forks will serve as support for the epiphytes that were not able to root and attach to the host tree. Therefore, it may be more efficient and effective to attach epiphytes to forks instead of trunks for long-term success.

Some epiphyte species responded positively to the amount of light measured within the area they were transplanted to. At IRA,

a denser canopy cover was recorded and individuals of *R. floccosa* that experienced greater light exposure had higher reproduction rates. This can be explained by a faster sexual maturation in areas that boast a more open environment (Cascante-Marín et al., 2006). In SBO, a more open environment, the species *C. fimbriatum* showed higher sprouting and attachment rates under a denser canopy cover. Studies have shown that light stimulates production of gems and shade stimulates tissue elongation in this orchid species (Moraes and Almeida, 2004; Suzuki et al., 2010). To explain the pattern observed in our study, individuals could have received light stimulus during the dry season to produce buds (Fig. 3) and then those which were located in shaded areas received stimulus to elongate pseudobulbs and roots.

Epiphyte species differed greatly among each other regarding survival and development. Such differences in mortality and reproductive abilities may lead to distinct populations within a community (Nadkarni and Solano, 2002; Winkler et al., 2005; Cascante-Marín et al., 2009). However, our objective here was not to define which species are most successful in transplantations and which are the most dominant epiphytes, but instead, to perform effective transplants for as many species as possible. This highlights the importance of understanding the biology of epiphyte species in order to make successful transplantations. One important outcome is that it would be recommendable to do pilot tests before transplanting threatened species, to previously check if this is the best relocation for them.

An interesting observation found during this study was that species that were not very successful in producing flowers and fruit could perform better in sprouting and vice versa. Studies show that plants maintain trade-off between allocating resources to sexual reproduction or vegetative propagation (Sutherland and Vickery, 1988; Westley, 1993), which is justified by the fact that epiphytes do not have access to large amount of resources (Zotz, 2000). From an ecological point of view, we can say that all species could invest in either sexual or asexual reproduction and, consequently, in their persistence of a new environment, which is an encouraging result.

5. Conclusion

Results obtained from this study indicate that enrichment of forests undergoing restoration can be a successful short-term and potential long-term investment. Even though we were not able to affirm the long-term survival and development of the epiphyte transplantations against ecological filters and persistence in the new environment, they have at least played a temporary role in the community during the course of their existence. Epiphytes' presence in an ecosystem can provide micro-habitats, water, food (Cestari, 2009; Fernandez Barrancos et al., 2016) and even pollen (Dulmen, 2001), seeds (Cascante-Marín et al., 2009) and ramets (Callaway et al., 2002). Our transplanted plants were able to stay in the area for one year and, at least temporarily, contribute to its enrichment. This study showed that simple cost effective techniques (Fernandez Barrancos et al., 2016) in conjunction with practical and efficient methods can create resourceful habitats for epiphytes from areas to be clear-cut, and use them to enrich forests undergoing restoration. Nevertheless, we still lack information regarding population dynamics of epiphyte species after transplanted, in order to establish a viable number of individuals to use for an effective enrichment, especially in a context of global climate changes (Mondragón et al., 2004). Future research may involve further study into the knowledge gap in the relationship between restoration forests and epiphytes, especially regarding their long-term permanence in the new environment, to further increase the success rate of epiphyte enrichment.

Author contributions

SG, MMD conceived the research; MMD, SG set up experiments; MMD carried out field observations; MMD performed statistical analyses with help of professionals; MMD, SG discussed data; MMD wrote manuscript; SG edited manuscript.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.06.063>.

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