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The Conservation Value of Secondary Forests for Vascular Epiphytes in Central Panama

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ABSTRACT

Secondary forests that develop following land abandonment could compensate for the losses of diversity and structure that accompany deforestation of old-growth forests in tropical regions. Whether secondary forests can harbor similar species richness, density, and composition of old-growth forests for vascular epiphytes remains largely unknown for secondary forests older than 50 yr. We examined community structure (species richness, density, and species composition) of vascular epiphytes in older secondary forests between 35 and 115 yr after land abandonment and nearby old-growth forests to determine if the community structure of epiphytes in secondary forests approaches that of old-growth forests over time. The recovery of epiphyte species richness was rapid with 55-year-old forests containing 65 percent of old-growth epiphyte species richness. Secondary forest epiphyte communities were found to be statistically nested within secondary forests older in age and within old-growth forests. Similarity of epiphyte communities to old-growth forests increased to 75 percent, 115 yr after abandonment. This study suggests that secondary forests will likely recover old-growth epiphyte richness and composition given enough time. Epiphyte densities did not recover quickly with 55-year-old forests having 14 percent and 115-year-old forests having only 49 percent of the density of old-growth forest epiphytes. The low density of epiphytes in secondary forests could impact rainforest diversity and function. We conclude that in less than 115 yr, although secondary moist forests have high conservation value for some aspects of community structure, they are unlikely to compensate biologically for the loss of diversity and ecosystem function that high epiphyte densities provide.

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

Key words: Barro Colorado Nature Monument; chronosequence; holoepiphyte; hemiepiphyte; succession; tropical moist forest.

TROPICAL FOREST CANOPIES SUPPORT A HIGH DIVERSITY of plants and animals (Ellwood & Foster 2004, Kelly *et al.* 2004). The vascular epiphytic plants that inhabit the tropical canopy are a conspicuous and integral component of tropical rain forests. Not only do epiphytes contribute up to a third of the vascular species in tropical forests (Gentry & Dodson 1987), but they can also play an important role in nutrient and water cycling (Nadkarni 1986, Clark *et al.* 2005, Holwerda *et al.* 2010) and in providing habitat and food for an array of arboreal animals (Davis & Sutton 1998, Ellwood *et al.* 2002, Ellwood & Foster 2004). Thus, how quickly epiphyte communities recover after stand-destroying disturbances has important implications for conservation of tropical forest diversity and ecosystem functioning.

There has been a contentious debate about the conservation value of secondary tropical forests (Christensen & Peet 1984, Brown & Lugo 1990, Turner *et al.* 1997, Guariguata & Ostertag 2001, Chazdon 2003, Dent & Wright 2009). Secondary forests developing on lands that were not intensively used and are close to seed sources tend to have high conservation value for trees and lianas because they rapidly attain many aspects of the forest structure and species richness of old-growth forests, but species composition may take centuries to converge on old-growth forest (Brown & Lugo 1990, DeWalt *et al.* 2000, Guariguata & Ostertag 2001, Chazdon *et al.* 2007, Dent & Wright 2009). Thus, if conservation value is determined solely by the number of species and forest biomass of trees and lianas, then secondary forests that were not intensively used and are close to seed sources can reach species richness and biomass values comparable to old-growth forest within a few decades (Saldarriaga *et al.* 1988, DeWalt *et al.* 2000, Guariguata & Ostertag 2001). Some plants and animals, however, may be highly specialized to old-growth forest because of the resources and conditions found only in that habitat (reviewed in DeWalt *et al.* 2003). For example, many cavity-nesting animals require standing dead trees that are less abundant in secondary forests (DeWalt *et al.* 2003, Chazdon *et al.* 2009), and some rare shade-tolerant species are absent from secondary forests (Thomlinson *et al.* 1996, Guariguata & Ostertag 2001, Liebsch *et al.* 2008, Chazdon *et al.* 2009). Secondary forests may take centuries to recover the conservation value of old-growth forests for these more specialized taxa (Christensen & Peet 1984, Turner *et al.* 1997).

In particular, secondary forests may take much longer to attain high conservation value for epiphytes than for plants of other habits. Epiphytes are dispersal limited and may take 8–12 yr to colonize regenerating trees in secondary forests (Nadkarni 2000, Cascante-Marin *et al.* 2009). In addition, individual epiphytes grow very slowly and can take more than 10 yr to reach reproductive maturity (Gerold & Zotz 2002, Hietz *et al.* 2002, Laube & Zotz 2003). Finally, many epiphytes appear to be old-growth specialists (Barthlott *et al.* 2001, Acebey *et al.* 2003, Krömer & Gradstein 2003). In montane forests of Venezuela

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and Costa Rica, for example, orchids and ferns were much less common in secondary forests than in old-growth forests (Barthlott *et al.* 2001, Nadkarni 2004). Epiphytes may be old-growth specialists if they only establish on large trees, on host tree species present only in old-growth forests, or in conditions found only in older forests, such as the presence of canopy soil or particular microclimatic conditions including shade and high relative humidity (Barthlott *et al.* 2001, Callaway *et al.* 2002, Acebey *et al.* 2003, Krömer & Gradstein 2003, Zotz & Schultz 2008, Werner 2011). The conservation value of secondary forests for epiphytes thus depends to a large part on the degree to which secondary forest epiphyte communities contain species found in old-growth forests. If the species composition of a young secondary forest is a subset of old-growth forest and the similarity to old growth increases with secondary forest age, then it is likely that community composition of secondary forests will eventually approach that of old-growth forests.

To date, studies on epiphytes in secondary forests have been limited to forests younger than 50 yr (Barthlott *et al.* 2001, Krömer & Gradstein 2003, Nadkarni 2004, Benavides *et al.* 2006, Cascante-Marin *et al.* 2006). In those studies, epiphyte communities in secondary forests had substantially different species composition as well as lower epiphyte densities and species richness compared with old-growth forests. It is therefore not known when, if ever, epiphyte community structure (density, species richness, and composition) in secondary forests approaches that of old-growth forests.

In this study, we employed a chronosequence approach (secondary forest stands of different ages since land abandonment) in central Panama, focusing on older secondary forest stands ranging in age from 35 to 115 yr, to examine whether there is convergence on old-growth forests over time in secondary forests in terms of epiphyte community structure. All stands were in close proximity to old-growth forest and were located on relatively fertile soils. We studied the density, species richness, and composition of holoepiphytes (*i.e.*, plants sustained entirely by nutrients and water received non-parasitically from within the canopy in which they reside) as well as hemiepiphytes (*i.e.*, plants that spend only part of their life cycle with a terrestrial connection, Benzing 1990, Moffett 2000). We included primary hemiepiphytes, which start in the canopy and eventually send roots to the ground, and secondary hemiepiphytes, which start in the ground and eventually lose their terrestrial connection (Benzing 1990, Moffett 2000). For those species whose classification as either a vine or a hemiepiphyte is still unresolved (*e.g.*, *Monstera*, Andrade & Mayo 1998, López-Portillo *et al.* 2000), we included them as a hemiepiphyte. We surveyed trees, lianas, and downed coarse woody debris. For epiphytes occurring on trees, we also examined relationships between epiphyte occurrence and host-tree size.

METHODS

STUDY SITE AND PLANT SURVEY.—Secondary and old-growth forest stands were located within the Barro Colorado Nature Monument (BCNM) of central Panama, which includes Barro Colorado Island (BCI, 9°9′ N; 79°51′ W) as well as several adjacent mainland peninsulas (Fig. S1). Forests in the BCNM receive approximately 2600 mm of annual rainfall, predominantly during the wet season from May through December. The vegetation is classified as tropical moist forest and ranges in altitude from 120 to 160 m asl (Holdridge & Budowski 1956, Leigh *et al.* 2004).

We surveyed vascular epiphytes in ten forest stands that included two in each of four ages of secondary forest and two stands in old-growth. When our epiphyte survey was conducted in 2009, the secondary forests were approximately 35, 55, 85, and 115 yr old. The two old-growth stands provided a reference level of epiphyte species richness, density, and species composition. This chronosequence was established in 1994 by J. S. Denslow, during which time, trees ≥ 5 cm diameter at breast height (dbh) were measured in contiguous 10 × 10 m quadrats within transects of 160 × 10 m in each stand (Denslow 2000, Denslow & Guzman 2000). In 1994, two transects, totaling 0.32 ha, were established in nine stands, but only one transect was established in one of the 35-year-old stands, which was deemed too small for an additional transect. Stand ages were estimated by reference to early publications of the establishment of BCI (Kenoyer 1929, Standley 1933, Enders 1935, Chapman 1938), digitized aerial photographs taken in the late 1920s and between 1955 and 1983, and land-use history in the BCNM (Denslow & Guzman 2000, DeWalt *et al.* 2000). In 2002, trees ≥ 5 cm dbh were permanently tagged and remeasured. More detailed descriptions of the chronosequence design and census methods are provided in Denslow and Guzman (2000) and DeWalt *et al.* (2000).

Within each stand, we counted and identified all holo- and hemiepiphytes that occurred on trees ≥ 1 cm dbh (living or dead), lianas, or downed coarse woody debris. For epiphytes occurring on living trees ≥ 5 cm dbh, we noted the tag number of the tree to later determine the dbh from the 2002 dataset. Epiphytes occurring in crowns were identified with the help of binoculars or by climbing the trees using modified rope climbing techniques (Perry 1978), when binoculars were insufficient for proper identification. Given the low density of epiphytes in forests along the chronosequence (a maximum of 25 individuals/tree) and the fact that ground-based surveys have been found to capture >90 percent of epiphyte occurrences (Burns 2007), ground-based epiphyte surveys were conducted for all trees ≤ 60 cm dbh and most (63%) of the trees >60 cm dbh, as the canopies of these trees were easily visible from the ground. A total of 10 trees >60 cm dbh were climbed as these canopies were difficult to view from the ground. Species names of flowering plants followed the Flora of Panama Checklist and Index (D'Arcy 1987). Other sources were used for the identification of seedless vascular plants (Croat 1978, Lellinger 1989).

STATISTICAL ANALYSIS.—One sub-plot in Enders, a 55-year-old secondary forest, had a 10 × 20 m gap in which 150 individuals of one hemiepiphytic aroid, *Philodendron rigidifolium*, were found. There were no similar gaps in other stands, and such high densities of *P. rigidifolium* were not found elsewhere. This sub-plot was found to be an outlier of all sub-plots in Enders according to a Grubb's test ($Z = 3.28$, $P < 0.05$) and was therefore removed from the analysis.

To compare epiphyte species richness among forest ages, we conducted sample-based Mao Tau rarefaction analysis using EstimateS software v. 8.2 (Colwell 2009). We used the 10 × 10 m sub-plots within each stand as samples. The expected species accumulation curves were rescaled by individuals to compare the stands in terms of species richness (Gotelli and Colwell 2001). We compared the rarefied species richness among stands for 60 individuals, which is the maximum number of individuals found in 55-year-old forests.

All statistical analyses were conducted using R v. 2.11.0 (R Development Core, Team 2009). We examined the relationships between epiphyte density, species richness, and rarefied species richness (E_{60}) and secondary forest age using simple linear regression. Because their ages are unknown, old-growth stands were omitted from regression analyses, but are estimated to be >500 yr old (Piperno 1990). Stand age was $\log_{10}$ transformed for all analyses. We tested whether holoepiphytes and hemiepiphytes differed in their relationship with stand age using analysis of covariance (ANCOVA), with stand age as the covariate and epiphyte type as the categorical predictor variable. To determine at what age, if ever, epiphyte density, species richness, and rarefied species richness in secondary forests were similar to old-growth forests, we conducted analysis of variance (ANOVA) using *a priori* orthogonal linear contrasts that compared each secondary forest age to old-growth forests. ANOVA was also used to compare if the percentage, density, and basal area of trees colonized by epiphytes and the maximum dbh of trees in each stand differed between secondary forest and old growth. We used the latter measure because the same total tree basal area could be achieved in two stands, but be divided into a few large trees or many small trees. Maximum tree dbh values from the census in 2002 were used for this analysis. Although the values from 2002 may underestimate the maximum dbh of each stand, these differences would be small given the slow change in dbh of large trees (Lieberman *et al.* 1985, Clark *et al.* 2003).

We tested whether holoepiphytes and hemiepiphytes were more common on larger trees using logistic regression. Diameters of trees ≥ 5 cm from the census in 2002 were used for this analysis.

We examined whether similarity in epiphyte species composition of secondary forests converged on old-growth forests with time by conducting linear regression of community similarity on approximate forest age. We calculated similarity with two metrics: the Sørensen similarity index using species incidence (presence/absence) and the Morisita-Horn similarity index, which uses species relative abundance. Of the traditional abundance-based similarity indices, the Morisita-Horn index is the most robust to uneven and insufficient sampling (Chao *et al.* 2006). It examines the probability of two randomly chosen individuals being of the same, shared species (Chao *et al.* 2006). We applied the jackknife method to the Morisita-Horn index to remove biases associated with under-sampling and henceforth refer to the index as Jackknife Morisita-Horn. For each secondary forest age, we averaged the pairwise similarity indices between each secondary forest stand and each of the two old-growth stands (*i.e.*, four comparisons per forest age).

Finally, we tested whether epiphyte communities in secondary forests were statistically nested subsets of old-growth forests using the NODF (Nestedness metric based on Overlap and Decreasing Fill) index for incidence data and the WNODF (Weighted NODF) index for abundance data using the NODF-Program (Almeida-Neto & Ulrich 2010). Only the 21 species represented by at least two individuals across the chronosequence were included in this analysis.

RESULTS

In a total of 3.02 ha (eight stands of 0.32 ha, one stand of 0.30 ha, and one stand of 0.16 ha), we found 1099 individual epiphytes in 27 species and 7 families (Table S1). Three Araceae species (aroids) were identified only to morphospecies. Fifteen epiphyte species were classified as holoepiphytes, and 12 species were classified as hemiepiphytes (Table S1; Appendix S1). All of the hemiepiphytes were classified as secondary hemiepiphytes. No primary hemiepiphytes were found in the survey. Across the chronosequence, Araceae was the most diverse and abundant epiphyte family, representing 64 percent of all individuals and 39 percent of all species; Orchidaceae and Polypodiaceae were less abundant and speciose; Bromeliaceae and Cactaceae were found only in old-growth stands (Table S1).

Over 90 percent of epiphytes were found on living trees, but only 11 percent of trees ≥ 5 cm dbh as measured in 2002 hosted at least one epiphyte. For these host trees, the mean epiphyte load was 3.9 epiphytes/tree. The probability that a tree would host an epiphyte increased significantly with dbh for holoepiphytes ($Z = 11.63$, $P < 0.0001$) and hemiepiphytes ($Z = 10.82$, $P < 0.0001$; Fig. 1). Small trees had a higher probability of hosting a hemiepiphyte than a holoepiphyte, but both epiphyte types had equal probabilities of being on large trees (*i.e.,* >100 cm dbh; Fig. 1).

At the stand level, density ($R^2 = 0.03$, $P = 0.68$) and basal area ($R^2 = 0.3$, $P = 0.16$) of trees that hosted epiphytes did not increase with forest age. However, the maximum tree dbh of trees that hosted epiphytes increased with forest age ($R^2 = 0.74$, $P = 0.006$), with the highest maximum dbh found in 85-year-old forests (Fig. 2). The percentage of trees colonized by epiphytes also increased with forest age ($R^2 = 0.86$, $P < 0.001$) and was maximal in old-growth forests (Fig. 2).

DENSITY AND SPECIES RICHNESS.—Density of all epiphytes ($R^2 = 0.80$, $P = 0.003$), holoepiphytes ($R^2 = 0.62$, $P = 0.02$), and hemiepiphytes ($R^2 = 0.85$, $P = 0.001$) increased significantly with forest age (Fig. 3A). The youngest stands in the chronosequence were virtually devoid of epiphytes; in fact, no epiphytes were found in one 35-year-old stand (Saino) and only 11 individual holoepiphytes of two species were found in the other (Pedro Gomez). The density of hemiepiphytes across stands was

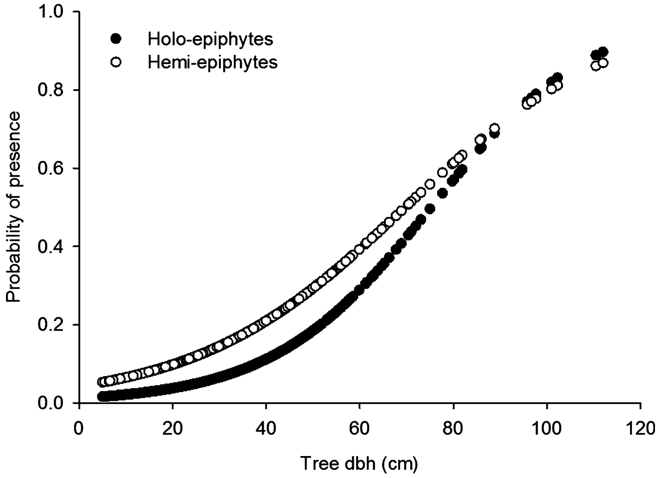

FIGURE 1. Logistic regression curves showing the relationship between tree dbh and predicted probability that a holoepiphyte ($e^{-4.4\ +\ 0.06(\mathrm{dbh})}/(1 + e^{-4.4\ +\ 0.06(\mathrm{dbh})})$) or a hemiepiphyte ($e^{-3.12\ +\ 0.04*\mathrm{dbh}}/(1 + e^{-3.12\ +\ 0.04*\mathrm{dbh}})$) occurred on the tree along a forest chronosequence in central Panama.

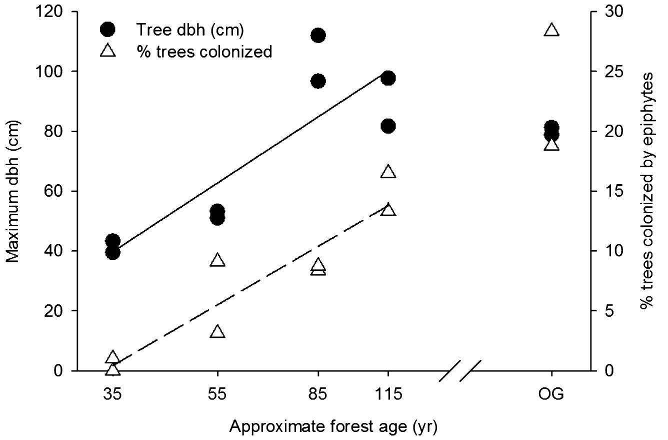

FIGURE 2. Relationship between maximum tree dbh (solid line) and percent of trees colonized by epiphytes (dashed line) with approximate forest age along a forest chronosequence in central Panama.

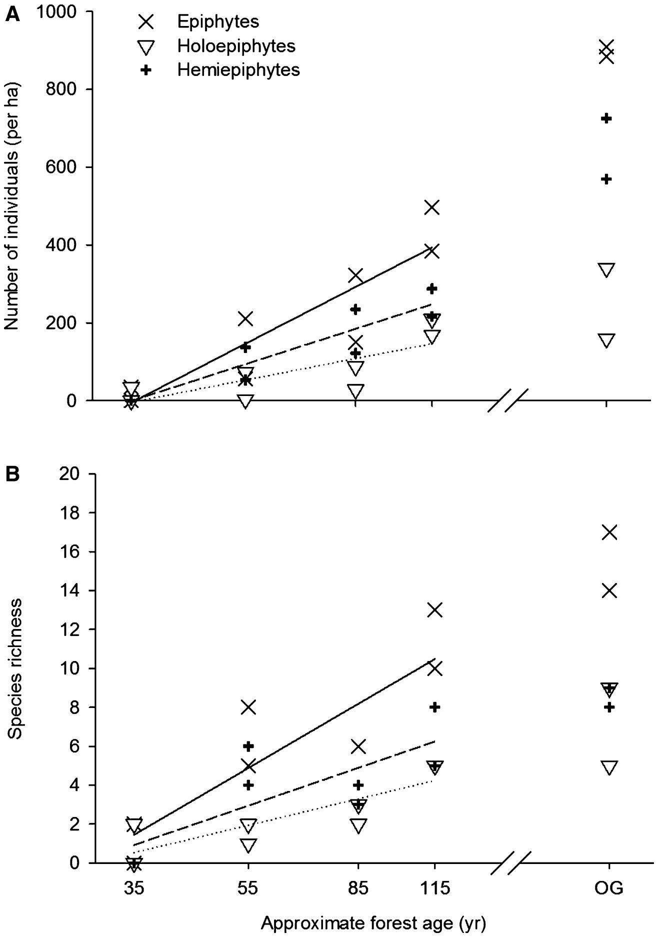

FIGURE 3. Relationship between density (A) and species richness (B) of epiphytes (solid line), holoepiphytes (dashed line), and hemiepiphytes (dotted line) and approximate forest age along a forest chronosequence in central Panama.

significantly higher than holoepiphytes ($F_{1,12} = 5.8$, $P = 0.03$), but there was no difference between holo- and hemiepiphytes in their responses to forest age (*i.e.*, no significant interaction of age and epiphyte type; $F_{1,12} = 1.9$, $P = 0.20$). Old-growth forests had significantly greater densities than all other forest ages for all epiphytes, holoepiphytes, and hemiepiphytes (Table 1). Epiphyte densities in 35-year-old forests were less than 1 percent of that in old growth, whereas epiphyte densities in 115-year-old forests were 49 percent of that in old-growth forests.

Species richness of all epiphytes ($R^2 = 0.77$, $P = 0.004$), holoepiphytes ($R^2 = 0.72$, $P = 0.008$), and hemiepiphytes ($R^2 = 0.60$, $P = 0.02$) increased significantly with forest age (Fig. 3B), with no overall difference between holoepiphyte and hemiepiphyte species richness ($F_{1,12} = 2.6$, $P = 0.13$) or their response to forest age ($F_{1,12} = 0.32$, $P = 0.58$). Species richness rarefied to 60 individuals increased significantly with forest age ($R^2 = 0.59$, $P = 0.03$). Compared to old-growth stands, epiphyte species richness in 35-year-old secondary stands was only 6 percent of the old-growth value, whereas it was 74 percent in 115-year-old secondary forests. Old-growth and 115-year-old stands were equivalent in species richness of all epiphytes, holoepiphytes, and hemiepiphytes, as well as rarefied species richness for all epiphytes (Table 1).

COMMUNITY COMPOSITION.—Similarity of secondary forests to old-growth forests in terms of species composition increased with forest age (Fig. 4; Jackknife Morisita-Horn index, $R^2 = 0.91$, $P = 0.04$; Sørensen index, $R^2 = 0.89$, $P = 0.05$). The slope for the incidence-based measure of similarity (Sørensen), however, was higher than the abundance-based measure (Jackknife Morisita-Horn), indicating faster convergence in the presence of species found in old-growth forests than in relative species abundance.

TABLE 1. *Density (mean per ha ± SE) and species richness (mean raw counts ± SE) of all epiphytes (All), holoepiphytes (Holo), and hemiepiphytes (Hemi), and species richness rarefied to 60 individuals (maximum number of epiphytes in 55-year-old forests) for all epiphytes found in different-aged secondary and old-growth forests (OG) along a chronosequence in the Barro Colorado Nature Monument in central Panama. The area sampled for each forest stand was 0.32 ha except for one 35-year-old stand of 0.16 ha and one 55-year-old stand of 0.30 ha. Values with different letters are significantly different from OG forests according to linear orthogonal contrasts (*$P < 0.05$*).*

	Density			Species richness			Rarefied species richness (E_{60})
Age	All	Holo	Hemi	All	Holo	Hemi	All
35	17.0 ± 24.0^{a}	17.0 ± 24.3	0 ± 0^{a}	1.0 ± 1.4^{a}	1.0 ± 1.4^{a}	0 ± 0^{a}	2.0 ± 2.4^{a}
55	133.0 ± 108.9^{a}	38.0 ± 49.6	95.0 ± 59.3^{a}	6.5 ± 2.1^{a}	1.5 ± 0.7^{a}	5.0 ± 1.4^{a}	8.0 ± 0.3^{b}
85	236.0 ± 121.6^{a}	58.0 ± 42.0	178.0 ± 79.2^{a}	6.0 ± 0^{a}	2.5 ± 0.7^{a}	3.5 ± 0.7^{a}	6.0 ± 0.5^{b}
115	440.5 ± 79.9^{a}	189.0 ± 28.7	252.0 ± 50.9^{a}	11.5 ± 1.2^{b}	5.0 ± 0^{b}	6.5 ± 2.1^{b}	9.0 ± 0.8^{b}
OG	896.5 ± 17.7^{b}	250.0 ± 128.2	647.0 ± 110.3^{b}	15.5 ± 2.1^{b}	7.0 ± 2.8^{b}	8.5 ± 0.7^{b}	9.0 ± 1.4^{b}
$F_{4,5}$	35.2^{***}	4.8	25.2^{**}	19.9^{**}	5.8^{*}	13.8^{**}	9.9^{*}

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

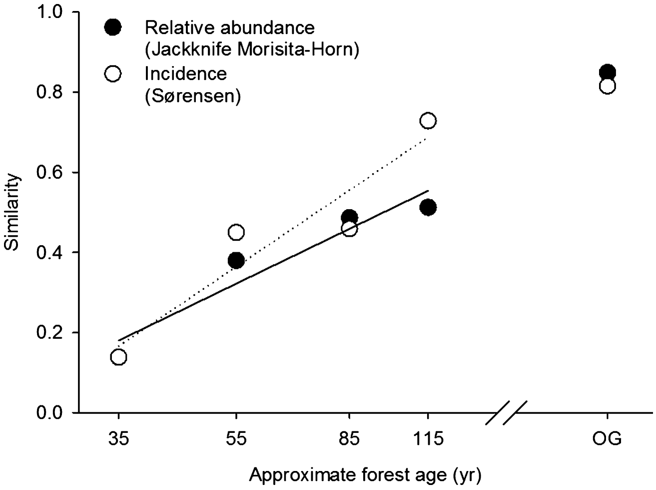

FIGURE 4. Linear regression of similarity in epiphyte species composition between secondary forest stands and old-growth forest stands and approximate forest age using a Jackknife Morisita-Horn similarity matrix on relative abundance and a Sørensen similarity matrix on incidence for epiphytes found along a forest chronosequence in central Panama. Pairwise distances between each secondary forest stand and each of the two old-growth stands were averaged for each secondary forest age. For clarity, the average similarity between each secondary forest age and old-growth stands is shown.

Epiphyte communities in secondary forests were nested subsets of the species found in older secondary forests and in old-growth forests, both in terms of the species present and their relative abundance (Fig. 5; NODF: $Z = -4.09$, $P < 0.001$; WNODF: $Z = -4.35$, $P < 0.001$). Of all the species found along the chronosequence, old-growth forests contained 81 percent, with only four species (each with fewer than seven individuals) being absent from old-growth stands.

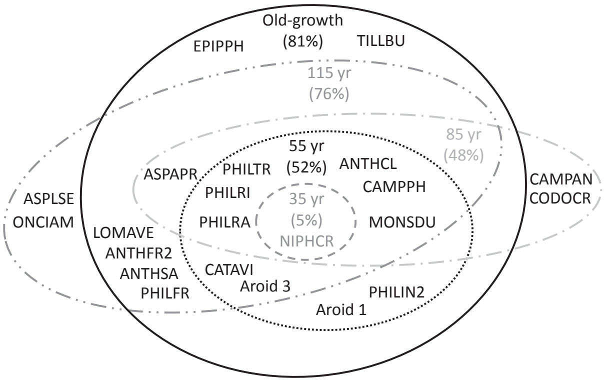

FIGURE 5. Nested diagram of species composition for epiphyte species in each forest age along a secondary forest chronosequence and old-growth forests in central Panama generated using Nestedness Overlap based on Decreasing Fill (NODF) index for incidence data. Species are denoted by codes defined in Appendix S1. Below each forest age is the percentage of species found along the chronosequence that were present in stands of that forest age.

DISCUSSION

Based on this chronosequence of secondary forests between 35 and 115 yr old, it appears that epiphyte community structure in secondary forests in central Panama becomes more similar to old-growth forest over time, and that 115 yr is sufficient for some community properties to attain levels found in old-growth forest. In our study, 115-year-old secondary forests and old-growth forests were equivalent in the density, basal area, and percent of trees colonized by epiphytes, as well as the species richness of epiphytes. Species richness increased with forest age and was 74 percent that of old-growth forests by 115 yr. Similarity in community composition to old-growth forest also increased with forest age and reached approximately 75 percent similarity in terms of species presence in 115-year-old forests. This increase in similarity to old-growth forest with time and the high degree of nestedness among forest stands suggest that, given sufficient time, epiphyte community composition in secondary forests would recover to old-growth forest composition. For epiphyte density, however, more time is needed to recover to old-growth levels. Secondary forests had substantially lower epiphyte densities than in old-growth forests, with 115-year-old forest having only 49 percent of the density of old-growth forest epiphytes.

Epiphyte succession in central Panamanian lowland forest appears to occur more slowly than in upper Amazonian and Costa Rican premontane forests, where epiphyte densities were almost 50 percent of old-growth levels by 30–40 yr after land abandonment (Benavides *et al.* 2006, Cascante-Marin *et al.* 2006). In contrast, 55-year-old secondary forests in our study site had only 14 percent of the density of old-growth forest epiphytes. Similarly, the density of epiphytes in old-growth forests in central Panama is lower than in other tropical forests with the number of epiphytes per ha averaging approximately 800 compared to 1550 in upper Amazonia (Benavides *et al.* 2006) and 2100 in premontane Costa Rican forests (Cascante-Marin *et al.* 2006). The low density of epiphytes in our study site compared with these aseasonal tropical wet forests may be due to drought stress resulting from the 4-month-long dry season and the lower annual rainfall in central Panama (2600 mm) compared to upper Amazonia (3200 mm, Benavides *et al.* 2006) and premontane forests in Costa Rica (3282 mm, Cascante-Marin *et al.* 2006). A low density of epiphytes would equate to fewer reproductive adults and fewer propagules, which may explain the slow colonization of secondary forests in central Panamanian lowland forest.

In contrast with density, the recovery of epiphyte species richness in central Panamanian forests appears quite rapid with 55-year-old forests containing 65 percent of the number of epiphyte species found in old-growth forests. The rapid recovery of epiphyte species in our secondary forests is similar to other lowland and premontane forests where almost 70 percent of old-growth epiphyte species richness was found in 30- to 40-year-old secondary forests (Benavides *et al.* 2006, Cascante-Marin *et al.* 2006). In our study, secondary forest plots are in close proximity to old-growth forest (DeWalt *et al.* 2003), which may explain the rapid recovery of species richness to old-growth levels (Chazdon 2003, Chazdon *et al.* 2009).

Similar levels of species richness between secondary and old-growth forests may not indicate high conservation value for secondary forests if there are large differences in species composition. In premontane forests in Costa Rica, for example, the number of species per ha between 35- and 40-year-old forests and old-growth forests was similar, but the identity of the dominant species changed dramatically between forest types (Cascante-Marin *et al.* 2006). Thus, the recovery of similarity of epiphyte species composition to old-growth forests may be a much better indicator of the value of secondary forests for this life form.

In central Panama, similarity in species composition of secondary forests to old-growth levels increased with forest age and recovered quite rapidly with 55-year-old forests having an average similarity to old-growth forests of 45 percent. The increasing similarity in species composition of secondary forests to old-growth forests with forest age may be due to the increasing heterogeneity in canopy structure, light, and microclimate that accompanies forest succession. The structural heterogeneity found in older forests results in a combination of drought-resistant epiphyte species common to hotter and drier secondary forests along with shade-tolerant epiphytes that specialize in moist and shady habitats of older forests (Barthlott *et al.* 2001, Acebey *et al.* 2003, Krömer & Gradstein 2003). In central Panama, epiphyte communities in young secondary forests were nested subsets of the epiphyte communities in older secondary forests and old-growth forests. The majority of epiphyte species that could inhabit drier sites in secondary forests in our study were also found within old-growth forests, and several species that had more specific microclimatic and structural requirements were only found in old-growth forests. For example, *Niphidium crassifolium* was found in all forest ages and can inhabit drought-prone microhabitats in tropical canopies on BCI (Andrade & Nobel 1997). In contrast, species that were only found in old-growth forests, such as *Vriesea gladioliflora* and *Guzmania lingulata*, require shady sites with high humidity (Merwin *et al.* 2003) that are probably not available in secondary forests (Barthlott *et al.* 2001, Krömer & Gradstein 2003).

Compared to other plant groups studied along the BCNM chronosequence, epiphyte communities need more time to approach old-growth forest species richness and density as they depend on the establishment of the forest before colonizing. Within 20 yr after land abandonment, secondary forests quickly attain old-growth levels of density and diversity for lianas and trees (Denslow & Guzman 2000, DeWalt *et al.* 2000, 2003). Epiphytes would thus require a minimum lag-time of approximately 20 yr before colonizing secondary forests in central Panama. Because epiphytes are inherently slow-growing, dispersal-limited plants that take a long time to establish on bare branches (Nadkarni 2000, Gerold & Zotz 2002, Cascante-Marin *et al.* 2009), the lag-time for successful establishment after forest development may be even greater than 20 yr. We found support for this hypothesis as 35-year-old forests had only 6 percent of the species richness of old-growth forests, whereas 55-year-old forests had 42 percent of old-growth epiphyte species richness. Epiphyte establishment in young secondary forests in the BCNM may be further inhibited by the 4-month-long dry season as epiphyte species richness in younger secondary forests has been found to be much higher in more aseasonal forests, such as in premontane Costa Rican forests (22% of old-growth species richness in 12-year-old forests, Cascante-Marin *et al.* 2006) and in upper Amazonian forests (36% of old-growth species richness in 16-year-old forests, Benavides *et al.* 2006).

As in other studies (Zimmerman 1992, Zotz & Vollrath 2003, Zotz & Schultz 2008), we found the probability of occurrence of all epiphytes to increase with tree dbh, potentially because small trees have less substrate on which epiphytes may establish, provide lower quality substrate (*e.g.*, lower water-holding capacity, Hyvärinen *et al.* 1992, Callaway *et al.* 2002), or represent less time for colonization (Zotz & Schultz 2008). Along the BCNM chronosequence, the highest number of large trees, and hence the greatest area of substrate on which epiphytes may establish, occurred in stands that were approximately 85 yr old (Denslow 2000). Despite the greater amount of substrate in 85-year-old forests, epiphyte density was highest in old-growth forests, suggesting that epiphyte colonization is not limited by tree size, but by time for colonization or a lack of suitable substrate in secondary forest trees. The high similarity in forest structure and epiphyte species composition between 115-year-old secondary forests and old-growth forests, however, suggests that the majority of old-growth epiphyte specialists are also colonizing 115-year-old secondary forests. Given that epiphytes are often dispersal limited (Cascante-Marin *et al.* 2009), less time for colonization better explains the low epiphyte densities in secondary forests.

In forests that were >55 yr, the density of hemiepiphytes was greater than that of holoepiphytes across the chronosequence and composed, on average, 70 percent of the total epiphyte density. Hemiepiphytes were, however, absent in 35-year-old forests, which may be due to hemiepiphytic vegetative fragments or seeds not surviving forest conversion (Benavides *et al.* 2006). The higher density of hemiepiphytes compared to holoepiphytes in mid- to old-secondary forests (*i.e.*, >55 yr) and old-growth forests could result from low host-tree specificity. Secondary hemiepiphytes generally are less host-specific than holoepiphytes and will ascend the closest tree, regardless of tree species identity or size (Atwell *et al.* 1999, Nieder *et al.* 2000). Holoepiphytes, on the other hand, are more commonly found on a particular subset of tree species that are generally large in crown volume (Zimmerman 1992, Nieder *et al.* 2000, Laube & Zotz 2006, Hirata *et al.* 2009, Burns & Zotz 2010). The size of trees climbed by hemiepiphytes in our study was generally smaller than holoepiphytes, which supports the idea that colonization of trees by hemiepiphytes is less dependent on the size of the tree.

CONCLUSION

Although other studies on epiphytes in secondary forests have been limited to sites less than 50 yr old, our study was able to examine epiphytes in older secondary forests to examine if epiphyte community structure ever approached old-growth levels. We found convergence in the number and identity of species with secondary forest age with 115 yr being sufficient time to recover old-growth species richness and composition. Epiphyte densities did not recover to old-growth levels, however, which may be due to a low probability of colonization of young host trees caused by epiphyte dispersal limitation. Given another 100 yr, epiphyte densities in secondary forests in central Panama might approach old-growth levels, but we conclude that, in the short-term, secondary moist forests are unlikely to compensate biologically for the loss of biological diversity and ecosystem functioning that high epiphyte densities provide. In tropical moist forests, old-growth forests are invaluable for the conservation of epiphytes, and secondary forests need more than 115 yr to recover all aspects of old-growth forest community structure.

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SUPPORTING INFORMATION

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

TABLE S1. *Number of individuals and number of species for all epiphytes (Total), holoepiphytes, and hemiepiphytes found in the seven most abundant plant families along a forest chronosequence in the Barro Colorado Nature Monument in central Panama.*

FIGURE S1. Map of the locations of studied secondary forest and old-growth stands on the Bohio and Gigante peninsulas and Barro Colorado Island in the Barro Colorado Nature Monument in central Panama.

APPENDIX S1. Number of holoepiphytes and hemiepiphytes for each epiphyte species of each family in two replicate stands of each forest age along a chronosequence in the BCNM, Panama.

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