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GERMINATION AND SEEDLING ESTABLISHMENT OF EPIPHYTES IN MEXICAN FORESTS AND COFFEE PLANTATIONS

Dissertation
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Eingereicht von
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“To copy one paper is plagiarism, to copy many is scholarship”

Anonymous

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Abstract

Shade coffee plantations can be important refuges for epiphytes, but are not suitable for all species. To test if the performance of early life stages, often the most sensitive phase, is responsible for the species' ability to colonize coffee plantations, we compared germination, growth and mortality rates of epiphyte species that differ in their ability to colonize shade trees in coffee plantations in central Veracruz, Mexico. We tested if germination rates of three bromeliad species (*Tillandsia juncea*, *T. heterophylla* and T*. viridiflora*) were related to their distribution between the three different habitats (forests, old coffee plantations and young coffee plantations) and to what extent either substrate or microclimate affected germination rates. We analyzed growth and mortality rates of transplanted juveniles of the same three bromeliad species and of two orchid species (*Jaquiniella teretifolia* and *Lycaste aromatica*) to see if the different habitat features affected growth and survival of plants. We also tested if tree and branch characteristics were related to growth and survival of the epiphytes growing on them. We found that germination rates, growth and mortality of our study species generally reflected the natural patterns of species occurrence and abundance in the three habitats, with species restricted to forests showing lower germination rates (*T. viridiflora*) and lower growth and survival rates (*T. viridiflora*, *L. aromatica*) in coffee plantations compared to forests, whereas the colonizing species showed higher germination rates (*T. juncea*) and higher growth rates (*T. juncea*, *J. teretifolia*) in coffee plantations. In coffee plantations, herbivory had a severe effect on some of the bromeliad juveniles during part of the wet season. Given the substantial contribution of herbivory to the mortality of juvenile plants and the significant differences between habitats, herbivory may partly impede the colonization of young coffee plantations by some epiphytic bromeliads. Our results also suggest that higher mortality rates of the forest species, at least of *L. aromatica*, as well as lower growth rates may co-limit the colonization of coffee plantations, especially in young plantations with small shade trees. We also found that a more humid microclimate favors germination and growth of the species restricted to forests.

Kurzfassung

Durch den Verlust natürlicher Lebensräume sind Kaffeeplantagen mit Schattbäumen zu wichtigen Refugien für viele Epiphytenarten geworden. Nicht alle Arten besitzen jedoch die Fähigkeit, auf diese Sekundärhabitate auszuweichen. In Zentralveracruz, Mexiko, untersuchten wir anhand von Keimungs- und Transplantationsversuchen, ob die Entwicklung in den frühen Lebensphasen von Epiphyten einen Einfluss auf ihre Fähigkeit hat, Kaffeeplantagen zu besiedeln. Dazu wählten wir Bromelien- und Orchideenarten mit unterschiedlicher Habitatpräferenz: A) reine Waldarten (*Tillandsia viridiflora, Lycaste aromatica*), B) Arten, die auch alte Schattbäume besiedeln (*Tillandsia heterophylla*) und C) Arten, die in der Lage sind, auch junge Schattbäume zu kolonisieren (*Tillandsia juncea, Jaquiniella teretifolia*). Wir untersuchten, ob die Keimraten der drei Bromelienarten im Zusammenhang mit ihrem Vorkommen in drei ausgewählten Habitaten (Wald, alte und junge Kaffeeplantagen) stehen, und in welchem Ausmaß Substrat und Mikroklima dabei eine Rolle spielen. Wir analysierten die Wachstums- und Mortalitätsraten von transplantierten Jungpflanzen aller fünf Arten, um herauszufinden, ob die unterschiedlichen Habitatbedingungen Wachstum und Mortalität beeinflussen. Unsere Ergebnisse zeigten einen deutlichen Zusammenhang zwischen Keim-, Wachstums- und Mortalitätsraten und dem natürlichen Verbreitungsmuster bzw. der Abundanz der untersuchten Arten in den drei Habitaten. Waldarten wiesen eine geringere Keimrate (*T. viridiflora*), geringere Wachstums- und höhere Mortalitätsraten (*T. viridiflora, L. aromatica*) in den Kaffeeplantagen auf, während die Siedlerarten dort höhere Keimraten (*T. juncea*) und höhere Wachstumsraten (*T. juncea, J. teretifolia*) zeigten. Während der Regenzeit wurde Wachstum und Mortalität der Bromelienarten in den Kaffeeplantagen (v.a. in den jungen Plantagen) gravierend durch Herbivorie beeinflußt. Höhere Mortalität und geringeres Wachstum scheinen ein limitierender Faktor bei der Besiedlung von Kaffeeplantagen durch die Waldarten zu sein, besonders bei jungen Plantagen mit niederen Schattbäumen. Ein feuchtes Mikroklima hingegen begünstigt Keimung und Wachstum dieser Arten. Angesichts des wesentlichen Beitrags von Herbivorie an der Mortalität von Jungpflanzen und des signifikanten Unterschieds dieses Einflusses zwischen den Habitaten, scheint Herbivorie für das Fehlen bestimmter Bromelienarten in jungen Kaffeeplantagen zumindest mitverantwortlich zu sein.

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1 Introduction

1.1 Biodiversity of humid montane forests in Mexico

Tropical montane rain forests are among the most species-rich forests worldwide. In Mexico, humid montane rain forest (bosque mesófilo de montaña) occupies only 0.8 percent of the territory but contributes 10 percent to Mexican biodiversity. It contains about 2500 plant species that grow preferentially or exclusively in this type of forest which accounts for 10 to 12 % of all estimated plant species of Mexico and which makes it the most species-rich forest compared to the area it occupies (Williams-Linera 2007). The organisms of the rain forest constitute a very diverse community. The high diversity is mainly a consequence of the great topographical and micro-environmental heterogeneity. We find a high number of endemics in plants (750 species), reptiles (102 species), amphibians (100 species), birds (201 species) and mammals (46 species) (Rzedowski 1996, Challenger 1998). Humid montane rain forest is the vegetation type with the largest number of epiphyte species with orchids, bromeliads, ferns, peperomias and mosses being the most abundant. In these forests, epiphytes account for 32 percent of vascular plant species, followed by shrubs and herbs (each 24%), trees (18 percent) and lianas (2 percent) (Williams-Linera et al. 2002).

1.2 Forest loss and fragmentation in cenral Veracruz

In Mexico, more than 50 percent of the area of humid montane forests has been lost (Challenger 1998). In the state of Veracruz the situation is even worse as the percentage of humid montane rain forest converted to other land uses is much higher than for all other tropical forest types (Doumenge et al. 1995, Aldrich et al. 2000). Until the beginning of the last century, the region around Xalapa had large extensions of continuous forest. In 1993 only 10 percent of undisturbed forest remained in central Veracruz, a percentage which probably has further decreased in the last years. Natural forests are mostly reduced to fragments on slopes, hill tops and in canyons, where the topography has impeded destruction. Since the 1960s, population increase has been one of the main causes for forest loss (Marchal & Palma 1985, Williams-Linera et al. 2002). Muñoz-Villers & López-Blanco (2007) analysed land use changes between 1990 and 2003 in central Veracruz and found depletion of tropical montane cloud forest to be by far the most important change over that period. The dominant land uses in the region are pastures (37 percent), urban zones (18 percent), secondary vegetation (17 percent) and disturbed forest (17 percent) (Williams-Linera et al. 2002).

Several studies have shown that humid montane forest and its biodiversity are especially sensitive to changes caused by fragmentation (e.g. Kattan et al. 1994, Williams-Linera et al. 1995, Bruijnzeel et al. 2010). The high number of endemic species makes this forest type particularly susceptible to species loss through fragmentation (Turner 1996). Habitat destruction directly reduces animal and plant populations and increases the risk of local extinction (Barthlott et al. 2001). The vulnerability of a species to fragmentation and to the danger of extinction depends on its specific conditions like rareness and population size. Habitat loss not only leads to a decrease of population size but inhibits or reduces the immigration of individuals between patches and isolates the population. Fragmentation increases the isolation of populations and can lead to the erosion of genetic variability (Young et al. 1996). The degree to which fragmentation affects genetic variability is depending on several factors like size and spatial isolation of remnant forest patches, elapsed time since land-use changes and traits inherent to the species (e.g. longevity, pollination, reproduction and dispersal mode). Edge effects change forest microclimate up to 60 m into the forest interior (Kapos 1989, Laurance 2004) and increase tree mortality (Williams-Linera 2002, Laurance et al. 2011), and are influenced by edge age, the number of nearby edges, and the quality of agricultural matrix between fragments.

Small forest fragments are often different in their species composition compared to the original forest, and the species richness can decrease in time. Still, due to the environmental heterogeneity of the region, each of these fragments contains plant populations that are only able to exist in those fragments because of the micro-environmental conditions special to this site, because of recent or past historical events or stochastic processes. Even small fragments can play an important role in plant population dynamics and in the plant composition at local and regional level (Williams-Linera et al. 2002). Therefore we need more information on the species response to landscape properties, like the area of fragments, the grade of isolation, and the type of matrix surrounding the fragments.

Fragmentation alters ecological processes like pollination, seed dispersal, nutrient cycles, and the consequences can indirectly affect many other species. In addition to efforts to protect remaining forests remnants, the management of the surrounding landscape matrix plays an important role in the conservation of forest species (Chazdon et al. 2009). High-quality agricultural matrix with vegetation types more closely resembling nearby forest fragments, especially shade-tree agroecosystems, can buffer the effects of fragmentation and serve as important refuges for forest species (e.g. Perfecto et al. 1996, Hietz 2005, Perfecto et al. 2007, Philpott et al. 2008)

1.3 Coffee agroecosystems in Mexico

Mexico occupies the 8th place in global coffee production with 781 million ha of cultivated area (SIAP 2010, FAO 2010). In Mexico, the main coffee growing areas have the same altitudinal range as humid montane forests and the conversion of native forest to coffee plantations accounts for the loss of considerable extents of forest. Along with Chiapas and Oaxaca the center of Veracruz is one of the main coffee growing regions of Mexico.

In Veracruz, 40 percent of humid montane forests were lost between 1984 and 2000, while the coffee-growing area increased by 58 percent (Manson et al. 2008).

Fig. 1 shows a classification of five different types of coffee plantations along a gradient of management intensification (Moguel & Toledo 1999). In rustic coffee plantations the original tree layer is left intact and coffee shrubs replace the original undergrowth. Tree species diversity is generally high with forest structure of 3 or more layers and a shade cover of 70 to 100 percent. In traditional polyculture some of the natural canopy is removed to add various tree and plant species for timber, fruit and vegetable production. Shade cover lies between 60 and 90 percent. For commercial polyculture the natural canopy is removed and replaced by timber and fruit trees that serve as shade trees for the coffee shrubs, usually 2 or 3 different species. The canopy is reduced to 2 layers (trees and coffee shrubs) and the shade cover is 30 to 60 percent. In these coffee cultures typically considerable quantities of agrochemicals are applied, the trees are regularly pruned and the epiphytes are sometimes removed. In shaded monoculture with shade cover of 10 – 30 percent coffee shrubs are much more densely planted than in polyculture, typically only one or two species, mostly Inga spp. of shade trees are planted and heavily pruned. Sun coffee is grown without shade. Due to the high percentage of small coffee producers (over 90 percent own less than 5 ha) 81 percent of Mexican coffee is still grown as shade coffee (Manson et al. 2008). Other studies report that 10 percent of Mexican coffee is managed as sun coffee, 25 percent as shade monoculture and commercial polyculture and 75 percent as rustic coffee and traditional polyculture (Rice & Ward 1996, Moguel & Toledo 1999, 2004).

While the conversion of many montane forests to coffee plantations for more than a hundred years contributed substantially to forest loss, shade coffee plantations have become important ecosystems for the conservation of Mexican biodiversity. The vegetation structure of low-impact shade coffee plantations is similar enough to native forests to harbor many of the forest species and serve as retreats and secondary habitats in lieu of erstwhile forest vegetation (Perfecto et al. 1996, Moguel & Toledo 1999, Schroth et al. 2004, Hietz 2005). Shade coffee plantations can maintain soil fertility, reduce erosion, keep up the input of organic material (litter) and nitrogen fixation.

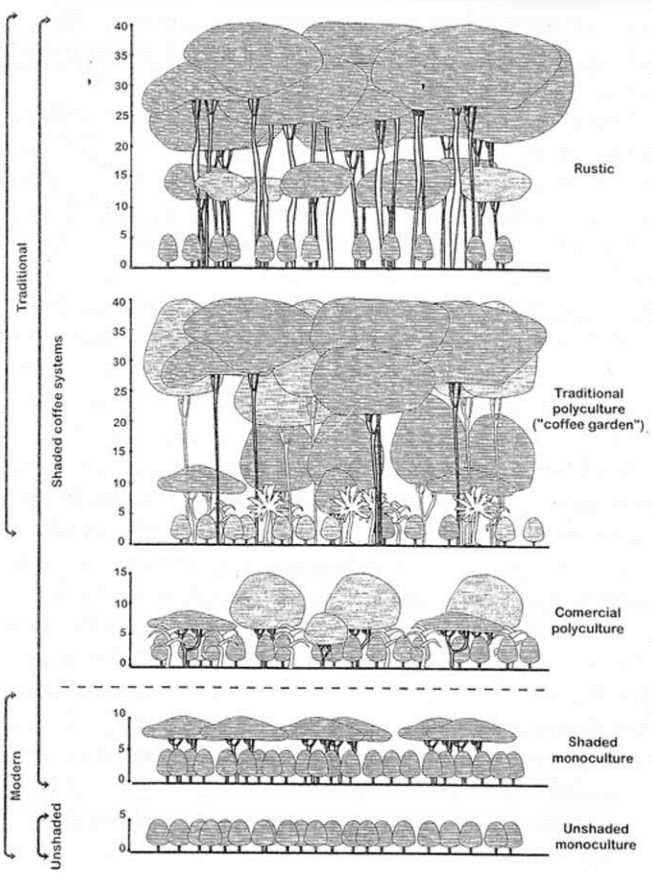

Figure 1. Classification of coffee agroecosystems (Moguel & Toledo 1999)

In recent years the ecological value of secondary arboreal vegetation, particularly of shade-tree agroecosystems, for the conservation of biodiversity and of ecological services was confirmed by a number of studies (Perfecto et al. 1996, Greenberg et al. 1997, Moguel & Toledo 1999, Rice and Greenberg 2000, Ricketts 2001, Perfecto & Vandermeer 2002, Perfecto & Armbrecht 2003, Philpott & Dietsch 2003, Mas & Dietsch 2004, Solis-Montero et al. 2005, Vandermeer & Perfecto 2007, Gordon et al. 2007, Rice 2010 and citations therein). Still, more studies on the ecological values of secondary habitats for the conservation of biodiversity and ecological services and their different capacities to harbor species, whose natural environment is increasingly lost, are necessary to predict the impact of land-use changes and to improve management of secondary vegetation.

1.4 Epiphytes in secondary habitats

Epiphytes account for 10 percent of the vascular plants worldwide, with about 30000 known species (Gentry & Dodson 1987). Vascular epiphytes are an important component of tropical forests and diversity and their abundance is particularly high in humid tropical montane forests, the lower altitudinal range of which is also most suitable for coffee cultivation. In Mexico, epiphytes represent only 6.8 percent of the known vascular plants, but comprise 30 percent of the endemic plants. Humid montane forest in Mexico hosts the largest number of epiphyte species accounting for 32 percent of the plant species (Williams-Linera et al. 2002). Epiphytes provide important resources to birds and arthropods (Cruz-Angón & Greenberg 2005, Cruz-Angón et al. 2009). Experimental removal of epiphytes from coffee shade trees led to strong decrease in insect abundance (90 percent less individuals) and species richness (22 percent less insect species) compared to trees with natural epiphyte cover (Cruz-Angón et al 2009).

Epiphytes are especially endangered by forest loss as they depend on host their host trees for their whole life cycle. In recent years a number of studies focused on the effects of forest loss and land use changes on epiphyte species and the role of secondary vegetation for the conservation of epiphyte biodiversity. Whereas epiphyte species in dry forests seem to be more resilient to habitat changes (Higuera & Wolf 2010), evidence suggests that epiphytes in wet forests are severely endangered by anthropogenic disturbance (Turner 1996) as they seem more sensitive to microclimatic changes (Sosa & Platas 1998, Nadkarni & Solano 2002, Zotz & Bader 2009). Compared to pristine forests secondary habitats generally have a more open vegetation with increased solar radiation and temperature, higher daily temperature fluctuations and stronger winds (Laurance 2004) leading to dryer microclimatic conditions. Most studies of epiphyte communities in secondary arboreal vegetation like disturbed forests, agroforestry sytems and isolated pasture trees show a generally lower total species richness (e.g. Wolf 2005, Barthlott et al. 2001, Poltz & Zotz 2011, Alvarenga et al. 2010, Moorehead et al. 2008, Haro-Carrión et al. 2009, but see Hietz 2005, Köster et al. 2009, Larrea & Werner 2010).

As different taxonomic and functional groups react differently to land use changes, shifts in floristic composition of epiphyte communities are common. Predominately drought-tolerant epiphyte species are often favored by disturbed habitats and show higher abundances than in natural forests (Engwald et al. 2000, Solis-Montero et al. 2005, Hietz et al 2006, Alvarenga et al. 2010). Individual remnant trees in pastures and other open vegetation have been found to host a number of epiphytic species per tree similar to that of undisturbed forests, but differences in species composition and a greater homogeneity of species assemblages were found (Hietz-Seifert et al. 1996, Flores-Palacios 2003, Larrea & Werner 2010). In a study of vascular epiphyte diversity in shade cacao plantations in Ecuador Haro-Carrión et al. (2009) reported a substantial decrease of total species richness and a downward shift in the vertical distribution of epiphytes in plantations compared to natural forests, but the decrease in species richness did not apply equally to all epiphyte families: aroids, *Peperomia* and ferns showed a strong reduction, whereas orchids and bromeliads did not differ at all. Similar results were reported by Larrea & Werner (2010) in their study of vascular epiphyte diversity in mature unmanaged montane wet forest, disturbed forest (cattle grazing) and isolated pasture trees in northeastern Ecuador. Although the total species richness did not differ between the three land-use types, they found a significant decrease in total species richness of pteridophytes on isolated trees compared to unmanaged forest, whereas Bromeliaceae, Orchidaceae and Piperaceae, comprising many xerotolerant species, showed an increase in species richness.

Still, comparisons of epiphytes in forests and different coffee agroecosystems (e.g. Hietz 2005, Moorehead et al. 2010, Hylander & Nemomissa 2008, 2009) show that coffee polyculture as well as traditional home gardens harbor more epiphyte species than more intensively manages farms and plantations and epiphyte richness is generally found to be positively correlated to tree size and stand basal area (Hietz-Seifert et al. 1996, Hietz 2005, Moorehead et al. 2010).Traditional coffee plantations with older shade trees and more diverse canopy structure were shown to host a surprising diversity of epiphytes and were about as rich as natural forests, per tree of a given size and per plot (Hietz 2005). Younger plantations had fewer species of epiphytes. Although species numbers were similar between forests and plantations with old shade trees, there was some difference in species composition, with epiphyte communities in coffee plantations generally more similar to each other than those of forests.

Secondary arboreal vegetation is clearly important for the conservation of epiphytes and habitat quality is an important factor influencing epiphyte occurrence and abundance, as epiphyte species differ in their ability to colonize alternative habitats. Knowledge about the species ability to regenerate, to germinate, grow and establish themselves in the different microhabitats is essential for a better management of forest fragments and secondary vegetation.

2 Project objectives

The objective of the FWF funded project "Epiphyte colonization of coffee plantations" was to explore the causes affecting epiphyte colonization, survival and diversity of differently managed coffee plantations. This knowledge is important to predict the consequences of changes to the present system of coffee cultivation and of other types of secondary arboreal vegetation, and to manage these in a way that maximizes their conservational value.

While coffee plantations had previously been shown to host a high number of epiphyte species, some species are seldom, if ever, found on coffee shade trees and many species are not present in coffee plantations with small shade (Hietz 2005).

We compared coffee plantations of different age and structure with natural forests in the same area. In these habitats, the epiphytic vegetation and stages in the population cycle that may be responsible for their ability or inability to colonize plantations, were compared among epiphytic species that are largely restricted to old-growth forests, species that are additionally found in old but absent from young plantations, and species occurring in all of these systems.

Recruitment and establishment of seedlings is crucial for the establishment and maintenance of plant populations, with the seedling stage being one of the most vulnerable periods in the life cycle of epiphytic plants (Zotz et al. 2001). Therefore we focused on the earliest life-cycle stages of epiphytes, germination and seedling establishment.

3 Study design

3.1 Study area and sites

The study area was located in central Veracruz, Mexico, near the village of Coatepec (19°27′ N, 96°57′ W), at altitudes between 1200 and 1350 m above sea level, which is the lower elevation range of humid montane forests. It is one of the main coffee-growing regions in Veracruz with a landscape dominated by coffee plantations, fields (mostly sugar cane), and pastures.

In central Veracruz, natural forests are reduced to fragments ranging between 0.04 and 2528 ha with an average size of 1.06 ha (Muñoz-Villersa & López-Blanco 2007) that stay as patches between pastures, coffee plantations or land dedicated to other land uses. According to Muñoz-Villersa & López-Blanco (2007) forests, secondary arboreal vegetation (agroecosystems) and non-arboreal vegetation (pastures, fields and sun coffee) cover ca. 21, 38 and 33 percent of the area.

The humid montane forest has a comparatively cool and relatively dry season from October/November to March, a dry and warm season from March/April to May and a wet and warm season from June to September/October. Mean annual temperature is ca 19.5°C and average precipitation is 1765 mm per year (Comisión Nacional de Agua http://smn.cna.gob.mx/productos/normales/estacion/ver/NORMAL30026.TXT).

As study sites we selected three natural forest fragments (Parque Ecológico, La Mascota, El Atorón F), three coffee plantations with large epiphyte-rich shade trees (Bola de Oro Co, La Pitaya Co, Nestlé La Orduña), and three plantations with small shade trees and much lower epiphyte cover (Bola de Oro Cy, El Atorón Cy, La Pitaya Cy). Study sites with the same name are located within a few hundred metres next to each other, different habitat types are then specified by the abbreviatens following the site name : (F) forest, (Co) old coffee plantation and (Cy) young coffee plantation.

Figure 2. Study sites. El Atorón F (above left). La Mascota (above middle), La Pitaya Co (above right), Bola de Oro Co (below left, picture by P. Hietz), El Atorón Cy (below middle) and Bola de Oro Cy (below right).

3.2 Study species

The study focused on orchids and bromeliad species, as they comprise two of the most prominent epiphyte groups.

Tillandsia viridiflora Beer (Baker) (Bromeliaceae) is usually found in the lower canopy, on stems and sometimes on rocks in closed forests.

Tillandsia heterophylla Morren (Bromeliaceae) is common in forests as well as old plantations, but not in young plantations

Tillandsia juncea (Ruíz & Pavón) Poiret (Bromeliaceae) is one of the most common bromeliads in the area and found in all three habitats.

Figure 3. Bromeliaceae. *Tillandsia viridiflora* (above left), *Tillandsia heterophylla* (above right, picture by P.Hietz) and *Tillandsia juncea* (below left, picture by P.Hietz)

Lycaste aromatica (Graham ex Hook) Lindl (Orchidaceae) is almost exclusively found in natural forests, in some places with very small populations, in others with several hundred individuals.

Jacquiniella teretifolia (Sw.) Britt. & P.Wilson (Orchidaceae) is a very common orchid in the area and found in forests as well as other woody vegetation, including coffee shade trees.

Figure 4. Orchidaceae. *Lycaste aromatic* (left), *Jaquiniella teretifolia* (right)

3.3 Experimental design

3.3.1 Germination

Seeds collected from wild plants were attached to artificial substrate or to branch surfaces and exposed on eight trees at each of the nine study sites. The artificial substrate was used to distinguish between microclimate and substrate effects on germination.

On each of eight trees per site, 20 seeds of each species were exposed on two branches in the lower crown and on two branches in the upper crown. Seeds were exposed at the end of the dry season, at the time of natural seed dispersal. Germinated seeds were counted and measured at several times but by the end of the wet and warm season in October most of the seeds that would germinate had done so.

We then tested if germination rates were related to their distribution within the canopy and between habitats and to what extent either substrate or microclimate affects germination rates in the three species.

Figure 5. Germination experiment. Branch sections with seeds attached with adhesive tape to the branch surface or to an artificial substrate (lower picture by P. Hietz).

3.3.2 Seedling establishment and survival

Orchid and bromeliad species were mass-propagated in a sterile jars from seeds collected in the area. After nine months plants were transferred to propagation trays with a mix of pine bark, oak charcoal and pumice and placed in a shadehouse (Mata-Rosas & Salazar-Rojas 2009). The trays were covered with translucent plastic lids during the first 30 days, then the lids were progressively lifted for the plants to adapt to ambient relative humidity, and plants were irrigated twice weekly with rainwater. After at least three month in the shadehouse seedlings were exposed on tree branches at the study sites.

On each of eight (orchids) and nine trees (bromeliads) per site, 5 seedlings of each species were exposed on two branches in the lower crown and on two branches in the upper crown. Orchid seedlings were exposed at the beginning of the dry and cold season. Bromeliad seedlings were exposed toward the end of the dry season and again in the wet and warm season. Seedling mortality, size and incidence of herbivory were noted at regular intervals.

Throughout the study we used shoot length as a measure of plant size. For the orchids, we defined both pseudobulbs (*Lycaste aromatica*) and stems (*Jaquiniella teretifolia*) as shoots and the sum of all shoot lengths of an individual as plant size.

We analyzed growth and mortality rates to see if the study species reflect the pattern of species occurrence and/or abundance in the three habitats and if habitat features affect growth and survival of plants. We also tested if tree and branch characteristics are related to growth and survival of the epiphytes growing on them (orchids: Chaper 5, bromeliads: Chapter 6).

Figure 6. Mass propagation of study species. Germination and growth in sterile jars (above left, picture by P. Hietz), study species in the shade house: *L. aromatica* and *J.teretifolia* (above right), *T. viridiflora* (below left), *T. heterophylla* (below middle), *T. juncea* (below right).

Figure 7. Orchid transplantation. One year old juvenile orchids shortly before exposition (above left: *L. aromatica*, below left: *J. teretifolia*) and experimental branch section with newly transplanted orchids (right).

Figure 8. Bromeliad transplantation. One year old juvenile bromeliads prepared for exposition (left) and experimental branch section with newly transplanted bromeliads (right).

3.4 Tree and branch parameter

To study differences in microclimate, temperature and relative humidity were recorded every 10 min with three HoboPro (Onest, Pocasset, MA, USA) and two TinytagPlus (Tinytag, Chichester, UK) dataloggers. Dataloggers were exposed at c. 2/3 of the canopy height between September 2006 and July 2007 and rotated between sites every 1 or 2 mo. We measured height and dbh of each experimental tree per site (Table S1).

For each branch section carrying seeds or transplanted seedlings, height above ground, inclination, diameter and canopy openness above the branch (using a spherical densiometer, Ben Meadows, Janesville WI, USA) were measured. The percentage of the upper branch surface covered by bryophytes, lichens, vascular epiphytes or bare bark, as well as the thickness of this substrate were estimated (Table S2).

Table S1. Description of study sites used for germination and transplantation experiments in central Veracruz. Sites with the same names (El Atorón, Bola de Oro, La Pitahaya) were within *ca.* 500 m from each other. Tree density includes all trees > 10 cm dbh from a 20 x 20 m subplot, dbh and tree height are mean ± SD from 8 experimental trees per site.

Habitat Site	Location N/W	Tree density /ha	Dbh (cm)	Tree height (m)
Forest		605	60.5 ± 22.3	17.8 ± 3.2
El Atorón F	19°29.57'/96°57.22'	525	61.4 ± 30.9	16.5 ± 2.8
La Mascota	19 27.54'/96 59.83'	325	57.6 ± 17.7	18.8 ± 3.9
Parque Ecológico	19 30.78'/96°56.38'	965	62.4 ± 18.7	18.3 ± 2.8
Old coffee plantation		133.3	52.2 ± 19.7	17.3 ± 2.4
Bola de Oro Co	19°28.34'/96°57.46'	150	63.7 ± 21.3	18.4 ± 1.4
La Pitaya Co	19°30.25'/96°56.97'	150	56.3 ± 16.7	18.9 ± 1.6
Nestlé,La Orduña	19°28.12'/96°55.72'	100	36.6 ± 9.6	14.8 ± 1.5
Young coffee		233.3	28.3 ± 5.2	9.6 ± 1.5
Bola de Oro Cy	19°28.34'/96°57.46'	275	25.3 ± 3.6	8.9 ± 1.1
El Atorón Cy	19°29.51'/96°56.99'	225	26.2 ± 2.4	8.7 ± 0.8
La Pitaya Cy	19°30.20'/96°56.85'	200	33.3 ± 4.9	11.3 ± 0.9

Table S2. Characteristics of experimental branches of forest, old and young coffee plantations selected for transplanting pre-growth juvenile bromeliads (mean ± SD, n = 32 – 35 branches per site and three sites per habitat). Different lower-case letters indicate significant differences between habitats (nested ANOVA and multiple comparisons by Tukey HSD test, *P* < 0.05).

Habitat	Inclination (°)	Height (m)	Diameter (cm)	Cover (%)				Substrate thickness (mm)	Canopy openness (%)
				Bryophytes	Lichens	Bark	Vascular plants		
Forest	52 ± 22 ^{a}	11.4 ± 3.8 ^{a}	14 ± 5 ^{a}	58 ± 35 ^{a}	13 ± 20 ^{a}	24 ± 28 ^{a}	5 ± 12 ^{ab}	3.1 ± 4.5 ^{a}	8 ± 6 ^{a}
Old plantation	47 ± 25 ^{a}	11.2 ± 3.6 ^{a}	17 ± 8 ^{b}	36 ± 33 ^{b}	33 ± 30 ^{b}	24 ± 25 ^{a}	8 ± 15 ^{a}	2.7 ± 3.0 ^{b}	10 ± 8 ^{ab}
Young plantation	59 ± 23 ^{b}	4.6 ± 2.1 ^{b}	13 ± 5 ^{a}	18 ± 27 ^{c}	29 ± 30 ^{b}	52 ± 35 ^{b}	2 ± 8 ^{b}	1.6 ± 2.5 ^{b}	12 ± 9 ^{b}

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Germination of Epiphytic Bromeliads in Forests and Coffee Plantations: Microclimate and Substrate Effects

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ABSTRACT

This study explores whether differences in germination ability shape habitat distributions among closely related epiphytic species, particularly in the context of the ability to colonize disturbed habitats. We compared the germination of three epiphytic bromeliad species differing in their ability to colonize secondary arboreal vegetation in natural forests, and in old and young coffee plantations. We asked if germination is related to their distribution within the canopy and between habitats, and the extent to which the substrate (branch) or microclimate affects germination success. *Tillandsia viridiflora*, a species that is largely restricted to closed forests, had highest germination success in natural forests, *Tillandsia juncea*, a pioneer species, germinated best in young coffee plantations, and *Tillandsia heterophylla*, an intermediate species, equally in forests and young plantations. Surprisingly germination rates of all three species were lowest in old plantations. Bryophyte cover on branches had a positive effect on germination of *T. viridiflora* and *T. heterophylla*, but *T. juncea* germination rates were largely independent of climate and substrate. These results show that germination can limit the ability of species to colonize disturbed habitats and also contributes to within-canopy distribution.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: coffee agro-ecosystem; epiphyte; germination; *Tillandsia*.

SEED GERMINATION IS CONTROLLED BY A RANGE OF ENVIRONMENTAL VARIABLES such as temperature or light regime, which affect both germination time and success (Baskin & Baskin 1998). There is scant information, however, as to what degree germination is related to habitat in closely related species and, in particular, if species distributions might be affected by their ability to germinate in different habitats. Considering the importance of secondary habitats for the survival of epiphytes, we tested whether germination rates differ between species, and if this might explain their presence in or absence from secondary vegetation.

The diversity of epiphytes is threatened by forest loss, but secondary arboreal vegetation might provide a refuge for many epiphytic species. Epiphyte species richness is mostly lower in secondary forests than in natural old growth forests (Barthlott *et al.* 2001, Krömer & Gradstein 2003, Benavides *et al.* 2006), though in some cases the diversity on isolated old trees was not lower than on trees within the forest (Hietz-Seifert *et al.* 1996, Flores-Palacios & Valencia-Diaz 2007). Epiphyte communities also differ in their distribution within the canopy (Kelly 1985, Hietz & Hietz-Seifert 1995, Zotz 2007), and the fact that those found in exposed canopy locations tend to be more common in secondary habitats suggests that species adapted to a harsher or sunnier microclimate are better able to colonize secondary vegetation (Hietz-Seifert *et al.* 1996, Acebey *et al.* 2003, Wolf 2005).

In the Neotropics, many humid montane forests have been replaced by coffee plantations. In areas where coffee is planted under shade trees, these plantations have become important reservoirs of biodiversity (Perfecto *et al.* 1996). Shade trees, when allowed to form large trees, can harbor about as many epiphyte species as trees in natural forest. Plantations with only small trees host a small minority of the epiphytes present in the region, and some forest epiphyte species are not found even on large shade trees (Hietz 2005). Given the importance of epiphytes for tropical biodiversity (Gentry 1987) and that their survival increasingly depends on secondary vegetation as primary forests in the tropics are lost, it is important to understand what affects the epiphytes' ability to colonize and survive in an anthropogenic landscape.

Independent of whether the habitat is primary or secondary, the establishment of any population requires diaspores to reach a given location and successfully germinate there. As germination rates of epiphytic bromeliads in the field differ widely between 3 and 60 percent (Benzing 1978, Mondragón *et al.* 2006, Cascante-Marín *et al.* 2008) while *in vitro* germination is often close to 100 percent (Mondragón *et al.* 2006, Paggi *et al.* 2007, Toledo-Aceves & Wolf 2008), germination could be a bottleneck, or at least a limiting factor, for the establishment of epiphyte populations. If this is the case, we would expect that germination rates are correlated with the relative abundance of species in different habitats, and even across different canopy strata within a forest based on microclimatic affinities.

Field experiments so far have found little or no correlation between the germination rates of epiphytes and the distribution

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of established plants within or between habitats (Graham & Andrade 2004, Winkler *et al.* 2005, Mondragón *et al.* 2006, Cascante-Marín *et al.* 2008). While these cases suggest that germination is not related to habitat preferences, not finding such an effect might also be due to confounding factors (*e.g.*, climate, genetic variation, small-scale variability in substrate quality).

Epiphytes, being decoupled from the soil, are sensitive to climate (Benzing 1998), and in the tropics montane cloud forests, which harbor large epiphyte biomass, are thought to be particularly vulnerable to climate change (Benzing 1998, Foster 2001, Zotz & Bader 2009). Microclimate is known to differ between closed forests and fragmented canopies and is generally used to explain differences in epiphyte communities (Acebey *et al.* 2003, Wolf 2005). As seeds require water to germinate, this could result in different germination rates among habitats.

Epiphyte preference has been shown to be related to the water holding capacity of branches, which depends on branch size, inclination, bark type and rugosity, and also on the branch substrate, including bryophytes, lichens, and canopy soil (Callaway *et al.* 2001, Callaway *et al.* 2002). The substrate found on branches is probably the result of both the canopy microclimate and branch type, hence distinguishing substrate from climate effects is difficult unless the substrate can be standardized among microclimates.

To investigate the relationship between germination and distribution patterns, we compared germination of three bromeliad species differing in their ability to colonize secondary habitats—one restricted to forests, one common in coffee plantations with old shade trees, and one rapidly colonizing even young shade trees. Seeds attached to artificial substrate, or directly to branch surfaces, were exposed in forests and in coffee plantations with old or young shade trees. We tested if germination can play a role in habitat selection and hypothesized that: (1) species germination rate is related to the pattern of species occurrences among habitats; (2) differences in germination rates between forest and coffee plantations will be greatest for the species restricted to forests and least for the 'early colonizing' species; and (3) differences among habitats are caused by the common effects of microclimate and substrate, which were distinguished by comparing germination on branches with germination on homogeneous artificial substrates. The substrate can also affect the ability of seeds to hold onto the branches, thus we further tested (4) if seeds differ in their ability to hold onto different branches.

METHODS

STUDY AREA.—The study was conducted in the vicinity of the town of Coatepec (19° 27′ N, 96° 57′ W) in the coffee-growing area of central Veracruz, Mexico. Average temperature (1971–2000) at 1252 m asl is 19.5°C and precipitation is *ca* 1760 mm per year. Three different habitats (natural forests, coffee plantations with large and presumably old shade trees and plantations with small shade trees) were selected with three individual sites for each habitat (Fig. 1; Table S1). The coffee system in the region has been studied in detail by Hernández-Martínez *et al.* 2009. The plantations we studied are the most common form in the region and classified as traditional or commercial polycultures, with most shade provided by planted *Inga* trees and a few native forest trees or fruit trees in between. To study differences in microclimate, temperature, and relative humidity were recorded every 10 min with three HoboPro (Onset, Pocasset, Massachusetts, U.S.A.) and two TinytagPlus (Tinytag, Chichester, U.K.) dataloggers exposed at about two-thirds of the canopy height between September 2006 and July 2007.

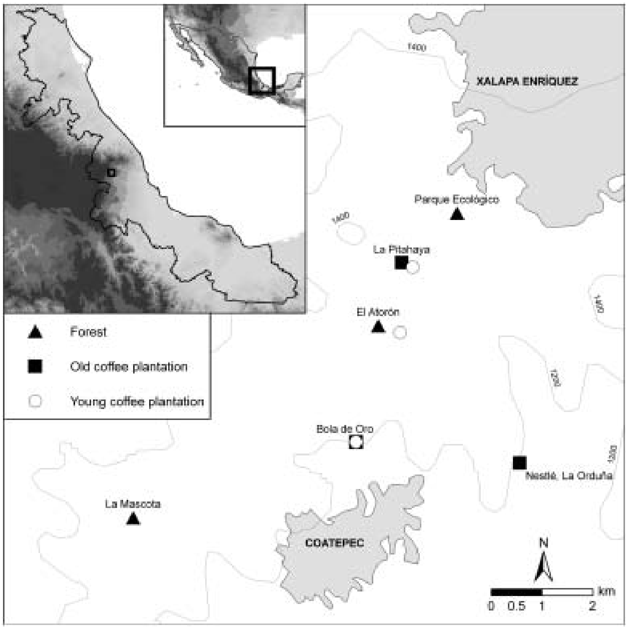

FIGURE 1. Study area and distribution of studied sites in central Veracruz. Background shapes were derived from the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) GIS portal http://www.conabio.gob.mx/informacion/gis/, and GTOPO30 from the US Geological Survey (http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30_info).

STUDY SPECIES.—Three bromeliad species were selected that are known to differ in their occurrence in forests and plantations (Hietz 2005; unpubl. data). *Tillandsia viridiflora* (Baker) Beer is a tank-forming species with broad-leaved juveniles, and is usually found in the lower canopy, often on stems and sometimes on rocks in closed forests. *Tillandsia viridiflora* was found in five out of six forests, in none of the four young coffee plantations, and only as a single individual in one of the eight old plantations. *Tillandsia heterophylla* Morren has narrow-leaved ('atmospheric') juveniles that start forming a compact tank at a size of 5–10 cm, and was found in all but one forest, and in all but one old coffee plantation. In three out of four young coffee plantations we found broad-leaved juvenile *Tillandsia* that were likely *T. heterophylla*, but they could not be identified with certainty at this size. *Tillandsia juncea* (Ruíz & Pavón) Poiret, an atmospheric species exhibiting Crassulacean acid metabolism, is one of the most common bromeliads in the area and was found in all plantations and forests.

FIELD EXPERIMENT.—Seeds were collected in February 2006 during the dry season when seeds become mature and disperse. To investigate whether the ability of seeds to persist on branches varies according to branch surface or seed species, we exposed 20 seeds from each of the three species on six different branch types, with branch types replicated five times (600 seeds per species). Branch types were A: branch diameter *ca* 50 cm, bark rough with fissures *ca* 10 mm deep, no bryophyte cover. B: 8–10 cm diameter with bark fissures up to 10 mm deep, partly covered with bryophytes up to 20 mm high, C: 6–7 cm diameter, bark with fissures up to 10 mm deep and no broyphytes, D: 6–7 cm diameter with bark fissures < 3 mm and bryophytes < 2 mm high, E: 5–6 cm diameter with thin, exfoliating bark and no bryophytes, F: 2–3 cm diameter with smooth bark and no bryophytes. After exposing the seeds on horizontal branches for 12 wk between June and September, the remaining seeds were counted.

Seeds from 10–15 individuals per species were thoroughly mixed and 20 seeds of each species were fixed to an adhesive tape with their hair-like appendages for wind dispersal so that the seeds were at a distance of 1 cm from the tape. The tapes were either fixed to a branch placing the seeds in direct contact with the branch surface (natural substrate), or to a carpet made of synthetic fibre with a pile of *ca* 5 mm, which provided a uniform artificial substrate. This was done to distinguish between the effect of the substrate and microclimate on germination. On each of eight trees per site, 20 seeds of each species were exposed on two branches in the lower crown and on two branches in the upper crown. As branches on one tree share all parameters related to the tree and the site, differences between branches within a tree must be related to branch or microclimatic parameters. The tapes of the three species were exposed with a distance of *ca* 10 cm between tapes, randomly altering the sequence of species. The same number of seeds was exposed on carpets, which were tied onto or close to the branches where seeds were exposed. The substrate on the branches ranged from bare bark of varying roughness, to lichens, bryophytes, and some canopy humus. Thus, seeds on all carpets shared the same substrate, but were exposed to the same microclimate as the seeds on the adjacent branches. For all branches, the proportion of the surface covered by bare bark, lichens, bryophytes or vascular plants, and the approximate thickness of any substrate (cryptogams or canopy soil) on the bark were estimated, branch diameter and height were measured with a tape, inclination with a clinometer, and light conditions with a spherical densiometer (Ben Meadows, Janesville, Wisconsin, U.S.A.) during the rainy season when all trees carry leaves. Experimental trees in forests were mostly *Quercus* spp., dominant trees in the forests, and in plantations mostly *Inga* spp., the most common shade tree in the region. Tree diameter at breast height (dbh) and height were also measured for all experimental trees. Average tree density was 605 stems/ha in forests, 133 in old and 233 in young coffee plantations. Average dbh for these three habitats was 60.5, 52.2, and 28.3 cm respectively, and tree height was 17.8, 17.3, and 9.6 m (Table S1). The selected branches in natural forests were significantly higher, less inclined, and had higher bryophyte and vascular plant cover and substrate thickness, but less lichen and bare bark surface than branches in young plantations. Forest and old plantations only differed in diameter, inclination and bryophyte cover (Table S2).

A total of 11,520 seeds for each species were exposed in February and March 2006. Very few seeds germinated until strong rains started in July. By September, most germinated seedlings had reached sizes ≥ 3 mm and only four seedlings had died, suggesting that at the time of the census in September to October 2006 most seeds that would germinate had done so. This was confirmed by another census in March 2007 when only 67 new germinations were recorded. A substantial number of seeds were lost due to various factors, including detachment from the tape, loss of the tape or the entire carpet. These were excluded from further analysis.

STATISTICS.—The effect of species and branch type on the arcsin-transformed proportion of seeds that remained attached to the branch after 12 wk of exposure was tested in a two-way ANOVA and the correlation between microclimate and average germination rate of a site by linear regression.

Observations within a cluster (tree, site) tend to be more alike than observations from different clusters (Agresti 2002) and are thus usually positively correlated. These cluster-related dependencies can be modelled using generalized linear mixed-effects models (GLMM; Saavedra & Douglass 2002, Thompson 2008). We fitted a GLMM with binary error distribution (logit link) for all species and habitats to test: (i) whether germination rates on branch surfaces differed between species and habitats. Separate models for each of the three study species were run to test; (ii) the impact of microclimate on germination by comparing germination rates on artificial substrate among habitats; (iii) the impact of the substrate on germination by comparing the germination rates on branch surfaces to that on an artificial substrate for each habitat; and (iv) which branch parameters reflect differences in germination rates. For the latter, starting with a model including all branch parameters, significant parameters were selected using a stepwise backward elimination procedure.

For each model the Laplace algorithm was chosen to approximate the log-likelihood criterion of parameter estimation. The numbers of germinated and non-germinated seeds per tape (originally 20) were used as the dependent variables. This is equivalent to using the proportion of germinated on total number of remaining seeds (*i.e.,* excluding those lost) on each tape weighted by the number of remaining seeds to account for varying numbers of lost seeds. Habitat was used as the only fixed effect in the first model of each species. In the second and third model substrate and the relative position in the crown, respectively, together with their interaction term with the habitat were used as additional fixed effects. The experimental design of the study comprises three nested levels of clustering (site and tree nested in site for all models; additionally branch nested in tree nested in site for the second model). Statistics were calculated with R 2.5.0 (R Development Core Team) using the package lme4 for GLMM.

RESULTS

SEED ATTACHMENT.—After 12 wk of being exposed to the rain on horizontal branches, between 58 and 73 percent of the seeds were still attached to the bark of different branch types. There was a

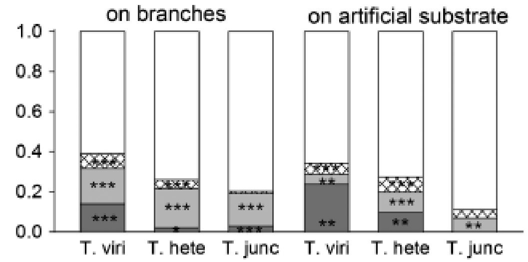

FIGURE 2. Variance of germination rates accounted for by Residual (within tree, ☐), Tree (⊠), Site (░) and Habitat (▓) effects. Asterisks mark significance levels for each component ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.0001$).

significant branch effect (ANOVA, $F_{2,72} = 3.9$, $P = 0.025$) and species effect ($F_{2,72} = 3.9$, $P = 0.022$), with attachment somewhat higher in *T. heterophylla* (71%) than in *T. juncea* (62%) and *T. viridiflora* (59%). There was no branch type × species interaction ($F_{10,72} = 0.76$, $P = 0.501$).

HABITAT EFFECT.—Out of 34,560 seeds exposed, 52.4 percent were still present after 7 mo, and of these 4372 (26%) germinated. Total germination rates were somewhat higher in young plantations (33.8%), than in forests (31.5%) and substantially lower in old plantations (14.9%). Variance in germination rates was mostly affected by habitats and sites within a habitat type and to a much lesser extent by trees within a site (Fig. 2). Habitat effects on germination differed significantly among species (Table 1; Fig. 3). In all habitats, germination was highest in the species restricted to forests (*T. viridiflora,* mean germination rate in all habitats was 35.4%), followed by *T. heterophylla* (23.9%) and least in the most widespread *T. juncea* (19.4%). Differences between species were more pronounced in forests than in plantations (Fig. 3). *Tillandsia viridiflora* had the highest germination rates in forests, and the strongest difference in germination rates between forests and plantations of all species. Germination rates of *T. juncea* were highest in young plantations and in *T. heterophylla* germination differed little between forests and young plantations (Fig. 3). The relative difference between habitats also held true in the cases where two sites were close to each other so that they should experience the same local climate (forest vs. young plantation in Atorón, old vs. young plantations in Bola and Pitahaya, data not shown).

SUBSTRATE AND CLIMATE EFFECT ON GERMINATION.—Germination on artificial substrates was generally lower than on adjacent branches and also significantly lower in old plantations than in forests or young plantations (Fig. 3). Similar to germination on branches, *T. viridiflora* showed the highest germination rates in forests, and *T. heterophylla* in young plantations. There was a strong habitat × substrate (branches vs. carpets) interaction (Table 2) in *T. juncea*, where germination in forests was higher on carpets than on branches (Fig. 3), a weaker interaction in *T. heterophylla* and none in *T. viridiflora.*

Differences between branches and carpets were least significant in young plantations (Fig. 3). Differences between habitats were most pronounced in *T. viridiflora* on branches as well as carpets (Table 3). For most comparisons, germination on branches and

TABLE 1. *Effects of species and habitat on germination rates of three* Tillandsia *species attached directly to branches. O, old coffee plantations; Y, young coffee plantations; TH:* Tillandsia heterophylla*; TJ,* Tillandsia juncea. *Effects were tested against* T. viridiflora *in forests. The analysis is based on a GLMM with binomial errors and logit link using Laplace estimation, random effects were tested using Wald tests. AIC = 1648,* N = *687.*

	Estimate	SE	*z* value	Pr(> |z|)
(Intercept)	0.378	0.378	1.002	0.316
Habitat: O	− 1.882	0.538	− 3.500	< 0.001
Habitat: Y	− 0.800	0.549	− 1.458	0.145
Species: TH	− 1.214	0.112	− 10.858	< 0.001
Species: TJ	− 2.078	0.125	− 16.616	< 0.001
Habitat: O Species: TH	0.838	0.170	4.923	< 0.001
Habitat: Y Species: TH	0.985	0.171	5.755	< 0.001
Habitat: O Species: TJ	1.539	0.187	8.242	< 0.001
Habitat: Y Species: TJ	1.662	0.183	9.070	< 0.001

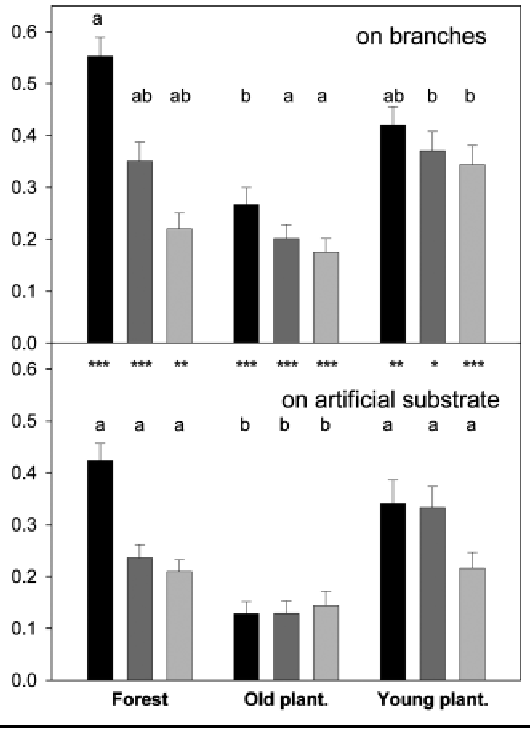

FIGURE 3. Germination rates of seeds of three bromeliad species (black bars: *Tillandsia viridiflora*, grey: *T. heterophylla*, empty: *T. juncea*) exposed directly on branches (upper pannel) and on artificial substrate (lower panel) in different habitats. Each habitat was replicated three times, with 20 seeds exposed on four branches or carpets each on eight trees per site. Error bars indicate SE. Different letters indicate significant differences ($P < 0.05$) among habitats within a species. Asterisks indicate significant differences between branches and artificial substrate ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$) tested for each species and habitat. Significance levels were derived from GLMM in both comparisons.

TABLE 2. *Effect of substrate on germination rates of three bromeliad species in three habitats. Habitat: O and Y are old and young coffee plantations, respectively, tested against forests. Substrate: A is artificial substrate (carpet) tested against natural substrate (branch surface).*

	Estimate	SE	*z* value	Pr(> |z|)
Tillandsia viridiflora				
AIC = 1279				
(Intercept)	0.28	0.25	1.13	0.260
Habitat: O	– 1.73	0.36	– 4.87	< 0.001
Habitat: Y	– 0.70	0.36	– 1.93	0.054
Substrate: A	– 0.72	0.10	– 7.15	< 0.001
Habitat: O substrate: A	– 0.27	0.18	– 1.47	0.141
Habitat: Y substrate: A	0.22	0.20	1.10	0.270
Tillandsia heterophylla				
AIC = 1196				
(Intercept)	– 1.13	0.32	– 3.54	< 0.001
Habitat: O	– 0.76	0.45	– 1.67	0.096
Habitat: Y	0.41	0.46	0.89	0.371
Substrate: A	– 0.44	0.12	– 3.83	< 0.001
Habitat: O substrate: A	– 0.44	0.19	– 2.33	0.020
Habitat: Y substrate: A	– 0.06	0.19	– 0.32	0.751
Tillandsia juncea				
AIC = 1189				
(Intercept)	– 2.00	0.20	– 9.98	< 0.001
Habitat: O	– 0.11	0.29	– 0.37	0.709
Habitat: Y	1.15	0.29	3.97	< 0.001
Substrate: A	0.41	0.12	3.32	< 0.001
Habitat: O substrate: A	– 0.91	0.20	– 4.58	< 0.001
Habitat: Y substrate: A	– 1.18	0.20	– 5.89	< 0.001

carpets showed similar habitat effects. Branch height had a significant and positive effect on germination of all species (Table 4). In *T. viridiflora* and *T. heterophylla* germination rates also increased with increasing bryophyte cover. Bark cover had a positive effect in *T. heterophylla,* whereas branch diameter in *T. viridiflora* and distance to the trunk in *T. heterophylla* had a negative effect (Table 4).

There was a significant ($P = 0.01$, $R^2 = 0.635$, df = 8) correlation between vapor pressure deficit (vpd) and germination rate of *T. viridiflora* at individual sites (Fig. 4). For *T. viridiflora* there was a somewhat weaker but also significant negative correlation with temperature ($P = 0.038$, $R^2 = 0.481$, df = 8) and positive correlation with relative humidity ($P = 0.030$, $R^2 = 0.511$, df = 8), both parameters that drive vpd. None of these parameters had a significant effect on germination of the other two species, although the effect of climate on germination in *T. heterophylla* appeared somewhat stronger ($R^2 = 0.33$ and 0.24, respectively, for temperature and relative humidity) than for *T. juncea* ($R^2 < 0.07$ for all climate parameters).

DISCUSSION

SEED FIXATION.—Although we found significant differences between species and effects of branch types on the seeds' ability to remain attached to branches, this is unlikely to explain differences in species abundance between habitats. If seed appendages of xeric or early colonizing species were adapted to their substrate, we would expect *T. juncea* to have, relative to other species, better establishment success on smaller and smoother branches, but this was not the case as there was no species × substrate interaction. The seed attachment experiment demonstrated that the seed appendages of

TABLE 3. *Summary of significant differences in germination rates of three bromeliad species exposed on branches and artificial substrates in forests, old and young coffee plantations. The diagonal (framed) gives the significance of the difference between branches and artificial substrates within one habitat, values above the diagonal the between-habitat effect of germination on branches and below the diagonal the between-habitat effect of germination on artificial substrates. Significance levels were derived from GLMM.*

	Forest	Old plantation	Young plantation
Tillandsia viridiflora			
Forest	< 0.001	< 0.001	0.118
Old plantation	< 0.001	< 0.001	0.052
Young plantation	0.154	< 0.001	0.003
Tillandsia heterophylla			
Forest	< 0.001	0.117	0.531
Old plantation	0.025	< 0.001	0.033
Young plantation	0.209	0.001	0.026
Tillandsia juncea			
Forest	0.001	0.473	0.078
Old plantation	0.001	< 0.001	0.013
Young plantation	0.719	< 0.001	< 0.001

TABLE 4. *Significant effects of branch parameters on the germination of three epiphytic* Tillandsia *species attached directly to branches in forests, old and young coffee plantations. Significance levels were derived from GLMM.*

	Estimate	SE	*z*-value	Pr(> |z|)
Tillandsia viridiflora				
(Intercept)	– 0.894	0.475	– 1.883	0.060
Diameter	– 0.020	0.009	– 2.156	0.031
Height	0.052	0.017	3.027	0.002
Bryophytes	0.009	0.002	3.880	< 0.001
Tillandsia heterophylla				
(Intercept)	– 2.000	0.495	– 4.036	< 0.001
Height	0.084	0.021	3.951	< 0.001
Distance from stem	– 0.229	0.071	– 3.205	0.001
Bryophytes	0.010	0.003	3.309	0.001
Bark	0.005	0.003	2.118	0.034
Tillandsia juncea				
(Intercept)	– 2.178	0.431	– 5.053	< 0.001
Height	0.089	0.019	4.552	< 0.001

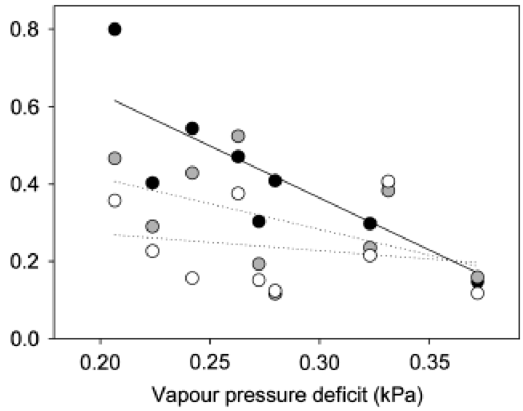

FIGURE 4. Correlation between the average vapour pressure deficit measured between September 2006 and July 2007 in the canopy of nine sites and germination rates of *Tillandsia viridiflora* (●, $R^2 = 0.64$), *T. heterophylla* (●, $R^2 = 0.24$) and *T. juncea* (○, $R^2 = 0.04$). The correlation is only significant ($P = 0.01$) for *T. viridiflora*.

Tillandsioides not only serve for dispersal, but also efficiently attach the seed to a twig. After almost 3 mo during the rainy season, more than half of all seeds that were initially only loosely attached to the bark were still present. By this time some seeds had germinated, though several more months were required until roots had grown sufficiently to serve as a holdfast. During this time the seed appendage was needed to hold the seedlings in place.

GERMINATION AND HABITAT PREFERENCE.—Germination was always highest in *T. viridiflora* and lowest in *T. juncea* (Fig. 3), even though *T. viridiflora* is rare and *T. juncea* very common in the area studied. These germination rates may reflect initial differences in seed quality or the seeds' ability to remain viable in the field. Thus, absolute germination rates are of less interest to explain the presence or absence of a species in a habitat than different site effects on species, *i.e.,* significant habitat × species interactions (Table 1).

The hypothesis that germination is higher in habitats where a species is common was confirmed for *T. viridiflora*, where germination was highest in forests, and in *T. juncea*, where most seeds germinated in young coffee plantations (Fig. 3). *Tillandsia heterophylla* is intermediate insofar as it germinated about equally well in forests and young plantations but, surprisingly, germination of all species was lowest in old plantations, a habitat we hypothesized to be intermediate in terms of suitability for establishment. Thus, germination may play a role in determining the occurrence between forests and young plantations, but it remains unclear why germination rates were generally low in old plantations.

A relationship between germination requirements and habitat preferences was also found in an *in vitro* experiment comparing two *Tillandsia* species (Bader *et al.* 2009). That study and ours contrast with results from Costa Rica, where germination of four bromeliad species was not related to distribution, although lower germination was also observed in late successional forest than in young successional or mature forests (Cascante-Marín *et al.* 2008).

WHICH FACTORS AFFECT GERMINATION?—The germination experiment on artificial substrate vs. branches was designed to test if germination is affected by the microclimate within the canopy or the substrate. If germination was determined only by substrate but not by microclimate, we would expect to find no habitat effect for seeds on carpets. This was clearly not the case. If germination were only determined by microclimate, we would expect similar germination on branches and adjacent carpets, a result that was indeed obtained (Fig. 3). Another way to test for the effect of climate vs. substrate is to correlate the germination on branches (differing by climate and substrate) with germination on carpets (differing only in climate). The high correlation in *T. viridiflora* ($R^2 = 0.66$, $P = 0.007$) and *T. heterophylla* ($R^2 = 0.60$, $P = 0.014$) shows that germination in these species is largely controlled by climate and substrate adds very little to variation between sites. In contrast, there was little correlation in *T. juncea* ($R^2 = 0.10$, $P = 0.40$).

Few of the branch parameters measured had a significant effect on germination. Branch height had a significant positive effect in all species (Table 4), though canopy openness did not. Two *Tillandsia* species were found to germinate equally well in darkness or red light (but failed to germinated in far-red light, Graham & Andrade 2004), thus neither light quantity or quality appear to play a role. In *T. viridiflora* and *T. heterophylla* germination was positively related to bryophyte cover, which tends to be higher in more humid forest strata and can provide humidity for germinating seeds and seedlings.

Hardly any seeds germinated during the dry season, which shows that water supply is limiting in all habitats. For *T. viridiflora* the importance of humidity is evident from the strong correlation between vpd and germination (Fig. 4), which was much weaker in *T. heterophylla* and not seen in *T. juncea*. The water holding capacity of branches in young plantations was likely lower than in old plantations or forests because branches of the smaller trees had smoother bark, less substrate and fewer bryophytes (Table S2). Substrate, therefore cannot explain why germination was higher in young compared to old plantations. The canopy in old plantations might, however, be drier than in young plantations because trees are higher and distance between trees is larger. As the ground vegetation in old and young plantations is essentially the same (herbs and coffee shrubs), the distance from the ground becomes important and trees and selected branches in young plantations were about half as high as those in old plantations.

GERMINATION AND OTHER LIFE STAGES.—Germination is clearly not the only stage determining distribution, not least because *T. viridiflora* germinated in all habitats but was very rare in coffee plantations, and because more individuals of *T. juncea* and *T. heterophylla* occurred in old plantations than in young ones despite lower germination in old plantations. We think it implausible that differences in dispersal abilities can explain the different distribution of the three bromeliads studied, because their seeds and appendages are very similar and unlikely to differ much in their aerodynamic properties. Most of the airborne seeds of *Tillandsia* land rather close to the mother plant, and though dispersal over hundreds of meters might be possible, it is certainly rare. Bromeliad seed rain broadly reflects the presence of adult plants within a 10 m radius (Cascante-Marín *et al.* 2009), and most seeds were trapped within 1.5 m of the source (Mondragón *et al.* 2006), though distances were further with increasing release height.

Tillandsia viridiflora may be dispersal limited insofar as seeds are unlikely to travel from the closed forest to relatively distant trees in coffee plantations. However, the reason other species are found in plantations is not because their seeds travel further and reach plantations at a greater distance from the remaining forests, but because their mother plants have been able to establish and reproduce outside of forests. Thus, even if seeds are equally likely to arrive, germinate and grow to adult plants in young plantations, epiphytes will still be much rarer because of the limited time the trees have been available and the long time it takes many epiphytes to reach reproductive size, which is evidenced by the fact that most epiphytes on young coffee trees are non-reproductive juveniles (Hietz *et al.* 2001, Zotz *et al.* 2005).

It has been suggested that dispersal limits the number of bromeliads on isolated trees in pastures (Cascante-Marín *et al.* 2009). Indeed, the number of epiphyte species on isolated trees decreases with distance from the forest (Hietz-Seifert *et al.* 1996), and the probability of epiphytes colonizing branches that had been previously cleared of epiphytes was higher in plots close to the forest (Werner & Gradstein 2008).

Many studies have reported different distributions of epiphyte species within the canopy and between habitats (Kelly 1985, Hietz & Hietz-Seifert 1995, Zotz 2007). A study of bromeliad seedling survival found no species × location interaction, and concluded that differences in vertical distribution cannot be explained by seedling survival, but that seed dispersal or germination may help to explain within-canopy distribution, although neither dispersal nor germination was tested (Zotz & Vollrath 2002). We found a significant effect of height in all species and of branch diameter and distance from the stem in single species (Table 4), which supports the idea that germination can play a role in the distribution of epiphytes within tree crowns. Differential seedling survival on different substrates may still play a role, as a previous study in one of the forest sites (Parque) showed that while germination on a relatively homogeneous substrate (branches attached in different canopy positions) was not related to canopy position, seedling survival was (Winkler *et al.* 2005).

We also found climate to be the main determinant of germination success, at least for *T. viridiflora*, the species restricted to forests. For *T. viridiflora* and *T. heterophylla* bryophytes can also facilitate germination. Whether the ability of forest-dependent species to colonize and survive in disturbed habitats depends exclusively on microclimate or substrate is relevant information if we are to manage secondary vegetation in a way that enables a large number of epiphyte species to survive. Dense stands of small trees will have a microclimate more similar to forests than sparse large trees, although if seed dispersal is limited, conserving larger trees as hosts of seed sources also becomes important.

Studies of epiphyte populations in natural forests show that the survival of mature plants is generally more important for population growth than the number of seeds germinating or seedling survival (Winkler *et al.* 2007, Zotz *et al.* 2005). Colonization cannot succeed without germination, but future studies looking into how epiphytes can survive in an anthropogenic landscape should look at other stages too. One is survival and growth of seedlings as these are particularly prone to suffer from drought (Zotz *et al.* 2001). Another question is how much seed exchange there is between individual trees and patches of trees within a fragmented landscape, how species with different dispersal modes differ and how this affects distribution and the ability of populations to survive in a patchy matrix. Dispersal and establishment limitation are known to affect tropical forest tree composition (Dalling *et al.* 1998) and dispersal limitation is important for plant migration under past and future climate changes (Svenning & Skov 2007).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Description of study sites used for germination experiments in central Veracruz.*

TABLE S2. *Characteristics of branches used for germination experiments in three habitats.*

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Seedling establishment of epiphytic orchids in forests and coffee plantations in Central Veracruz, Mexico

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Abstract: The distribution of epiphytes differs between branches within tree crowns as well as within habitats. Where the original forests have been lost, shade coffee plantations can be important refuges for epiphytes, but are not suitable for all species. To understand what affects habitat quality, we transplanted 1440 seedlings each of two orchids, one, *Lycaste aromatica*, restricted to forests, the other, *Jacquiniella teretifolia*, common on trees in coffee plantations and in forests. Seedling mortality and growth were compared between three forests, three young and three old coffee plantations to test for differences between habitats and to analyse which habitat features affect growth and mortality. In *J. teretifolia* there was no clear pattern of habitat effect on mortality (*c.* 0.08 mo^{-1}), but the production of new shoots was higher in coffee plantations than in forests. In *L. aromatica*, growth rates as well as seedling mortality increased over time. During the last census growth rates in forests (1.8 mm mo^{-1}) were significantly higher than in old (0.9 mm mo^{-1}) and young (1.2 mm mo^{-1}) coffee plantations, and seedling mortality was about four times higher in old (0.10 mo^{-1}) and young (0.11 mo^{-1}) coffee plantations than in forests (0.025 mo^{-1}), which may explain the natural absence of *L. aromatica* from coffee plantations. Mortality in *L. aromatica* at individual sites was negatively correlated with bryophyte cover on branches (Pearson $r = -0.75$) and positively with lichen cover ($r = 0.70$) and canopy openness ($r = 0.75$). Branch cover with non-vascular epiphytes, whether directly responsible by improving the water supply to epiphytes or indicative of differences in microclimate, may be a useful indicator of suitable habitats for vascular epiphytes.

Key Words: Coffee plantation, epiphyte, growth rate, mortality rate, Orchidaceae, transplantation experiment, tropical montane forest

INTRODUCTION

The composition of epiphyte communities differs between forest types (Hietz & Hietz-Seifert 1995), between natural forests and anthropogenic vegetation (Flores-Palacios & García-Franco 2008, Hietz 2005), and also within a tree where species are often observed to prefer different micro-habitats (Zotz 2007). As with other plants, preference of any habitat can be the result of differences in seed dispersal, germination, growth, survival or reproduction, which can be affected by biotic or abiotic factors.

In secondary habitats, the presence or absence of epiphyte species is determined by two processes. At first, seed dispersal can limit the colonization of new trees by epiphytes if external seed sources are scarce or far away (Cascante-Marín *et al.* 2009). Dispersal can also affect within-tree distribution of epiphytes with different dispersal modes (Fischer & Araujo 1995), but we consider it unlikely to be responsible for habitat selection in epiphytes with very similar diaspores and thus similar dispersal, such as orchids. After successful seed dispersal and germination, plants require a suitable environment for survival, growth and reproduction, which may not be found in secondary habitats. Though biotic interaction may also play a role, epiphytes are thought to be limited mainly by abiotic constraints, particularly water availability (Zotz *et al.* 2001). Microclimate, and thus abiotic stress, differs between habitats as well as between branches within a tree (Cardelús & Chazdon 2005), and other characteristics of branches such as bark

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Table 1. Elevation and mean tree density of habitat (each with three replicates) and size of trees used for transplanting juvenile orchids. Different lower-case letters indicate significant differences among habitats (nested ANOVA and multiple comparisons of linear contrasts by the Scheffé method, $P < 0.05$).

			Experimental trees	
	Altitude (m asl)	Tree density (ha^{-1})	Height (m; mean ± SD)	dbh (cm; mean ± SD)
Forest	1350	605	19.4 ± 2.8^{a}	59.0 ± 25.1^{a}
Old plantation	1200–1300	133	18.5 ± 2.9^{a}	61.4 ± 15.9^{a}
Young plantations	1250–1300	233	9.3 ± 1.5^{b}	27.2 ± 4.6^{b}

roughness and the cover by cryptogams may affect vascular epiphytes growing on it (Callaway *et al.* 2002).

The seedling stage is one of the most vulnerable periods in the life cycle of many plants, including epiphytes (Zotz & Hietz 2001) and may constitute the bottleneck for colonizing new sites. Seedling performance is therefore often used to compare the suitability of habitats for different species and to understand what habitat characteristics determine habitat selection (Pearson *et al.* 2003). A few studies have analysed the survival of transplanted epiphyte seedlings, either within the canopy (Winkler *et al.* 2005, Zotz & Vollrath 2002) or between habitats but without a replication of habitat types (Cascante-Marín *et al.* 2008).

Understanding what limits a species from any habitat and particularly secondary habitats is also of importance for conservation. For instance, shade trees in coffee plantations are an important refuge for many groups of organisms (Armbrecht *et al.* 2005, Gordon *et al.* 2007, Perfecto *et al.* 1996) including epiphytes in areas where little natural forest remains (Hietz 2005, Sosa & Platas 1998). However, not all epiphytes are found on shade trees and not all coffee plantations are equally suitable (Hietz 2005). Understanding why some are able to colonize plantations whereas others cannot, or are found in some types of plantations but not in others, may help to design ‘epiphyte friendly’ or generally diversity-conserving ways to grow coffee and to manage the cultural landscape.

Asking what affects the suitability of different habitats and different branches within a tree, we analysed seedling mortality and growth of two species of epiphytic orchids, one, *Jacquiniella teretifolia*, a common colonizer of secondary vegetation, the other, *Lycaste aromatica*, mostly limited to natural forests. Plants were transplanted to forests, coffee plantations with old and plantations with young shade trees. In addition to the comparison of habitats we asked which habitat features affect growth and survival of plants. We hypothesize that seedlings of the forest species have low growth and high mortality rates in coffee plantations, which may restrict this species to closed forests. *Lycaste aromatica* is also found in substantially drier forests at lower altitudes in the area, and in any forest is found mostly on larger branches (Hietz & Hietz-Seifert 1995). We therefore hypothesize that the survival of *L. aromatica* is related to branch size, bryophyte cover or the thickness of any substrate on the branch, all of which may affect the branch’s water-holding capacity. In contrast, seedlings of the generalist *J. teretifolia* are expected to grow in plantations as well as or better than in forests and have higher growth rates on exposed branches receiving more light. Finally, we expected to find the highest mortality in the dry season in both species.

MATERIALS AND METHODS

Study area and sites

Field work was carried out between October 2006 and February 2008 in the vicinity of Coatepec (19°27′N, 96°57′W), a centre of coffee cultivation in Central Veracruz, Mexico, at altitudes between 1200 and 1350 m asl. The climate is humid temperate with a comparatively dry and cool season from October/November to March, a dry and warm season from April to May and humid and warm season from June to September/October. Mean annual temperature in Coatepec is 19.5 °C and precipitation is 1765 mm y^{-1} (Comisión Nacional de Agua http://smn.cna.gob.mx/productos/normales/estacion/ver/NORMAL30026.TXT).

The study area is in the lower elevational range of the humid montane forest. The natural vegetation is mostly reduced to forest fragments in locations difficult to access such as steep slopes, crests and canyons. Agricultural landscape is formed by coffee plantations, fields (mostly sugar cane) and pastures.

Three habitats were included in the study and three individual sites selected for each habitat (Table 1). We transplanted seedlings to forests and two types of coffee plantations, one with old shade trees and the other with young shade trees. Size and species of all trees >10 cm diameter at breast height (dbh) were recorded on a 20 × 20-m plot within each study site. All forests were dominated by *Quercus* spp., all plantations by *Inga* spp.

Study species

Lycaste aromatica (Graham ex Hook.) Lindl. has ovate pseudobulbs up to 7 cm tall with large plicate leaves up to

60 cm long, which are shed in the dry season. This species was almost exclusively found in natural forests, in some places with very small populations, in others with several hundred individuals. *Jacquiniella teretifolia* (Sw.) Britt. & P. Wilson is a caespitose erect bulbless plant up to 30 cm tall with linear fleshy distichous leaves regularly distributed along the stems. It is a very common orchid in the area and found in forests as well as other woody vegetation, including coffee shade trees.

Experimental design

Seeds were collected from plants growing in the region, surface sterilized, and cultivated in sterile jars on 25 ml of half-strength Murashige and Skoog medium (Murashige & Skoog 1962) plus 30 g l^{-1} sucrose adjusted to pH 5. Cultures were incubated at 25 °C ± 1 °C, under a 16-h photoperiod provided by cool-white fluorescent lamps (50 µmol m^{-2} s^{-1}). After 9 mo the seedlings were transferred to propagation trays with a mix of pine bark:oak charcoal:pumice (3:1:1) and placed in a shade-house. The trays were covered with plastic translucent lids during the first 30 d, then the lids were progressively lifted for the plants to adapt to ambient relative humidity, and plants were irrigated twice weekly with rainwater. After 3 mo in the shade-house seedlings were transplanted to the study sites.

At each of the nine study sites we selected 16 trees that reached the upper canopy from which eight trees were randomly chosen. On each tree, two branches in the upper and two in the lower part of the crown were selected for transplantation. We measured height and dbh of each experimental tree. For each branch section carrying transplanted seedlings height above ground, inclination, diameter and canopy openness above the branch (using a spherical densiometer, Ben Meadows, Janesville WI, USA) were measured. The percentage of the upper branch surface covered by bryophytes, lichens, vascular epiphytes or bare bark, as well as the thickness of this substrate were estimated.

To study differences in microclimate, temperature and relative humidity were recorded every 10 min with three HoboPro (Onest, Pocasset, MA, USA) and two TinytagPlus (Tinytag, Chichester, UK) dataloggers. Dataloggers were exposed at *c.* 2/3 of the canopy height between September 2006 and July 2007 and rotated between sites every 1 or 2 mo.

In total, 1440 seedlings of each species (5 seedlings per branch × 4 branches × 8 trees × 3 sites × 3 habitats) were transplanted by climbing trees with single-rope technique and tying their roots with strips of elastic synthetic gauze to the branches. Labels with seedling number were pinned next to their position.

In *L. aromatica* the height of each pseudobulb, in *J. teretifolia* the height of each stem from the base of the stem to the tip of the uppermost leaf were measured to the nearest mm. Throughout the study we used shoot length as a measure of plant size. While we define both pseudobulbs and stems as shoots and the sum of all shoot lengths of an individual as plant size. Plant size was measured at the beginning of the transplantation experiment in October 2006, and again in March 2007, August 2007 and February 2008. Initial size (mean ± SD) was 65.7 ± 25.8 mm for *J. teretifolia* and 22.9 ± 9.5 mm for *L. aromatica* with an average of 2.1 ± 0.8 and 2.1 ± 1.3 shoots, respectively. At each census seedling mortality and size was noted.

Statistical analysis

Monthly growth rates per seedling were calculated as the increment of plant size divided by the months passed since the last census. Monthly mortality rates (m) were calculated at branch level using the following equation (Sheil *et al.* 1995):

$$m = 1 - \left(1 - \left(\frac{(M_{t1})}{(A_{t1} + M_{t1})}\right)\right)^{\left(\frac{1}{(t1-t0)}\right)}$$

where M_{t1} is the number of plants dead at census time t_1, A_{t1} the number of plants alive at census time t_1 and $t_1 - t_0$ the time between censuses. A few plants that were missing rather than found dead were assumed to have dropped and were eliminated from the analysis.

Growth and log (m + 1)-transformed mortality rates were analysed using a nested analysis of variance (ANOVA) with habitat as main fixed factor and site and tree as random factors, each fully nested in the respectively higher level. When the response differed significantly between habitats pairwise post hoc comparisons for linear contrasts were conducted using the Scheffé test.

Growth and mortality rates between the upper and lower branches were compared with paired t-tests with growth/mortality averaged for two branches of a tree. Influence of various branch parameters on growth and mortality rates of the study species were analysed using simple and multiple linear regressions.

Statistical analyses were performed using R 2.5.0 (R Development Core Team, http://www.R-project.org).

RESULTS

Growth

Temperature and precipitation during the experiment are shown in Figure 1a. During the first 6 mo after transplantation (October 2006–March 2007) the

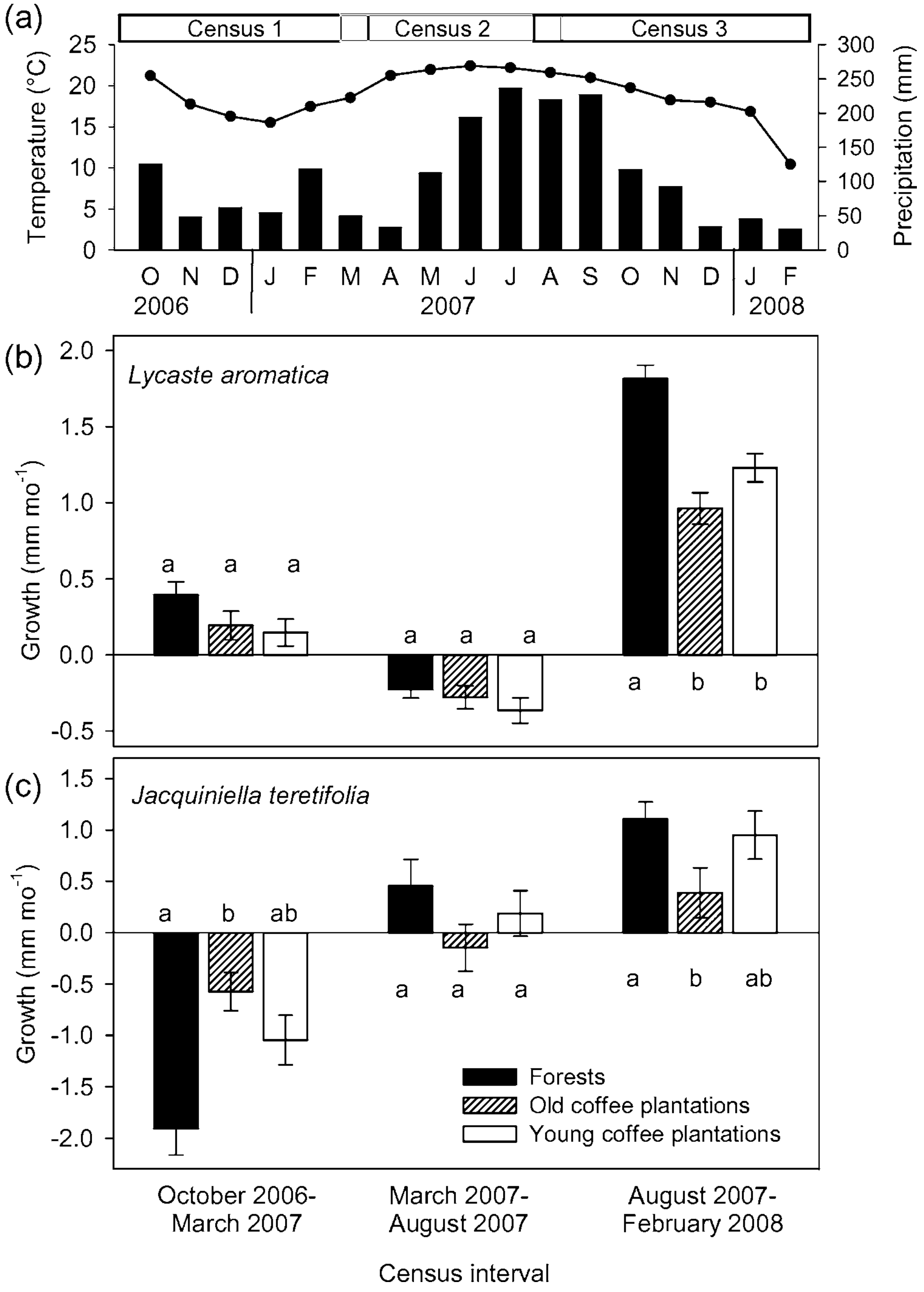

Figure 1. Climate and monthly growth rates of seedlings of two orchid species transplanted to trees in three different habitats during three census intervals. Monthly mean temperature (line) and total precipitation (bars) in the area during the observation period. Bars on top indicate the census periods (a). Growth rates of *Lycaste aromatica* (b), and *Jacquiniella teretifolia* (c). Error bars indicate standard error. Different lower-case letters indicate significant differences (nested ANOVA and multiple comparisons of linear contrasts by the Scheffé test, $P < 0.05$).

monthly growth rate of *L. aromatica* seedlings was highest in forests and lowest in young coffee plantations (Figure 1b) although the difference was not significant ($F_{2,1293} = 2.19$, $P = 0.11$). From March 2007 to August 2007 seedling growth rates were negative as shoots of many seedlings died. Habitat had no significant effect ($F_{2,1101} = 0.95$, $P = 0.39$) on growth, but in coffee plantations the reduction in shoot numbers was significantly higher than in forests ($F_{2,1052} = 10.9$, $P < 0.001$). Between August 2007 and February 2008 seedling growth rates increased strongly. Growth rates varied significantly between habitats ($F_{2,916} = 22.74$, $P < 0.001$) and were higher in forests than in coffee plantations.

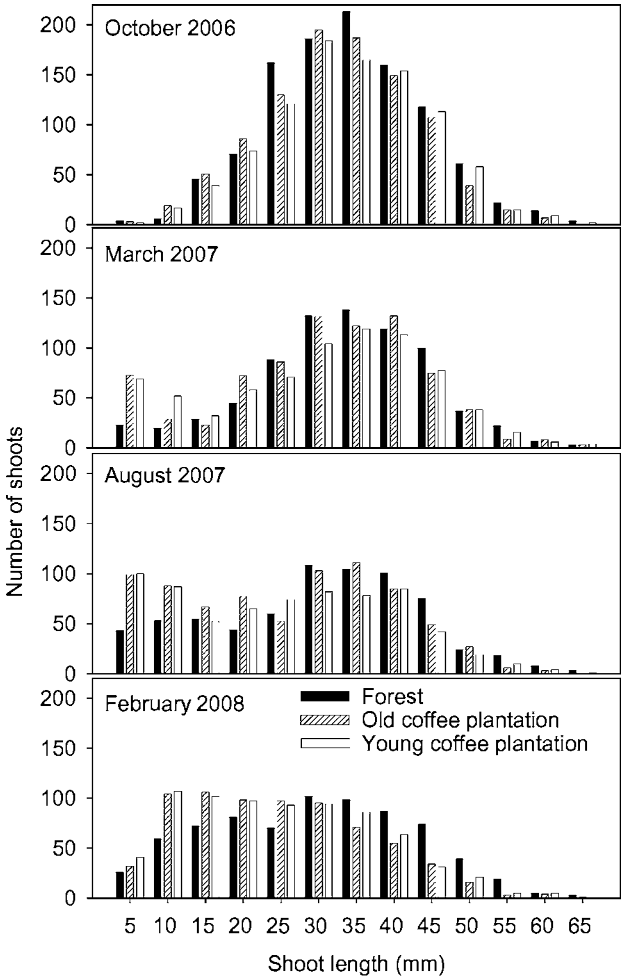

Figure 2. Change in the frequency of shoot size classes of *Jacquiniella teretifolia* seedlings transplanted to trees in three different habitats after transplantation in October 2006.

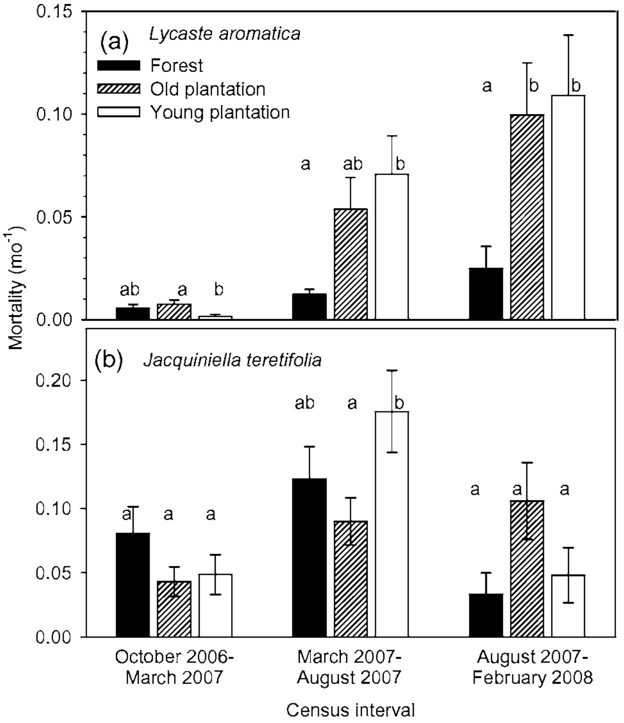

Figure 3. Mortality rates of seedlings of epiphytic orchids transplanted to three different habitats. *Lycaste aromatica* (a), and *Jacquiniella teretifolia* (b). Error bars indicate standard error. Different lower-case letters indicate significant differences (nested ANOVA and multiple comparisons of linear contrasts by the Scheffé test, $P < 0.05$).

In *J. teretifolia* initial growth was negative because shoots were lost or died at the apex. Habitat had a significant effect on growth ($F_{2,1053} = 9.13$, $P < 0.001$, Figure 1c) with the strongest reduction in size in forests and least in old coffee plantations. Between March and August 2007 growth was low but positive (except for old plantations) with no significant habitat effect ($F_{2,746} = 1.69$, $P = 0.18$). In the last interval growth was generally higher, differed between habitats ($F_{2,661} = 3.23$, $P < 0.05$) and was significantly higher in forests than in old plantations.

The fact that the initial decline in size was highest in forests and least in old plantations but later positive growth was highest in forests and lowest in old plantations is explained by changes in shoot size and numbers (Figure 2). At the first census, all plants had lost shoots in most size classes, but plants in coffee plantations developed more new shoots than in forests. Subsequently, plants in plantations continued to grow more new shoots, but plants in forests lost fewer large shoots.

Root growth was not measured, but in both species the original roots did not attach themselves to the new branches but withered and died. New roots began to emerge about 6 mo after transplantation in *J. teretifolia* and after about 12 mo in *L. aromatica*. Root growth in both species began first in coffee plantations, and later in forests.

Mortality

During the first 6 mo after transplantation (October 2006–March 2007) mortality in *L. aromatica* was low and showed nearly significant differences between habitats ($F_{2,267} = 3.01$, $P = 0.05$, Figure 3a) with the lowest mortality in young and the highest in old coffee plantations. From March to August 2007 monthly mortality rates increased and differed significantly between habitats ($F_{2,267} = 6.17$, $P < 0.01$) with mortality rate in young coffee plantations being almost six times higher than in forests. Between August and February 2008 mortality increased again and differed between habitats ($F_{2,261} = 4.67$, $P = 0.01$) being about four times higher in young plantations than in forests.

Table 2. Characteristics of experimental branch of three different habitats selected for transplanting juvenile orchids in Veracruz, Mexico. Mean ± SD is shown for 96 branches per habitat. Different lower-case letters indicate significant differences between habitats (nested ANOVA and multiple comparisons of linear contrasts by the Scheffé method, $P < 0.05$).

			Cover (%)					
	Inclination (°)	Diameter (cm)	Bryophytes	Lichens	Bark	Vascular plants	Substrate thickness (mm)	Canopy openness (%)
Forest	51.6 ± 21.7^{ab}	14.1 ± 5.0^{a}	57.8 ± 34.6^{a}	13.0 ± 19.5^{a}	23.8 ± 27.9^{a}	5.4 ± 12.6^{ab}	3.2 ± 4.5^{a}	8.6 ± 5.6^{a}
Old plantation	46.2 ± 24.7^{a}	17.0 ± 8.1^{b}	35.5 ± 32.4^{b}	33.3 ± 30.4^{b}	24.0 ± 25.0^{a}	7.3 ± 14.8^{a}	2.7 ± 3.1^{a}	9.9 ± 8.1^{ab}
Young plantation	59.1 ± 22.8^{b}	12.4 ± 5.3^{a}	18.4 ± 27.9^{c}	28.7 ± 29.7^{b}	51.3 ± 34.6^{b}	1.6 ± 8.0^{b}	1.5 ± 2.4^{b}	11.7 ± 8.6^{b}

In *J. teretifolia* mortality was generally higher than in *L. aromatica*, particularly during the first months after transplantation when there was no significant habitat effect on *J. teretifolia* mortality ($F_{2,266} = 1.60$, $P = 0.21$, Figure 3b). Between March and August 2008 mortality increased in all habitats with a significant habitat effect ($F_{2,258} = 3.16$, $P < 0.05$; Figure 3b) and higher mortality in young than in old plantations. During the last period mortality was somewhat lower again with a nearly significant habitat effect ($F_{2,237} = 2.97$, $P = 0.05$).

Effect of branch characteristics and climate

In both species growth was faster on upper branches than on lower branches in forests and old coffee plantations and faster on lower branches in young plantations (Figure 4), although we detected a significant difference only for *L. aromatica* in the young plantations (paired t-test; $t = 3.76$, $P < 0.01$). Mortality was mostly lower on the upper branches in forests and old plantations but higher in young plantations, though none of these differences was significant. When growth and mortality on individual branches were tested, none of the branch parameters (Table 2) had a significant effect (data not shown).

Branch parameters differed significantly between habitats with selected branches in forests having higher bryophyte and lower lichen cover than plantations, in young plantations having more bare bark area than in forests or old plantations and lower substrate thickness and higher canopy openness than in forests, and in old plantations having higher branch diameter than in forests and young plantations (Table 2). *Lycaste aromatica* mortality was negatively correlated with mean bryophyte cover per site and positively with lichen cover and canopy openness (Table 3).

Air temperature and relative humidity recorded at individual sites over most of the time of the experiment were not related to growth or mortality (data not shown).

DISCUSSION

Transplantation experiments are simple tools to test for environmental effects on plants, and epiphytes are easier to transplant than most ground-rooting plants. Compared with our artificially propagated plants, local field-grown plants (Zotz & Vollrath 2002) likely suffer less transplantation stress, and using entire epiphyte mats resulted in no increased mortality (Nadkarni & Solano 2002). For our study sampling a high number of rare orchids from the field was not an option, thus we relied on artificial propagation. Transplantation stress was likely to have had an effect on initial growth and mortality, which is obvious in *J. teretifolia* where initial growth was

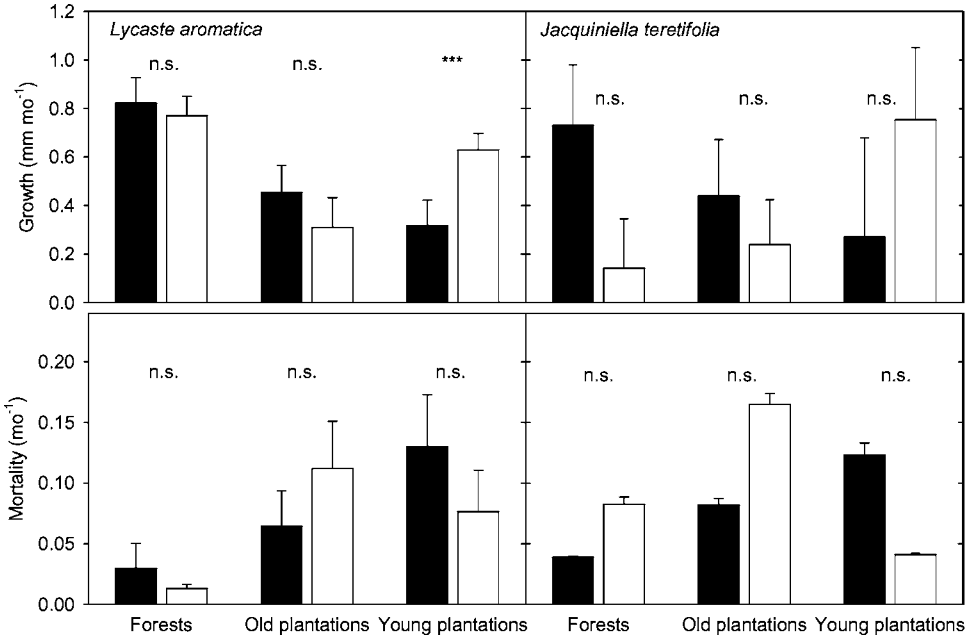

Figure 4. Growth (upper graphs) and mortality (lower graphs) of epiphytic *Lycaste aromatica* (left) and *Jacquiniella teretifolia* (right) seedlings transplanted to branches in the upper (black bars) and lower (empty bars) crown on trees in three different habitats. Error bars indicate standard error, ** indicates significant difference (paired t-test, $P < 0.01$).

negative. During the last census interval the mortality rates of transplanted seedlings in forests (0.025 mo^{-1}), which were *c.* 2.5 y old, were in the range of juvenile plants beyond the seedling stage in the field at the Parque site (average mortality over 3 y was 0.014 and 0.017 mo^{-1} for *L. aromatica* and *J. teretifolia* respectively; Winkler 2005), so apparently after some adaptation the transplanted plants reflect the situation in the field well. Mean natural growth rates of up to *c.* 2-y-old seedlings at the Parque site were 0.7 mm mo^{-1} (SD = 0.8 mm mo^{-1}, n = 84) and 1.1 mm mo^{-1} (SD = 0.5 mm mo^{-1}, n = 11) for *J. teretifolia* and *L. aromatica*, respectively (M. Winkler unpubl. data).

After very low or even negative growth rate during the first two census intervals, growth rates of *L. aromatica* seedlings were higher in forests than in coffee plantations. During the last period the difference between forests and coffee plantations was especially pronounced with growth rates in forests about 60% higher than in plantations and mortality dramatically higher in plantations than in forests. Seedling mortality in *L. aromatica* increased over time even though the final interval overlaps more with the wet season than the second interval, and other studies found that seedling mortality of epiphytes declines with increasing size (Benzing 1978, Benzing 1981, Hietz 1997, Winkler 2005). Apparently, death in *L. aromatica* is a drawn-out process and individuals that for whatever reason do not achieve a positive growth balance die slowly as the reserves in their pseudobulbs are exhausted. The 1-y-old seedlings transplanted were grown under near-optimum conditions and were certainly larger than seedlings would be at this age in the field. Considering transplantation stress, the fact that roots were initially

Table 3. Correlations (Pearson r) between branch characteristics of nine sites (three forests, three coffee plantations with old and three with young shade trees) and growth and mortality of epiphytic *Jacquiniella teretifolia* and *Lycaste aromatica*. Significant correlations ($P < 0.05$) are printed in bold.

	J. teretifolia		*L. aromatica*	
Correlations	Mortality	Growth	Mortality	Growth
Bryophytes	0.077	0.571	**−0.751**	0.583
Lichens	0.045	−0.658	**0.704**	−0.573
Bare bark	−0.170	−0.243	0.419	−0.231
Vascular plants	0.121	0.165	−0.076	−0.227
Substrate thickness	0.143	0.225	−0.001	−0.069
Canopy openness	−0.216	−0.657	**0.748**	−0.352
Inclination	−0.274	0.437	−0.258	0.039
Diameter	0.207	−0.336	0.236	−0.354

not attached to the substrate and at least some habitats were likely unsuitable for the species, mortality was surprisingly low and only 15%, 35% and 32% had died after 17 mo in forests, old and young plantations, respectively. In *J. teretifolia*, the 43%, 44% and 45% of seedlings died in forests, old and young plantations, respectively. If final seedling mortality in *L. aromatica* is several-fold higher in coffee plantations (about 10% mo^{-1}) than in forests, this likely excludes the species from establishing in coffee plantations.

Disturbed forests and open vegetation are generally drier than the forest interior (Laurance 2004), but the difference between our study sites is subtle and neither mortality nor growth were related to temperature or air humidity. Also, *L. aromatica* occurs in much drier oak forests at lower elevations in the area (Hietz & Hietz-Seifert 1995) and mostly grows on larger branches in the lower canopy (Winkler & Hietz 2001), so the hypothesis was that branch parameters play a bigger role in this species. Branches of experimental trees in old plantations were even somewhat thicker than in forests and similar in rugosity and substrate thickness, but had lower bryophyte and higher lichen cover. Though the within-site effect of branch parameters was not significant, bryophyte cover had a positive effect on *L. aromatica* survival and growth when individual sites were compared. Lichens typically cover branches in more exposed conditions and drier sites and lichens and canopy openness were negatively correlated with *L. aromatica* survival. Bryophytes can improve the water-holding capacity of branches (Pypker *et al.* 2006) and for epiphytic orchids, which, unlike bromeliads, absorb water primarily through their roots, the substrate on the branch may be more important than the microclimate in defining suitable habitats.

For *J. teretifolia* seedlings we predicted growth rates to be equal or higher in coffee plantations than in forests. This prediction holds true only for the first 6 mo when fewer shoots died after transplanting in plantations. Later shoot growth, measured as the difference in length of all shoots, tended to be higher in forests but the number of shoots was much higher in coffee plantations, and higher in young than in old plantations, with no clear pattern in mortality. An analysis of shoot size distribution shows that while more of the larger shoots present at the time of transplantation died in coffee plantations, plants in plantations at the same time produced more new shoots. Thus it appears that shoots produced before transplantation may have been adapted to higher humidity and were not completely acclimatized, but the potential for growth is higher in coffee plantations. Although the death of many shoots following transplantation in *J. teretifolia* confounds the outcome, we interpret the significantly higher production of new shoots in coffee plantations as supporting our initial hypothesis. In all three old coffee plantations included in the study *J. teretifolia* is naturally abundant (but found only in two young plantations and one forest). A detailed study at La Orduña found high densities of over 800 plants ha^{-1} and a great abundance of small and young plants, showing that conditions were adequate for seed germination and establishment (Solis-Montero *et al.* 2005).

Some other studies have tried to correlate the performance of epiphyte seedling with distribution. Zotz & Vollrath (2002) found no effect of position within the tree crown on seedling mortality of three bromeliad that could explain their within-crown distribution, but for a hemiepiphytic strangling fig (*Ficus stupenda*) the preference of knotholes concurred with higher seedling survival in these microsites with substantially higher moisture retention (Laman 1995). In an attempt to explain different colonization of secondary forests by some species, seedling survival and growth were higher in early successional forests than in mature forest in Costa Rica, but this was not related to habitat preference and thus does not explain species distribution (Cascante Marín *et al.* 2008). By contrast, in the area of an Ecuadorean moist montane forest, survival rates of two xeric epiphytes were higher than those of two mesic species on isolated trees (Werner & Gradstein 2008), but sample numbers (5–19 individuals) were low.

One reason for the high variance found in epiphyte performance in many studies may be the difficulty of accurately describing the relevant micro-environment for each plant. For instance, if branches were described as having an area of 40% covered by bryophyte, this could effectively mean that two plants are rooting in bryophyte mats but the other three are not. Also, chance or stochastic processes may play a more important role in the fate of individual epiphytes than generally recognized, complicating attempts to analyse the effect of environmental parameters. For orchids with minute seeds, this starts with the chance if and where exactly on a branch a seed lands, and ends with the danger of falling to the ground with a breaking branch.

This does not exclude alternative explanations. Substantial differences in dispersal characteristics are unlikely in orchids, all of which have minute, dust-like and wind-dispersed seeds. However, orchids require a mycorrhizal partner to germinate, some orchid mycorrhiza can be quite specific (McCormick *et al.* 2006), and the presence or absence of fungi may limit orchids to certain substrates or habitats (Bayman *et al.* 1997, Tremblay *et al.* 1998). Unfortunately, studying orchid mycorrhizal associations in the field is often difficult and our germination trials with epiphytic orchids failed.

In Central America many montane forests have been replaced with coffee plantations. Where few natural forests are left, traditional coffee plantations with large shade trees play an important role in conserving biodiversity (Perfecto *et al.* 1996), but are not a suitable habitat for all species (Hietz 2005). In our study, seedling mortality during the last interval, which was about 10% mo^{-1}, is sufficient to explain the absence of *L. aromatica* from coffee plantations and was correlated with the low bryophyte cover on branches in coffee plantations. Bryophytes may be directly responsible by improving the water supply or indicative of differences in microclimate and could thus be useful indicators of habitat quality for vascular epiphytes. Understanding what permits individual species to thrive and identifying suitable habitats is important to manage coffee plantations as well as other non-natural ecosystems to maximize their value for conserving biodiversity.

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Survival and Growth of Juvenile Bromeliads in Coffee Plantations and Forests in Central Veracruz, Mexico

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ABSTRACT

Shade coffee plantations can be important refuges for epiphytes, but are not suitable for all species. To test if the performance of early life stages, often the most sensitive phase, is responsible for the species' ability to colonize coffee plantations, we compared growth and mortality rates of three epiphytic bromeliad species that differ in their ability to colonize secondary arboreal vegetation by transplanting juveniles to trees in forests, and shade trees in old and young coffee plantations in Central Veracruz, Mexico. Growth rates of *Tillandsia viridiflora*, generally restricted to forests, and *Tillandsia juncea*, an early colonizer, were related to the pattern of the species occurrence among habitats with growth rates of *T. viridiflora* being generally higher in forests and growth of *T. juncea* higher in coffee plantations. Performance of the third species, *Tillandsia heterophylla*, which is intermediate in habitat preference, was not clearly related to habitat. No difference in growth rates was found between plants transplanted in wet or dry season. In general, mortality in transplanted bromeliads was relatively low (mostly < 5% per month). In coffee plantations herbivory had a severe effect during part of the wet season, when mortality in young coffee plantations reached between 15 and 24 percent per month. Given the substantial contribution of herbivory to the mortality of juvenile plants and the significant differences between habitats, herbivory may be co-limiting the colonization of young coffee plantations by some epiphytic bromeliads.

Abstract in Spanish is available in the online version of this article.

Key words: Bromeliaceae; coffee plantation; epiphytes; herbivory; survival; transplantation experiment.

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Mexican humid montane forests, classified as 'bosque mesófilo de montaña' in Mexico, occupy 0.8 percent of the country's territory, but contain 10–12 percent of all plant species of Mexico (Williams-Linera 2007), with a particularly high diversity of epiphytes (Aguirre-León 1992, Rzedowski 1996). More than 50 percent of Mexican montane forest has been lost (Challenger 1998). Forest loss and fragmentation particularly endanger the diversity of epiphytes, which depend on host trees during their whole life cycle. With primary forests lost and fragmented, conservation in secondary habitats becomes increasingly important.

One of the most extensive forms of land-use replacing humid montane forests, particularly in the Neotropics, are coffee plantations. In Veracruz, 40 percent of humid montane forests were lost only between 1984 and 2000, while the coffee-growing area increased by 58 percent (Manson *et al.* 2008). In Mexico, most coffee is still grown under shade trees with only 11 percent of coffee cultures in seven coffee-growing areas being without shade (Moguel & Toledo 1999). Shade coffee plantations play an important role in conserving biodiversity (Perfecto *et al.* 1996, Armbrecht *et al.* 2005, Gordon *et al.* 2007). They do act not only as secondary habitats for many species, but also serve as stepping stones interconnecting forest fragments or buffering the edge effect of forest remnants.

Many epiphytes are able to colonize shade trees in coffee plantations, which have become important refuges for biodiversity in areas where little natural forests remain (Sosa & Platas 1998, Hietz 2005, Solis-Montero *et al.* 2005, García-Franco & Toledo-Aceves 2008). Not all epiphytes do well in these habitats, however, and not all coffee plantations are equally suitable (Hietz 2005), but very little is known about why some epiphyte species are able to colonize plantations, whereas others are restricted to natural forests.

Recruitment and establishment of seedlings is crucial for the establishment and maintenance of plant populations, and the seedling stage is also one of the most vulnerable periods in the life cycle of epiphytic plants (Zotz *et al.* 2001). For epiphytes, the probability of a seed to land in a safe site is low because seeds of anemochorous species moving away from the branch carrying the mother plant will more likely land on the forest floor than on a new branch suitable for germination and survival. Germination is affected by the structure, water holding capacity, and chemical composition of the substrate (Frei & Dodson 1972, Callaway *et al.* 2001), and after germination, the survival of seedlings can be low, with mortality, particularly high in the dry season (Benzing 1978, Zotz 1998, Castro-Hernández *et al.* 1999, Winkler *et al.* 2005a, Zotz *et al.* 2005). Field germination experiments of epiphytic bromeliads found germination rates between 7 and 67 percent (Winkler *et al.* 2005a, Cascante-Marín *et al.* 2008, Hietz *et al.* 2011), with subsequent survival in the first year

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after germination between 7 and 18 percent (Winkler *et al.* 2005a, Cascante-Marín *et al.* 2008).

In this study, we examined the growth and survival of juveniles of three epiphytic bromeliads that differ in their ability to colonize shade trees in coffee plantations. We transplanted pre-grown juveniles to forests, coffee plantations with large old shade trees and coffee plantations with small and younger shade trees. We asked if growth and mortality rates of the study species reflect the pattern of species occurrence and/or abundance in the three habitats, and if tree and branch characteristics are related to growth and survival of the epiphytes growing on them. Another aspect of the study was to quantitate how transplanted plants fare, as this had been suggested as a potential strategy to repopulate trees with endangered species (Toledo-Aceves & Wolf 2008).

MATERIALS AND METHODS

STUDY AREA AND SITES.—Fieldwork was carried out from February 2007 to February 2008 near Coatepec (19°27′ N, 96°57′ W), at altitudes between 1200 and 1350 m asl, which is the lower elevation range of humid montane forests. The humid montane forest has a comparatively cool (and relatively dry) season from October/November to March, a dry (and warm) season from March/April to May and a wet (and warm) season from June to September/October. Mean annual temperature is *ca* 19.5°C and precipitation is 1765 mm per year (Comisión Nacional de Agua http://smn.cna.gob.mx/productos/normales/estacion/ver/NORMAL30026.TXT).

The study area is one of the main coffee-growing regions in Veracruz with a landscape dominated by coffee plantations, fields (mostly sugar cane), and pastures. Natural forests are mostly reduced to fragments on slopes, hill tops, and in canyons. For this study, we selected natural forests, coffee plantations with large shade trees that were generally rich in epiphytes, and plantations with small shade trees with much less epiphyte cover, with three individual sites for each habitat (Table S1). Size and species of all trees > 10 cm diameter at breast height (dbh) were recorded on a 20 × 20 m plot at each study site. The forest sites were dominated by *Quercus* spp., the plantations by *Inga* spp.

STUDY SPECIES.—The three bromeliad species selected differ in their occurrence in forests and plantations (Hietz 2005). *Tillandsia viridiflora* Beer (Baker) forms water-impounding tanks with the bases of broad, overlapping leaves. The rosette of *T. viridiflora* is less compact than in *T. heterophylla* and it is usually found in the lower canopy, on stems and sometimes on rocks in closed forests. *Tillandsia heterophylla* Morren is heteroblastic with the leaf form changing from very narrow in small juveniles (the so-called 'atmospheric' life-form of bromeliads that do not form tanks) to broad and tank-forming in plants > 5–10 cm. It is common in forests, as well as in old plantations, but we never found adult plants in young plantations. Small juveniles of *T. heterophylla* cannot be distinguished from those of other species, but juveniles of any broad-leaved or heteroblastic *Tillandsia* are uncommon in young coffee plantations. *Tillandsia juncea* (Ruíz & Pavón) Poiret is atmospheric, exhibiting Crassulacean acid metabolism-type photosynthesis and is one of the most common bromeliads in the area and is found in all three habitats.

EXPERIMENTAL DESIGN.—In previous experiments, seeds were affixed to the branches in the field (Hietz *et al.* 2011), but because many of the resulting seedlings were poorly affixed and lost after germination and we feared that extremely high mortality or loss might limit the experiment, we opted for pre-growing seedlings in the laboratory. We herein use the field-germinated seedlings only to compare mean growth and mortality rates with somewhat larger pre-grown plants.

Seeds were collected from plants growing in the region, surface-sterilized, and cultivated in sterile jars on 25 mL of half-strength Murashige and Skoog medium (Murashige & Skoog 1962) plus 30 g/L sucrose adjusted to pH 5. Cultures were incubated at 25 ± 1°C, under a 16-h photoperiod provided by cool-white fluorescent lamps (50 μMol/m^2/sec^1). After 9 mo, plants were transferred to propagation trays with a mix of pine bark: oak charcoal: pumice (3:1:1) and placed in a shadehouse. The trays were covered with translucent plastic lids during the first 30 d, then the lids were progressively lifted for the plants to adapt to ambient relative humidity, and plants were irrigated twice weekly with rainwater.

At each site, we selected 16 trees, from which nine trees were randomly chosen for the transplantation experiment. On each tree, two branches in the upper and two in the lower part of the crown were selected for transplantation. For each branch section carrying transplanted plants, we measured height above-ground, inclination, diameter, canopy openness above the branch (using a spherical densiometer; Ben Meadows, Janesville Wisconsin, USA), and estimated the percentage of the branch surface covered by bryophytes, lichens, vascular epiphytes, or bare bark, and the thickness of this substrate (Table S2).

In February 2007, after 3 mo in the shadehouse, 3240 bromeliad juveniles (three species × five seedlings per branch × four branches × six trees × three sites × three habitats) were attached with non-toxic glue to strings that were tied around the branches. A number of these plants (54% in *T. juncea*, 39% in *T. heterophylla*, 14% in *T. viridiflora*) were lost because of poor adhesion between the rudimental roots and the glue. At the beginning of July 2007, an additional 1620 plants (three species × five plants per branch × four branches × three trees × three sites × three habitats) were transplanted after 8 mo in the shadehouse. Until then, the root length of the plants was sufficient for them to be tied to the branches with strips of elastic synthetic gauze. For each individual plant, the longest leaf of each shoot from the base of the rosette to the tip of the leaf was measured to the nearest mm and the sum of all shoot lengths of an individual was taken as plant size. Very few plants had more than one shoot when transplanted. Plants transplanted in February 2007 were measured before transplanting and again in May 2007, August 2007, and February 2008. The three census intervals correspond approximately to the warm dry season, the warm wet season, and the cool season. Initial size was 32.2 ± 8.5 (mean ± SD) mm for *T. viridiflora,* 20.4 ± 5.3 mm for *T. heterophylla*, and 17.0 ± 4.5 mm for *T. juncea*. Plants transplanted in July were measured again in September 2007 and February 2008. Initial size was 48.9 ± 14.7 mm for *T. viridiflora,* 45.0 ± 9.5 mm for *T. heterophylla*, and 38.0 ± 11.5 mm for *T. juncea.* At each census, plant mortality and evidence of herbivory were noted. Leaves affected by pathogens or abiotic stress were dead, but still attached to the plant (the oldest leaves in growing bromeliads die more or less continuously, but this was not quantified). In contrast, when leaves were clearly cut off, this was attributed to herbivory. We did not test if individual plants affected by herbivory had lower growth rates (which mostly was obvious because at least their leaf tips were missing), but instead tested if herbivory affected the mean growth rates of a population by comparing growth rates of all plants to growth rates of plants not affected by herbivory. When the attached roots were still present but leaves had been cut to the base, this was recorded as herbivore-induced mortality and such plants were not found to produce new leaves at a later census. Plants that were lost without traces were excluded from the analysis as we assume that they were poorly attached and consequently dislodged.

STATISTICS.—Monthly growth rates per plant were calculated as the increment of plant size divided by the months passed since the last census. Monthly mortality rates (M) were calculated at branch level as

$$m = 1 - \left(1 - \left(\frac{(M_{t1})}{(A_{t1} + M_{t1})}\right)\right)^{\left(\frac{1}{(t1-t0)}\right)}$$

where M_{t1} is the number of plants dead at census time t_1, A_{t1} is the number of plants alive at census time t_1, and t_1–t_0 is the time between two censuses (Sheil *et al.* 1995).

We did not use relative growth rates or size as a co-variable in an analysis of covariance because the correlation between size and growth was very low (Pearson $r^2 < 0.05$). Log-transformed growth rates were analyzed using a nested Analysis of Variance (ANOVA) with habitat as main fixed factor and site and tree as random factors, each fully nested in the respective higher level. Multiple comparisons between the three habitats were tested using Tukey HSD tests. Apart from these ANOVAs testing the habitat effect for each census interval and species, we calculated repeated measurement ANOVAs that included season × habitat interactions for each species. The ANOVAs with all species and habitats were calculated only over the entire time span to test species × habitat interactions, but the first and second batch of plants was not pooled. The effect of habitat on mortality was tested with generalized linear models using a binary response variable (alive/dead). For habitat × species effects, we analyzed survival over the entire census, again not pooling plants transplanted at different times. Tree and branch characteristics of habitats were analyzed using nested ANOVAs with habitat as main fixed factor and site as random factor.

Any possible difference between habitats must be related to some environmental variables the plants are exposed to. As some of these will be captured by the branch parameters measured, we did not include these as co-variables in the analysis of the habitat effect because this likely would have removed at least part of the habitat effect. Rather, we tested for significant differences between habitats and independently for a significant effect of branch parameters on growth and mortality. If plant performance and a branch parameter differ between habitats and the branch parameters significantly affect plant performance, this parameter will be a plausible candidate for explaining habitat effects.

Influence of tree and branch characteristics on growth and mortality rates of the study species was determined using generalized additive models (GAM) of the R library mgcv (Crawley 2007). For GAMs, site and tree were ignored assuming that any differences between these were represented by the branch parameters recorded for each branch. Mortality and growth rates were averaged per branch. For GAMs, we tested overall growth and mortality, *i.e.,* between transplantation and the final census, but keeping time of transplantation (first or second batch) as an additional variable. Full GAMs, including all branch parameters (height, inclination, diameter, percent cover by bryophytes, lichens and bark, substrate thickness, and canopy openness) were reduced by stepwise elimination of non-significant parameters until only parameter with a significance of $P < 0.1$ remained. Statistical analyses were calculated with *R* 2.12.1 (www.r-project.org).

RESULTS

HERBIVORY.—While the effect of herbivory on growth rates was negligible most of the year (as seen in the May 2007 and February 2008 census, Fig. 1), it was notably high between May and September, the wet season. In the August census of plants transplanted in February, 12.2, 12.9, and 0.9 percent of *T. viridiflora, T. juncea*, and *T. heterophylla*, respectively, had signs of herbivory and in the September census of plants transplanted in July 27.0, 20.3, and 7.8 percent were affected. Herbivory significantly decreased mean growth rates of *T. viridiflora* in young and old plantations and of *T. juncea* in young plantations, but had no significant effect on *T. heterophylla* (Fig. 1).

Although all the damage was probably not caused by a single herbivore, the most likely and prominent herbivore in the coffee plantations was the grasshopper *Taeniopoda cf. eques* (Romaleidae), which in August and September is extremely common in coffee plantations, generally found on or close to the ground but also seen on branches.

GROWTH.—Growth rates over the entire period were highest in *T. juncea* (4.3 ± 2.5 mm/mo for plants transplanted in February, 2.7 ± 2.3 mm/mo for plants transplanted in July). *Tillandsia heterophylla* transplanted in February grew faster (2.2 ± 1.3 mm/mo) than *T. viridiflora* (0.5 ± 0.8 mm/mo). *Tillandsia heterophylla* and *T. viridiflora* transplanted in July had low overall growth rates (−0.05 ± 1.7 and 0.1 ± 1.3 mm/mo, respectively). Negative growth resulted when the oldest and longest leaves were

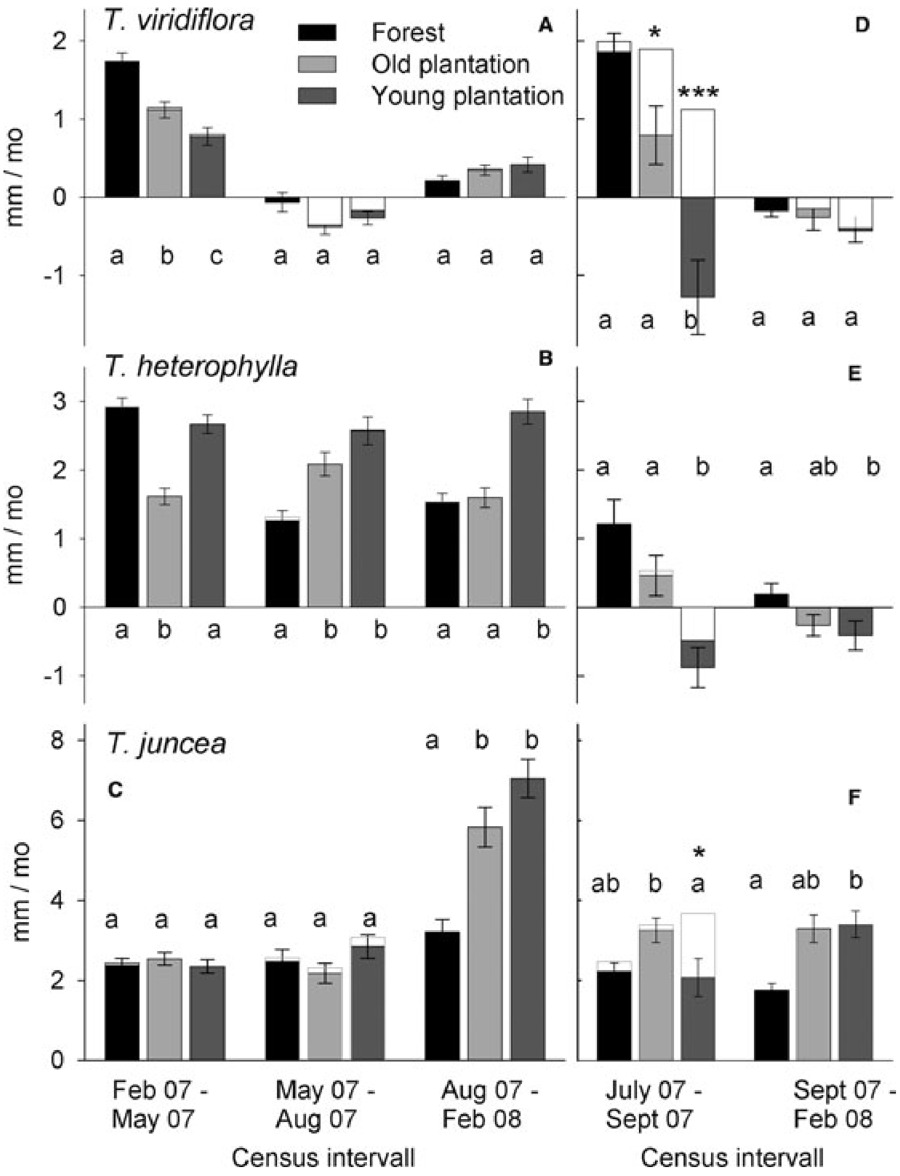

FIGURE 1. Growth rates (mm per month) of juveniles of three bromeliad species transplanted to trees in three different habitats. Plants were either transplanted in February in the dry season (A–C), or in July at the beginning of the wet season (D–F). White bars indicate growth rates after excluding plants that were still alive but had evidence of herbivory. Whiskers indicate standard errors, different lowercase letters indicate significant differences (nested ANOVA and multiple comparisons of linear contrasts by the Tukey HSD test, $P < 0.05$). Asterisks indicate that mean growth rates were significantly (*$P < 0.05$, ***$P < 0.001$) higher if individuals affected by herbivory were excluded.

lost without sufficient growth of younger leaves to compensate this.

Overall, habitat and species, as well as habitat × species interactions had highly significant effects on growth rates (Table 1). Growth rates, generally, differed between seasons or at least showed significant season × habitat interactions, except for *T. heterophylla* transplanted in July (Table 2). Growth rates of *T. viridiflora*, declined after transplantation and during the first census, were significantly lower in coffee plantations than in forests (Fig. 1). Growth rates of *T. heterophylla* decreased less with time than in *T. viridiflora*, and although there were significant habitat effects, there was no clear pattern and in individual intervals, different habitats had significantly lower rates than the others (Fig. 1). Growth in *T. juncea* did not decrease over time and when differences between habitats were significant, plants in forests had lower growth rates than in coffee plantations (Fig. 1).

MORTALITY.—Mortality differed significantly between species and habitats (Table 3). Mortality of plants transplanted in February was generally low with an overall of 80.0, 82.0, and 82.6 percent of plants of *T. viridiflora*, *T. heterophylla*, and *T. juncea*, respectively, still alive after 1 yr. For plants transplanted in February, only

TABLE 1. *Effect of habitat and species on growth rates of juveniles of three bromeliad species transplanted to forests, old and young coffee plantations. As plants transplanted in February and July were sown at the same time, those transplanted in July were older and larger at the time of transplantation.*

Start–end of experiment	*df*	Sum Sq	*F* value	*P*
February 07–08				
Habitat	2	4.37	39.5	<0.001
Species	2	86.56	782.6	<0.001
Habitat × Species	4	4.95	22.4	<0.001
Residuals	1194	66.04		
July 07–February 08				
Habitat	2	0.99	10.7	<0.001
Species	2	19.87	213.0	<0.001
Habitat × Species	4	2.46	13.2	<0.001
Residuals	1046	48.78		

TABLE 2. *Significance (*P*) of season and habitat on growth of juvenile bromeliads transplanted to forests, old and young coffee plantations (Habitat).*

	T. viridiflora	T. heterophylla	T. juncea
February 07–08			
n	912	737	437
Habitat	**<0.001**	**<0.001**	**0.002**
Season	0.161	**0.0027**	**<0.001**
Habitat × Season	**<0.001**	**0.003**	0.726
July 07–February 08			
n	431	438	408
Habitat	**<0.001**	**<0.001**	**0.006**
Season	**<0.001**	0.125	**<0.001**
Habitat × Season	**<0.001**	0.837	**<0.001**

n is the number of seedlings with at least one growth measurement, $P < 0.05$ indicated by bold numbers. Significances were tested with repeated measurement ANOVAs for three seasons (i.e., census intervals) between January 07 and February 08 and two seasons between July 07 and February 08.

TABLE 3. *Significance (*P*) of habitat and species on mortality of juveniles of three bromeliad species transplanted to forests, old and young coffee plantations. Plants transplanted in July were 12-mo old and larger than plants transplanted in February, which were 17-mo old.*

Interval	February 07–08	July 07–February 08
n	1670	1506
AIC	1617	1662
	P	P
Habitat: old coffee (OC)	0.519	**0.006**
Habitat: young coffee (YC)	0.274	**<0.001**
Species: T. viridiflora *(Tv)*	0.923	**0.001**
Species: T. heterophylla *(Th)*	0.374	**0.001**
OC: Tv	0.323	**0.010**
YC: Tv	**0.030**	**0.008**
OC: Th	0.577	**0.001**
YC: Th	0.113	**0.002**

$P < 0.05$ indicated by bold numbers.

T. viridiflora during the last census interval had significantly higher mortality in young coffee plantations than in old plantations or forests (Fig. 2).

In February 2008, 71.5, 76.1, and 77.1 percent of *T. viridiflora*, *T. heterophylla*, and *T. juncea* transplanted in July 2007 were still alive. Mortality was assigned to herbivory when leaves were cut to the base with little above the roots left. This was observed almost exclusively in the September census, but accounted for 45.9, 18.0, and 55.0 percent of mortality in *T. viridiflora*, *T. heterophylla*, and *T. juncea* transplanted in July 2007 and for a substantially higher proportion of deaths in young coffee plantations (Fig. 2). During the second census interval, mortality was generally lower and only *T. juncea* had higher mortality rates in young plantations than in forests (Fig. 2).

Mean mortality rates of the plants that had germinated in the field during the first 5–6 mo after germination (3.3, 6.2, and 3.0% per month for *T. viridiflora*, *T. heterophylla*, and *T. juncea*, respectively) were similar to those of larger pre-grown plants. However, mean growth rates of the seedlings germinated in the field (0.46, 0.58, and 0.42 mm/mo) were lower.

Effects of tree and branch characteristics.—Branch height and bryophyte cover were positively and canopy openness was negatively related to growth of *T. viridiflora*. The effects of branch diameter and substrate thickness on growth in this species were also significant, but not uniform across the range of branch sizes and substrate thickness (Table 4). Branch diameter and the cover with lichens affected mortality of *T. viridiflora*. Growth of *T. juncea* was negatively correlated with bryophyte cover, and mortality in *T. heterophylla* was higher in larger diameter branches (Table 4).

Trees in younger plantations were smaller than that in forests and old plantations, but forest and old plantation trees were of similar size (Table S1). Forest branches selected for transplantation had higher bryophyte and lower lichen cover than those in plantations, whereas branches in young plantations showed a higher percentage of bark area than both forests and old plantations (Table S2). Substrate thickness was lowest in young plantations and highest in forests, canopy openness above branches was highest in young plantations and lowest in forests, and branch diameter was highest in old coffee plantations.

DISCUSSION

Transplantation effect.—The seedling stage is often the most sensitive with high mortality rates (Harper 1977). Seedlings that had germinated in the field had lower growth but similar mortality rates compared to pre-germinated larger plants. While mortality of naturally regenerating seedlings in their first year is often higher (Zotz & Vollrath 2002, Winkler *et al.* 2005a, Cascante-Marín *et al.* 2008), mortality rates of the larger plants we

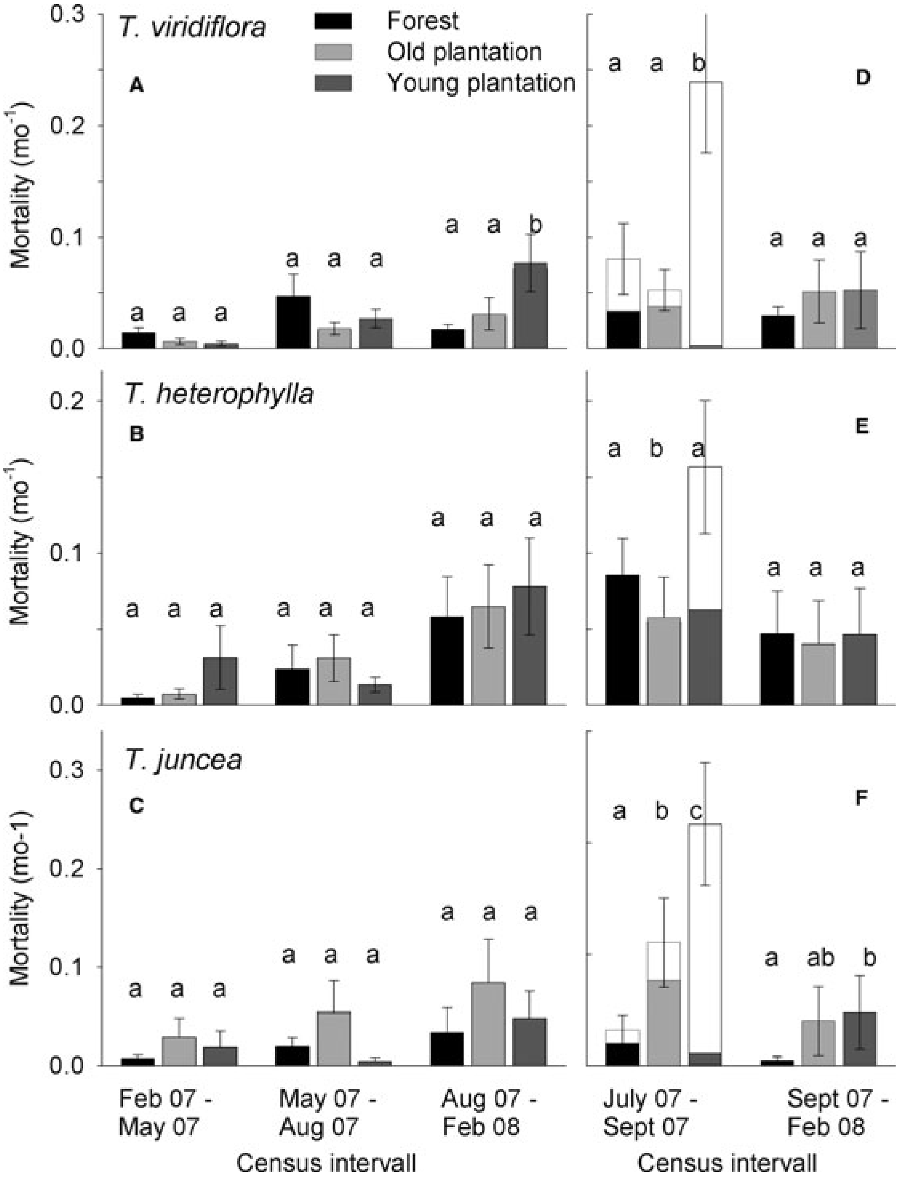

FIGURE 2. Mortality rates (per month) of juveniles of three bromeliad species transplanted to trees in three different habitats. Plants were either transplanted in February in the dry season (A–C) or in July at the beginning of the wet season (D–F). White bars indicate mortality caused by herbivory when nearly all leaves were missing but the roots were still attached to the substrate. Whiskers indicate standard error, different lowercase letters indicate significant ($P < 0.05$) differences tested with GLM.

transplanted were very similar to annual mortality rates ranging between 0.2 and 0.39 in juveniles between 1 and *ca* 10 cm length of five bromeliad species in one of the study forests (Winkler *et al.* 2007). Growth rates of transplanted plants in the forests mostly ranged between 1.5 and 2.5 mm/mo, which are very similar to the 1.5–2.5 cm/yr seen in naturally growing *Tillandsia* spp. in one of the sites (Hietz *et al.* 2001). Thus, mean mortality and growth in our experimental plants reflect normal rates.

This, however, does not mean that plants suffer no transplantation stress at all. In general, we expected growth rates to be higher in the wet season and higher for larger plants. While this was the case for *T. juncea*, the opposite was found in *T. viridiflora*, and may be due to the fact that the drought-sensitive *T. viridiflora* was affected more by transplantation stress than the drought-tolerant *T. juncea*.

HABITAT AND BRANCH EFFECTS.—The main hypothesis that growth rates reflect the pattern of species occurrence among habitats was confirmed for *T. viridiflora* and *T. juncea*. Where differences were significant, the forest species, *T. viridiflora* had generally higher growth rates in forests than in coffee plantations, and growth of *T. juncea* was higher in coffee plantations than in forests (Fig. 1). For the intermediate *T. heterophylla*, there was no clear pattern of which habitat is more suitable.

TABLE 4. *Significance (*P*) of branch parameters on growth and mortality of three bromeliad species transplanted to branches in various habitats.*

Number of branches	T. juncea		T. heterophylla		T. viridiflora	
	232		298		309	
Branch parameter	Growth	Mortality	Growth	Mortality	Growth	Mortality
Diameter				~0.010	~0.043	~0.011
Height		~0.100			+0.000	
Substrate					~0.007	
Bryophytes	−0.002				+0.001	
Lichens						+0.089
Canopy openness					−0.017	

Significance was tested with generalized additive models (GAM) that were reduced by stepwise elimination until only parameters with a significance $P < 0.1$ remained. Branch inclination was never significant. The date of transplantation (February or July) was included in the model and had always a highly significant effect on growth rates, but only for *Tillandsia heterophylla*, a significant effect on mortality rates. Sign indicates a generally positive (+), negative (−), or non-uniform (~) effect.

Factors, such as light intensity, water, and nutrient availability through precipitation and runoff, substrate moisture, bark stability, and surface structure vary within a given host tree canopy and can influence epiphyte germination, distribution, and abundance (Castro-Hernández *et al.* 1999, Callaway *et al.* 2002 Zotz 1998, Winkler *et al.* 2007). Differences in growth or mortality must be explained by factors that plants are experiencing on the microsites where they are growing, and we therefore tested for the effect of branch parameters on plant performance (Table 4) and compared these parameters between habitats (Table S2). In general, growth and to a lesser extent, survival of *T. viridiflora* were more affected by branch parameters than in the other two species. Bryophyte cover, canopy openness, and the height of the branches affected growth in this species (Table 4), which is consistent with differences in these branch parameters between forests, old and young plantations (Table S2). Bryophyte cover has previously found to positively affect the survival of juvenile orchids (Scheffknecht *et al.* 2010) and the germination of *T. viridiflora* and *T. heterophylla* (Hietz *et al.* 2011). Other studies have found positive as well as negative correlations between vascular epiphytes and bryophyte patches (Zotz 2003). Correlation, however, is not the same as causation, and epiphytic vascular plants and bryophytes may grow together more often than if distributed randomly if both have similar microsite preferences. Whether bryophytes directly facilitate other epiphytes or only share their habitat, the abundance of bryophytes is nearly always related to humidity, old trees and large branches, and may thus serve as an indicator of the suitability of a habitat for other drought-sensitive epiphytes.

Tree species can differ in their suitability as host trees for epiphytes (Callaway *et al.* 2002, Cardelús 2007). While different trees dominate the coffee plantations (*Inga* spp.) and forest (*Quercus* spp.) studied, we think this very unlikely to explain the differences in *Tillandsia* performance because *Inga*, as well as *Quercus* are generally good epiphyte hosts in the region (Hietz & Hietz-Seifert 1995, Hietz 2005). The choice of trees, however, might have a substantial effect on the suitability of plantations for epiphytes in general. For instance, *Trema micrantha* and *Bursera simaruba*, both occasional shade trees in coffee plantations, carry fewer epiphytes than *Inga* or *Quercus*.

UNEXPECTED HIGH HERBIVORY.—Herbivory was thought to be of little relevance to epiphytes (Benzing 1990, Zotz 1998), but recent studies challenge this assumption. In a 3-yr study of *Werauhia sanguinolenta*, (Schmidt & Zotz 2000) report a herbivore-induced annual leaf area loss in their population of up to 4.4 percent, leading to a herbivore-induced mortality rate of 2.2 percent. In one of our studied forests (Parque Ecológico), herbivore damage of meristematic tissue and reproductive organs contributed significantly to mortality and reduced fecundity in epiphytic orchids and bromeliads, while less than 1.5 percent of leaf area was eaten in orchids and bromeliads (Winkler *et al.* 2005b).

While herbivory was negligible during the dry season, the severe effect of herbivory on juvenile *T. viridiflora* and *T. juncea* in August and September in the coffee plantation sites was quite unexpected. The grasshopper *Taeniopoda* was not observed during the dry season but was very abundant in coffee plantations in August and September. Remarkably, herbivory was substantially higher in plants transplanted in July than in plants transplanted in February (Fig. 2) and was higher in young than in old plantations, although grasshoppers were present in both. Leaves of plants transplanted in the dry season may have become better defended than plants recently moved from the protective environment of the shadehouse. *Taeniopoda*, while mainly ground-dwelling, was also seen on branches but may reach the branches in young plantations more frequently than those in old plantations, where plants were transplanted more than twice as high (Table S2). Although the plants were observed only for 1 yr, we have observed the high abundance of *Taeniopoda* in several summers in various coffee plantations, and therefore believe that the herbivory reported was not unusual. Given the substantial contribution of herbivory to juvenile mortality and the significant differences between habitats, this is a situation where an herbivore may be co-limiting the colonization of a habitat by epiphytes.

LIMITS TO COLONIZATION OF COFFEE PLANTATIONS.—Shade coffee plantations retain some important characteristics of natural forests and can provide important refuges for many species (Perfecto *et al.* 1996), including epiphytes (Hietz 2005). The suitability depends on many factors, but for epiphytes, the size and/or age of the shade trees are of prime importance and it has been pointed out that sparing large forest trees is an important management strategy for forestry operations (Wolf 2005). Similarly, the conservation value of old coffee shade trees should be recognized.

Except for rustic coffee plantations, where some of the original forest trees are spared and the understory is cleared for coffee (Hernández-Martínez *et al.* 2009), all shade trees are planted and need to be colonized by epiphytes at some point. The ability of epiphytes to colonize new environments have been discussed in terms of limitations to seed dispersal (Cascante-Marín *et al.* 2009), pollination limitation (Ackerman *et al.* 1996), the presence of mycorrhizal fungi necessary for germination of orchids (Bayman *et al.* 2002, Otero *et al.* 2005), and physiologic adaptations to the microclimate (Acebey *et al.* 2003, Hietz 2005, Wolf 2005).

Although seed dispersal may limit the colonization of coffee shade trees, this is unlikely to differ between the three species, whose seeds and appendages for air dispersal are very similar. Dispersal will, however, limit the colonization of *T. viridiflora* simply because potential source populations are restricted to few remaining forests, which are at a substantial distance to most coffee shade trees. *Tillandsia juncea* is self-compatible and in part self-pollinating (fruit set in bagged flowers without pollinator was still 48 percent Hietz *et al.* 2006), which is an advantage for plants colonizing new habitat where conspecific plants for cross-pollination are rare. We have no information of possible pollinator limitation in the other two species, which have no colored bracts and creamish or green flowers typical for moth-pollinated species, but autogamy does not appear to be common in bromeliads (Kessler & Krömer 2000). In the case of the three bromeliads studied herein, habitat and microsites play a significant role for early survival and growth as seen in this study. The proportion of seeds germinating was also related to the habitat with *T. viridiflora* having highest germination rates in forests and *T. juncea* in young coffee plantations (Hietz *et al.* 2011). For germination, branch characteristics appear to be somewhat less and climate somewhat more important than for early survival and growth. Germination on branches, which differed substantially in surface cover, was similar to germination on artificial homogeneous substrate exposed at the same location, and mean vapor pressure deficit of a site was significantly correlated with germination in *T. viridiflora*, but not with the performance of juveniles.

To what extent the unexpected high herbivory also explains the distribution is hard to say. As our design includes a true replicate of habitats, the results can be generalized at least for the region of our studies. Herbivory certainly cannot explain the presence or absence of our study species alone, as *T. viridiflora* is also absent from large trees in old plantations where herbivory is much lower than in young plantations, and herbivory appears to affect the very common *T. juncea* about as much as *T. viridiflora*. Summarizing, the lack of *T. viridiflora* in the plantation can be explained by a combination of lower germination and lower juvenile growth and survival than in forests because of a drier microclimate, which also makes the substrate less suitable, and high loss through herbivory.

POSSIBLE USE OF TRANSPLANTATION.—In spite of transplantation stress and unexpected herbivory-driven mortality, on average *ca* 80 percent of plants transplanted in the dry season and 70–80 percent of those transplanted in the wet season were still alive after 12 and 7 mo, respectively. Transplantation of propagated epiphytes has been suggested as a way of reintroducing endangered species in places where suitable habitat exists and it was recommended to use plants as large as possible to reduce mortality (Toledo-Aceves & Wolf 2008). Large plants certainly have lower mortality and take less time to reproduce, but this has to be weighed against the effort, time, and space needed to produce larger plants. Our plants were 12–17 mo when transplanted, larger than field-germinated seedlings, which at this age rarely exceed 1 cm (Mondragón *et al.* 2004, Winkler *et al.* 2007), and had mortality rates similar to field-germinated plants of the same size, thus caring for plants much longer may not be necessary. If transplantation to re-establish a species or support a dwindling population of epiphytes is attempted, our study suggests that it is important to choose a habitat of suitable substrate and microclimate, and consider unexpected high mortality from herbivores, which may or may not be limited to certain canopy zones. Once adjusted to their new environment, transplanted plants have growth and mortality rates similar to plants germinated *in situ*.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Habitat and tree characteristics of forests, old and young coffee plantations selected for transplanting pre-growth juvenile bromeliads.*

TABLE S2. *Characteristics of experimental branches of forest, old and young coffee plantations selected for transplanting pre-growth juvenile bromeliads.*

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7 Conclusions

In recent years several studies have confirmed the benefit of shade coffee agroecosystems for the conservation of biodiversity in the face of ongoing forest loss, as they retain many important characteristics of natural forests and can serve as secondary habitats for many plant species (Perfecto et al. 1996, Moguel & Toledo 1999, Hietz 2005). Secondary arboreal vegetation is especially important for epiphytes, which depend on host trees through all their life stages. The suitability of coffee plantations as secondary habitats depends on factors like tree age and size, tree density and diversity, but also on management measures such as intensity and frequency of pruning, removal of epiphytes from the branches (a widely practiced measure) and intensity and frequency of agrochemical application (Moorehead et al. 2010).

To know what affects the suitability of different coffee plantations, to understand, why some epiphytes are able to colonize them, whereas others do not, is important for taking adequate conservation measures and recommending epiphyte-friendly coffee cultivation systems.

This study focused on the early stages in the life cycle of epiphytes, i.e. the recruitment and establishment of seedlings, which are not only essential for the maintenance of existing plant populations, but also play a crucial role in the colonization of new habitats .

We found that germination rates, growth and mortality of our study species generally reflect the natural patterns of species occurrence and abundance in the three habitats, with species restricted to forests showing lower germination rates (*T. viridiflora*) and lower growth and survival rates (*T. viridiflora*, *L. aromatica*) in coffee plantations compared to forests, whereas the colonizing species showed higher germination rates (*T. juncea*) and higher growth rates (*T. juncea*, *J. teretifolia*) in coffee plantations.

Our results suggest that higher mortality rates of the forest species, at least of *L. aromatica*, as well as lower growth rates may co-limit the colonization of coffee plantations, especially in young plantations with small shade trees. Leaf herbivory in young plants may additionally limit the successful establishment in some species.

Overall, in spite of these significant habitat effects, the explanatory value of parameters like vegetation cover, substrate thickness, diameter, height and inclination of branches was not as conclusive as expected. Still, results indicate that a more humid microclimate favors germination and growth of forest species. Germination rates of the forest species *T. viridiflora* decreased with increasing vapour pressure deficit and temperature, and increasing canopy openness negatively affected seedling growth rates. Bryophyte cover was positively correlated with germination and growth rates, either through direct facilitation or because they share a preference of the same microhabitat. Increasing canopy openness negatively affected growth rates of *T. viridiflora*. For *L. aromatica*, we found a positive correlation of canopy openness and lichen cover with mortality, and a positive effect of bryophyte cover on survival.

These results are consistent with our observation of species preferences of different microclimatic environments inside natural forests, where the colonizing species often prefer more open, drier forest patches or higher canopy regions, whereas the forest species tend to grow in more humid areas or in the lower canopy.

Although mortality in epiphyte seedling is generally higher than in larger plants, at the end of this study a high percentage of the transplanted juveniles of each species was still alive in coffee plantations. (50.5 and 76.5 percent for *J. teretifolia* and *L. aromatica*, respectively; 81.4, 79.6 and 78.7 percent for *T. juncea*, *T. heterophylla* and *T. viridiflora* exposed in dry season, respectively; 71.2, 76.6 and 70.2 percent for *T. juncea*, *T. heterophylla* and *T.*

viridiflora exposed in wet season, respectively). A survival rate of over 70 percent in the forest species *L. aromatica* and *T. viridiflora* is certainly encouraging if we consider the possibilities of re-establishing rare species by artificial propagation and transplantation. In terms of what causes the absence of even juvenile forest plants in coffee plantations, it raises further questions that need to be answered.

In a study on bromeliad establishment in different successional habitats in Costa Rica, Cascante-Marín et al. (2009) found that seed exchange between habitats was low and the presence of species likely dispersal-limited. We know that the seeds our study species share very similar dispersal properties (orchids and bromeliads, respectively) and that the possibility to reach a certain site should be the same within each group. However, what may contribute to the differences in actual species distribution is the low abundance of natural populations of the forest species in the area. The percentage of juveniles in some of these populations was quite low (Winkler & Hietz 2001, personal observation), which can be a sign of low fecundity. Dwindling size, low fecundity and low seed quality of source populations are possible explanations for the absence of seedlings and juveniles of forest species in the coffee plantations of the area.

It has been argued that the survival of mature plants is generally more important for population growth than germination and seedling survival. Many epiphytes need 10 to 20 years to reach reproductive maturity (Benzing 1981, Larson 1992, Zotz 1995, Winkler & Hietz 2001), as is also the case with our forest species. Young tree age, heavy pruning and a high tree turnover rate likely explain the absence of adult *T. viridiflora* and *L. aromatica* plants in young coffee plantations.

What causes the absence of adult forest plants in coffee plantations with old shade trees, however, is not so easily inferred. In contrast to *T. viridiflora*, whose leaves and floral bracts are only rarely used as ornaments in the construction of the floral arches covering the church fronts of the villages around Xalapa during festivities of the local saint, *L. aromatica* is valued in the region for its beautiful yellow flowers and often illegally collected and sold as ornamental plant. Trees in coffee plantations are much more easily accessible than forest trees, which makes the collection of wild plants relatively easy. Additionally, lower tree density leaves the tree canopy more vulnerable to strong winds, which we observed several times a year, and which left the ground strewn with fallen epiphytes, some still attached to the branches they had been growing on. This may be particularly precarious to species with an already isolated occurrence. We also may have to consider the management history of the individual plantation as cause for the absence of adult plants. While realizing this study we did not observe any incidence of epiphyte removal at our sites, but we lack information on former management strategies.

Further studies on the suitability of coffee plantations and other secondary arboreal vegetation in sustaining epiphyte diversity in the area need to address the subject of seed dispersal and seed exchange in a fragmented landscape, as well as study the demography of the remaining populations of rare forest species to evaluate their adequacy as source populations for the survival of the species. It would be also very interesting to monitor if and to what extent our transplanted individuals survive during the next years and if some of them will reach reproductive age.

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9 List of figures

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10 CV

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