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Abstract
We compared Araceae abundance among mature forests, secondary forests, and plantations (8–14 years) in central Panama. Araceae colonization was virtually nonexistent in secondary forests and plantations. Low humidity, relatively short forest stature, and time could drive this absence. These results highlight the conservation value of forests containing intact populations of Araceae.

Keywords
epiphyte, Araceae, recolonization, forest restoration, Agua Salud, Panama

Secondary forests are becoming increasingly abundant in the neotropics (Aide et al., 2013; Chazdon et al., 2009), but they do not always offer the complete array of biotic and abiotic conditions necessary to sustain the full range of biota found in mature forests (Gibson et al., 2011). Vascular epiphytes are a good example of the problem of biodiversity conservation in secondary forests. They represent up to 50% of the vascular flora in Neotropical forests, but their recolonization after disturbance is very slow (Gentry & Dodson, 1987; Nadkarni, 2000). This feature is particularly aggravated in fragmented landscapes (Cascante-Marín et al., 2009; Kanowski, Catterall, Wardell-Johnson, Proctor, & Reis, 2003; Woods & DeWalt, 2013). Comparing epiphyte communities in secondary, planted, and mature forests can help researchers and restoration practitioners determine whether arrested epiphyte recolonization requires manual assistance, via for example, epiphyte transplants (Duarte & Gandolfi, 2017; Fernandez Barrancos, Reid, & Aronson, 2017).

Araceae are among the most diverse groups of epiphytic plants (Croat, 1988; Gentry & Dodson, 1987) and provide nectar, fruit, and nesting sites for a wide array of arboreal animals such as birds, insects, primates, and bats (Cestari & Pizo, 2008; Kraemer & Schmitt, 1999; Maia, Schlindwein, Navarro, & Gibernau, 2010; Ripperger, Kalko, Rodríguez-Herrera, Mayer, & Tschapka, 2015; Vieira & Izar, 1999). In Panama, they have high rates of endemism (Correa, Galdames, & De Stapf, 2004), are the fifth most diverse group of vascular plants (Ortiz & Croat, 2017), and have exponential rates of new species discoveries (Croat, 2015).

Given Araceae's role in sustaining tropical biodiversity, it is important to know how Araceae populations are responding to land use change. Monitoring intact and recolonizing populations of Araceae can help elucidate the effects of land degradation on Araceae populations and to develop strategies to restore Araceae communities. Here, we focus on hemiepiphytic Araceae because they are suitable for monitoring from the ground: As secondary hemiepiphytes, their roots are often close to or connected to the ground which makes it easy to detect them without the need to climb to the canopy. This makes it possible to study the

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recolonization of hemiepiphytic Araceae communities across a relatively large number of sites in a small amount of time (Dent & Wright, 2009; Wolf, Gradstein, & Nadkarni, 2009).

The goal of this study is to (a) determine whether hemiepiphytic Araceae from mature forests are able to colonize nearby naturally regenerating secondary and planted forests, and (b) to test for differential rates of recolonization by forest type. We address the following questions:

1. Are hemiepiphytic Araceae from mature forests recolonizing nearby young secondary forests and plantations?
2. Are there any differences in hemiepiphytic Araceae recolonization between naturally regenerating and planted forests?

The study took place within the Agua Salud study area in the central part of the Panama Canal Watershed (9°13' N, 79°47' W). The area is classified as tropical moist forest (Holdridge, 1967). Elevation is 330 masl. Annual rainfall and temperature are 2,700 mm and 24°C, respectively, with a dry season that goes from December to May (Ogden, Crouch, Stallard, & Hall, 2013). The landscape consists of a mosaic of cattle pastures, agricultural fields, fallows, plantations, and secondary forests of various ages (van Breugel et al., 2013). Hemiepiphytic Araceae were monitored in secondary forests (8–14 years old), native plantations (9 years old), and mature forest fragments (>100 years old). Secondary forest and plantation plots were adjacent to Soberania National park. All plots were connected by a dense network of forest patches along streams and were located less than 100 m from old secondary forest fragments (van Breugel et al., 2019). A total of 17 plots were used for Araceae monitoring: six 20 m × 50 m (0.6 ha) plots in secondary forests, seven 30 m × 30 m (0.63 ha) plots in plantations, and four 20 m × 50 m (0.4 ha) plots in mature forests. Secondary forest plots used in this study constitute a subset of the plots used in van Breugel et al. (2013).

Vegetation in secondary forests (stem density of 7,990 stems/ha; ≥1 cm diameter at breast height [DBH], and basal area of 23.5 m^2/ha) consisted of medium-sized trees that formed a heterogeneous canopy cover: While the forest had recovered relatively quickly, secondary forests had not yet reached the light levels found in older forests (van Breugel et al., 2013), and regions with small trees, tree fall gaps, and high liana densities (Lai, Hall, Turner, & van Breugel, 2017) had higher canopy openness. The understory was relatively dense and was composed of tree seedlings, herbaceous plants, and vines. The most abundant species in secondary forest sites were *Byrsonima crassifolia* (L.)

Kunth, (Malpighiaceae), *Miconia argentea* (Sw.) DC. (Melastomataceae), and *Xylopia frutescens* (Aubl.) (Annonaceae). The percentage of stems for each of these species was 21%, 15%, and 13.5% respectively. Mature forest vegetation (stem density of 3,656 stems/ha; ≥1 cm DBH and basal area of 26.1 m^2/ha; Hassler, Zimmermann, van Breugel, Hall, & Elsenbeer, 2011) consisted of large trees that formed a dense canopy and of low densities of vines and herbs. The most abundant species in mature forests were *Oxandra longipetala* R.E. Fr. (Annonaceae), *Perebea xanthochyma* H. Karst. (Moraceae), and *Socratea exorrhiza* (Mart.) H. Wendl. (Arecaceae). The percentage of stems for each of these species was 9%, 9%, and 6%, respectively. Plantations (stem density of 1,282 trees/ha; ≥1 cm DBH and basal area of 12.66 m^2/ha; Mayoral, van Breugel, Cerezo, & Hall, 2017) hosted a mix of five timber species native to Panama, namely, *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae), 38% stems; *Tabebuia rosea* (Bertol.) DC. (Bignonicaceae), 11% stems; *Pachira quinata* (Jacq.) W.S. Alverson (Malvaceae), 21% stems; *Dalbergia retusa* (Hemsl.) (Fabaceae), 21% stems; and *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels (Anacardiaceae), 10% stems. Of these species, *Anacardium excelsum* is present in mature forests (0.2% stems) and *Terminalia Amazonia* is present in secondary forests (7% stems).

As part of study plot maintenance, plantation plots are cleaned 4 times a year using machetes to remove ruderal vegetation, and these plots have the lowest canopy cover (Mayoral et al., 2017). Annual tree diameter measurements are performed in secondary forests and plantations, and every 5 years in mature forests. When hemiepiphytes or climbers are present, tree diameter measurement is performed by placing the measuring tape underneath their roots, being careful to minimize disturbance to root connections between climbing plants and the ground or the tree trunk (Condit, 1998).

The presence of Araceae was recorded on all trees with DBH ≥5 cm. A total of 1,479 trees were surveyed: 571 in secondary forests, 433 in plantations, and 475 in mature forests. Araceae specimens were identified with the help of Dr. Thomas Croat, Dr. Michael Grayum, and Dr. Orlando Ortiz.

To compare Araceae abundance between forest types, we standardized Araceae abundance to a density of Araceae per hectare. To test whether there was a significant difference in Araceae abundance between mature forests, secondary forests, and plantations, we bootstrapped data 10,000 times to calculate the 95% confidence intervals of the mean abundance of Araceae in each land use. Bootstrapping with replacement was performed using the "boot" (Bootstrap Resampling) function from the "boot" package in R version 3.2.3 (R. Development Core Team, 2008). An overlap in

confidence intervals from different forest types would indicate that Araceae abundance was not significantly different between forest types while the absence of an overlap would indicate that the number of surveyed Araceae was significantly different between forest types (Cumming, 2009).

A total of 818 Araceae were recorded over the three forest types including nine species and nine morphospecies. Ninety-four percent of the surveyed Araceae individuals were identified to species and to genus. Araceae were abundant in mature forests but were nearly absent in secondary forests and plantations. Mean Araceae abundance was 2,014.9 Araceae/ha (95% CI [1781, 2255]) in mature forests, 13.4 Araceae/ha (95% CI [0, 30.33]) in secondary forests, and 4.8 Araceae/ha (95% CI [0, 10.75]) in plantations (Table S1). Mature forest confidence intervals did not overlap with those of secondary forests nor plantations, indicating that Araceae abundance was significantly different between mature forests and these two forest types. Secondary forest and plantation confidence intervals overlapped, showing no difference in Araceae abundance between these two forest types (Table S1). This pattern was observed for hemiepiphytic Araceae, in general, as well as for six species and two genera. On average, Araceae were 152 and 420 times more abundant in mature forests than in secondary forests and plantations respectively (Table 1).

Although differences in abundance are expected, the fact that hemiepiphytic Araceae are virtually absent in secondary forests and plantations is surprising because these two forest types are located close to mature forests (see earlier) and many Araceae are dispersed by generalist birds (Snow, 1981). Dispersal limitation has been shown to partially structure secondary forest tree communities at the landscape but not local scale at Agua Salud (van Breugel et al., 2019). Given these results for trees and the fact that our study included only a subset of plots that are in one block of the Agua Salud study site, we believe that seed dispersal limitation is unlikely to be driving the absence of Araceae. Generalist seed dispersing fauna are known to use secondary forests as well as mature forests (Chazdon et al., 2009). In addition, mature forest tree species have regenerated rapidly in secondary forests in our study area, and many produce abundant amounts of seeds that are dispersed by both birds and bats throughout the landscape (Van Bael, Zambrano, & Hall, 2013; van Breugel et al., 2013).

It is possible that research or other management could have influenced hemiepiphyte abundance. In our study plots, plantations are regularly cleared of ruderal vegetation, and in all study plots (plantation, secondary, and mature forest), tree diameters are measured with a DBH tape (Condit, 1998), which might impact hemiepiphytes when the roots are pulled from the trunk during measurement. Neither of these impacts is sufficient to explain our observation that hemiepiphytes were depauperate in plantations and secondary forests. First, ruderal clearing is only done in plantations, but hemiepiphytes were depauperate in both plantations and secondary forests, where ruderals are not removed. Second, many hemiepiphytes grow quickly (1.5–8 m/year; Patiño, Gilbert, Zotz, & Tyree, 1999), and passing a DBH tape beneath their roots would not likely cause mortality (T. Croat, personal communication, 12 February 2019). Furthermore, an analysis of Araceae data from a study by Reid, ChavesFallas, Holl, and Zahawi (2016a, 2016b) in southern Costa Rica showed that secondary forests and plantations (9–11 years old) also did not differ in their Araceae abundance (Table S2). As such, we expect that other dispersal and establishment filters are more likely to explain the lack of hemiepiphytes in recovering forests.

Table 1. Mean Araceae Abundance Standardized by Unit Area (Hectare).

Species	Mature forest	Secondary forest	Plantation
Araceae sp.	12.5 [3, 22]	1.3 [0, 2]	0.2 [0, 1]
Anthurium salvinii Hemsl.	50 [0, 125]	0	0
Monstera dubia (Kunth)Engl. & K. Krause	18 [0, 42]	0	0
Philodendron alliodorum Croat & Grayum	375 [217, 534]	0	0
Philodendron findens Croat & Grayum	3 [0, 7]	0	0
Philodendron fragrantissimum (Hook.) G. Don	190 [8, 372]	0	0
Philodendron radiatum Schott	8 [0, 20]	0	0
Philodendron sp. 1	1248 [976, 1523]	0	3 [0, 10]
Philodendron sp. 2	8 [0, 16]	0	0
Zingonium sp. 1	8 [0, 20]	2 [0, 5]	0
Total Araceae	2,018	13	5

Note. Araceae sp. stands for all unidentified specimens. All other species were identified to species or genus level. The number of transects surveyed was four in mature forests, six in secondary forests, and seven in plantations. Bootstrapped 95% confidence intervals are given within square brackets.

Canopy cover in secondary forests and plantations in our area is lower than that of mature forests (van Breugel et al., 2013), and hemiepiphytic Araceae are adapted to dark moist microhabitats (Croat, 1988). It is possible that the conditions needed for Araceae growth are not met in restoration plantations and secondary forests where the young trees do not have fully developed canopies (van Breugel et al., 2013) and lack vertical stratification complexity. In addition, time plays a key role in the recovery of species diversity during succession (Aide, Zimmerman, Pascarella, Rivera, & Marcano-Vega, 2000; Barthlott, Schmit-Neuerburg, Nieder, & Engwald, 2001; Woods & DeWalt, 2013) and a time lapse of 8 to 14 years of regeneration may be too short to see any significant colonization of hemiepiphytic Araceae despite the proximity of secondary forests and plantations to mature forests in our study sites.

It is too early to determine whether hemiepiphytic Araceae communities in our secondary forests and plantations will require manual transplantation to recover. Our observations of hemiepiphytic Araceae suggest a considerable lag time required for recolonization of secondary forests, even when they are in close proximity to mature forests with large populations. In this sense, hemiepiphytic Araceae recolonization conforms to the slow recolonization pattern observed for other types of vascular epiphytes (Martin & Siedow, 1981; Woods & DeWalt, 2013). Araceae are a major component of epiphytic communities and an important food resource for canopy dwelling organisms: This highlights the importance of conserving mature forests harboring healthy populations of Araceae. Further research is required concerning the factors affecting recolonization of hemiepiphytic Araceae in disturbed areas.

Acknowledgments

Data Availability

The data used in this study is available from the corresponding author upon request.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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