# Tropical forest restoration enriches vascular epiphyte recovery

John Leighton Reid, José Miguel Chaves-Fallas, Karen D. Holl & Rakan A. Zahawi

**Reid, J.L.** (corresponding author, leighton.reid@mobot.org)[1],
**Chaves-Fallas, J.M.**
(chamiguel@gmail.com)[2,3],
**Holl, K.D.** (kholl@ucsc.edu)[4],
**Zahawi, R.A.**
(zak.zahawi@tropicalstudies.org)[2]

[1]Center for Conservation and Sustainable Development, Missouri Botanical Garden, PO Box 299, St. Louis, MO 63166-0299, USA;
[2]Las Cruces Biological Station, Organization for Tropical Studies, Apdo. 73-8257, San Vito, Costa Rica;
[3]Current address: Department of Biology and Whitney R. Harris World Ecology Center, University of Missouri   St. Louis, St. Louis, MO 63121, USA;
[4]Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA

## Abstract

**Questions:** Vascular epiphytes constitute a large proportion of tropical forest plant biodiversity, but are among the slowest plants to recolonize secondary forests. We asked whether tree planting for ecological restoration accelerates epiphyte community recovery. Does the spatial configuration of tree planting matter? What landscape contexts are most suitable for epiphyte restoration?

**Location:** Restored pastures in premontane Coto Brus County, Puntarenas, Costa Rica.

**Methods:** We surveyed vascular epiphyte species growing on the lower trunks of 1083 trees in 13 experimental restoration sites. Each site contained three 0.25-ha treatment plots: natural regeneration, trees planted in patches or 'islands' and tree plantations. Sites spanned elevational (1100–1430 m) and deforestation (4–94% forest cover within a 100-m radius around each site) gradients.

**Results:** Vascular epiphytes were twice as diverse in planted restoration plots (islands and plantations) as in natural regeneration; we observed this at the scale of individual host trees and within 0.25-ha treatment plots. Contributing factors included that trees in planted restoration plots were larger, older, more abundant and composed of different species than trees in naturally regenerating plots. Epiphyte species richness increased with surrounding forest cover within 100–150 m of restoration plots. Epiphyte communities were also twice as diverse at higher (1330–1430 m) vs lower (1100–1290 m) elevation sites. Epiphyte groups responded differently to restoration treatments and landscape factors; ferns were responsible for higher species richness in planted restoration plots, whereas angiosperms drove elevation and forest cover effects.

**Conclusions:** Tree planting for ecological restoration enriched epiphyte communities compared to natural regeneration, likely because planted forests contained more, bigger and older trees. Tree island plantings were equally effective compared to larger and more expensive plantations. Restoration sites nearer to existing forests had richer epiphyte recolonization, likely because nearby forests provisioned restoration sites with angiosperm seeds. Collectively, results suggest that restoration practitioners can enrich epiphyte community development by planting trees in areas with higher surrounding forest cover, particularly at higher elevations.

## Introduction

A modern conservation dilemma is that forest biodiversity is increasingly dependent on secondary forests, but secondary forests do not support complete species assemblages (Chazdon et al. 2009; Gibson et al. 2011). As old-growth forest fragments shrink and degrade, their constituent plant populations are less likely to recolonize new secondary forests (Vellend 2003), and it is unknown whether extinction debts in old-growth forest fragments will be paid before mature forest species reassemble in current secondary forests (Vellend et al. 2006; Jackson & Sax 2010). These challenges highlight the need to develop strategies to assist the recovery of mature forest conditions

and facilitate recolonization by late successional species (Martínez-Garza & Howe 2003).

Vascular epiphytes (hereafter 'epiphytes') are dependent on host trees and thus represent a model system for examining forest colonization (Taylor & Burns 2015). In tropical forests, epiphytes comprise up to a third of vascular plant diversity (Gentry & Dodson 1987) and provide important ecosystem functions, including canopy water storage, soil accumulation, food provisioning for animals and microclimatic buffering (Duellman 1988; Nadkarni & Matelson 1989; Clark et al. 1998; Scheffers et al. 2013).

A growing literature shows that epiphytes are among the slowest plants to recolonize secondary forests (Lisboa et al. 1991; Kanowski et al. 2003; Martin et al. 2013; Woods & DeWalt 2013). In fragmented landscapes, epiphytes face obstacles to propagule dispersal (Cascante-Marín et al. 2008), and secondary forest colonization is further impeded through establishment barriers, including relatively homogenous tree architecture, a lack of old-growth microhabitats (e.g. deep canopy soils) and poor microclimate differentiation (Barthlott et al. 2001; Woods et al. 2015). Ecological restoration can address both dispersal and establishment limitations for terrestrial species, but despite recent calls for canopy restoration (Lowman & Schowalter 2012), there are few examples of ecological restoration projects attempting to stimulate epiphyte recolonization in secondary tropical forests (Bare & Tello 2010).

Among the many unanswered questions about epiphytes and tropical forest restoration are: (1) does tree planting accelerate epiphyte recovery relative to natural forest regeneration; (2) does the spatial configuration of tree planting make any difference; and (3) what landscape contexts are most suitable for epiphyte community recolonization? We aimed to answer these questions by sampling epiphytes in a long-term experiment in southern Costa Rica.

We predicted that tree plantations established to restore degraded pastures would enhance epiphyte species richness compared to naturally regenerating forests, on the basis of increasing the number of trees available for colonization after a decade of recovery. Tree plantations could also increase epiphyte richness as they have been shown to attract seed-dispersing birds (Lindell et al. 2013) and to create shady microclimates (Meli & Dirzo 2013). We further expected that individual trees in planted forests would host more epiphyte species compared to trees in naturally regenerating forest because the trees may be older and larger in planted forests (Merwin et al. 2003; Zotz & Vollrath 2003).

Within planted restoration plots, we predicted that more heterogeneous planting configurations would contribute to higher epiphyte richness compared to homogenous configurations. Planting small patches or 'islands' of trees in lieu of extensive tree plantings is an alternative restoration strategy called 'applied nucleation' (Corbin & Holl 2012). This approach can reduce restoration costs and increase habitat heterogeneity (Robinson & Handel 2000), including heterogeneity in canopy structure and light environments (Holl et al. 2013; Zahawi et al. 2015a) – both potential axes of epiphyte diversification (Bennett 1986).

Finally, we expected that local epiphyte richness would vary depending on a restoration site's landscape context (Flores-Palacios & García-Franco 2006; Werner & Gradstein 2008). We predicted that larger surrounding landscape forest cover would contribute to epiphyte species richness via higher propagule availability.

## Methods

### Study area

The 13 restoration sites studied are located on the Pacific slope of premontane southern Costa Rica, in the landscape surrounding Las Cruces Biological Station (8°47′ N, 82°57′ W) and the town of Agua Buena (8°44′ N, 82°56′ W). The area encompasses ~100 km$^2$ of hilly terrain with elevations ranging from 1060 to 1430 m a.s.l. Annual precipitation varies with microtopography (3000–4000 mm·yr$^{-1}$), with most rain falling between Apr and Nov. Mean annual temperature at Las Cruces is 21 °C. The native ecosystem is tropical pre-montane humid forest (Holdridge et al. 1971), but most of this was cleared for coffee cultivation between 1960 and 1980 (Zahawi et al. 2015b). Currently the study area is a mixed, agricultural mosaic of cattle pastures, coffee plantations, various vegetable crops, small forest fragments and riparian corridors.

### Experimental design

Restoration sites were established in 2004–2006 on post-agricultural lands (mostly cattle pastures) that were farmed for ≥18 yrs (Holl et al. 2011). Each site contained three, randomly assigned, 0.25-ha treatment plots with one of three restoration strategies: (1) natural regeneration, (2) applied nucleation or tree islands, and (3) tree plantations (Appendix S1). Natural regeneration plots were fenced to exclude cattle, but otherwise recovered without intervention. Plantation plots were planted entirely with tree seedlings (313 seedlings·plot$^{-1}$), and island plots were planted with six patches of trees, two each of 4 m × 4 m, 8 m × 8 m and 12 m × 12 m (86 seedlings·plot$^{-1}$). Different patch sizes in island plots were initially planted to test for optimal patch size (Zahawi et al. 2013); however, in recent years islands have become less discrete due to tree branching and seedling recruitment in the in-between spaces. As such, we do not address optimal patch size questions here. All plots were hand-cleared by machete for

36 mo following planting to allow seedlings to grow above the height of the pasture grasses, thus, planted trees were at least 3 yrs older than the oldest naturally recruited trees. Plots within a site were separated by ≥5 m and sites were separated by ≥0.7 km.

Seedlings in islands and plantations included four tree species: *Erythrina poeppigiana* (Fabaceae), *Inga edulis* (Fabaceae), *Terminalia amazonia* (Combretaceae) and *Vochysia guatemalensis* (Vochysiaceae). Trees species were chosen based on their availability in local nurseries. *Inga* produces an indehiscent fruit with an edible pulp consumed by primates, whereas the other three species produce wind-dispersed seeds. A more detailed description of the treatments is provided in Holl et al. (2011).

### Epiphyte sampling

We sampled vascular epiphyte communities on 1083 planted and naturally recruited trees within each restoration site. We selected trees with DBH ≥5 cm. Sampled trees were located ≥5 m from the plot edge to minimize edge effects.

A common challenge in epiphyte studies is how to effectively sample individuals that are high in tree canopies. Some researchers overcome this challenge by climbing trees (Flores-Palacios & García-Franco 2001; Gradstein et al. 2003) or using a canopy crane (Zotz & Vollrath 2003), often at the cost of a reduced sample size (Freiberg 1996). Other researchers have sampled only the lower trunks of trees (Moran et al. 2003; Mehltreter et al. 2005) or have observed epiphytes with binoculars (Taylor & Burns 2015). In our study system tree climbing would have been difficult and destructive as most trees lack stout branches, and the epiphyte community was too diverse to confidently identify small individuals with binoculars, so we elected to sample epiphytes on lower trunks and branches, defined here as ≤4 m height. This sampling area corresponded roughly to Johansson's (1974) zones 1–2, although some tree species branched below 4 m, and in these cases we sampled epiphytes on lower branches (zone 3) as well.

On each tree, we recorded the identity and abundance of all vascular epiphytes, including those that complete their life cycles on another plant (holoepiphytes) and most of those that spend at least part of their life cycle as an epiphyte (hemiepiphytes). We did not record lianas, and we excluded several instances where non-epiphytic species were growing on trees opportunistically [e.g. a seedling of *Conostegia xalapensis* (Melastomataceae), a pioneer tree, that had germinated in an *I. edulis*].

Our observations suggested that epiphytes in these young forests were discrete and counting individuals did not pose a challenge, which has been raised as an issue in some epiphyte studies in more mature forests (Wolf et al. 2009). Species were identified in the field or with photographs using the reference collection at the Luis Diego Gómez Herbarium (www.tropicalstudies.org/plantdatab ase; accessed 15 Jul 2015).

### Landscape forest cover

Restoration sites span a landscape deforestation gradient, with some sites adjacent to remnant forest and others surrounded almost entirely by crops and cattle pastures. Nearby forests likely serve as propagule sources for recovering epiphyte communities, but the spatial scale for this effect probably varies among epiphytic taxa. We approximated the scale of landscape forest cover effects on epiphyte communities by calculating tree cover within eight concentric circles (radii 50–650 m) around each treatment plot using digitized aerial photographs from 2003 and 2005 (Fahrig 2013), the period when restoration sites were established. Forest cover included old-growth and regrowth forest fragments, and native and non-native trees growing in fence rows, gardens and tree plantations measured at a 2-m spatial resolution (Mendenhall et al. 2011).

### Tree density

Planted and naturally recruited trees with DBH ≥10 cm were counted across the entirety of each 0.25-ha restoration plot in 2014 (K.D. Holl & R.A. Zahawi, unpubl data). Natural recruits with DBH 5–10 cm were counted in 8-m wide belt transects covering 256 m$^2$ in natural regeneration and plantation plots and 576 m$^2$ in island plots (following methods in Zahawi et al. 2013); tree density was standardized to trees ≥5 cm DBH per 0.25 ha.

### Data analysis

We sampled and analysed epiphyte species richness at the tree scale and subsequently scaled up to the 0.25-ha plot scale (Mendieta-Leiva & Zotz 2015). For tree-scale analyses, we used observed species richness ($S_{obs}$). This measure included higher-level taxa in cases where, e.g. an individual was identified only to family or genus.

At the tree scale, we estimated the effects of restoration strategy, elevation and landscape forest cover on $S_{obs}$ using generalized linear mixed effects regression (GLMER) with Poisson error (R package lme4 v 1.1-9; R Foundation for Statistical Computing, Vienna, AT). Models included a random, variable intercept term for site. Significance of fixed factors was calculated using *F*-tests (R package lmerTest v 2.0-29). To determine an appropriate scale for landscape forest cover effects, we compared deviance in fully specified

models with landscape forest cover measured within differently sized buffers around each restoration plot (50–650 m). We inspected model residuals for homogeneity.

After observing an effect of restoration strategy on $S_{obs}$, we tested whether this effect could be attributed to differences in tree size or tree composition between restoration strategies. We repeated our GLMER procedure but excluded restoration strategy as a fixed factor. We then compared the residuals from this reduced model across host tree sizes using linear regression and across the seven most frequently sampled tree species (>40 individuals sampled) using two-sided $t$-tests with Bonferroni correction for family-wise error. As a measure of tree size, we used the sum of DBHs for all stems on a given host tree ($\Sigma$DBH; range: 1–3 stems). We compared tree sizes across restoration strategies using two-way ANOVA with site as a blocking factor and pair-wise, *post-hoc* Tukey tests.

We tested our model for sensitivity to epiphyte composition by repeating our GLMER procedure with $S_{obs}$ calculated for different taxonomic subsets and comparing estimates to a model including all epiphyte species. We sequentially excluded one of the following groups at a time: ferns, angiosperms, Polypodiaceae, Orchidaceae, Bromeliaceae, Gesneriaceae and Ericaceae. We observed at least 100 individuals in each group.

At the plot scale, we analysed estimated epiphyte species richness ($S_{est}$) by extrapolating a sample-based species accumulation curve to the number of trees ≥5 cm DBH expected in each plot (EstimateS v 9; purl.oclc.org/estimates). $S_{est}$ and tree densities were compared among restoration strategies using two-way ANOVA with site as a blocking factor and pair-wise, *post-hoc* Tukey tests. Tree densities were log or log + 1 transformed to meet the normality assumption.

Analyses were conducted in R v 3.2.2. Data are available at merritt.cdlib.org/m/ucsc_lib_hollzahawi.

## Results

We recorded 4267 individual epiphytes belonging to 76 species and 108 genera in 23 families (Appendix S2). Ferns comprised 70% of individuals; angiosperms comprised 30%. We identified 78% of individuals to family, 71% to genus and 53% to species. Of individuals not identifiable to family, 99% were juvenile ferns. Thirteen species (17%) were endemic to southern Costa Rica and/or western Panama, including five orchids, four aroids, two Polypodiaceae ferns and one species each from Araliaceae and Gesneriaceae.

Epiphyte communities were twice as diverse in planted restoration plots (islands and plantations) as in natural regeneration plots. This effect was observable at the scale of individual trees (Fig. 1a, Appendix S3), as well as at the

plot level (Fig. 1b). On average, individual trees in island and plantation plots were 22% larger than in natural regeneration plots (Fig. 2a), and larger trees had more epiphytes than smaller ones (Fig. 2b). Naturally recruiting species dominated natural regeneration plots but comprised a comparatively small percentage of larger trees in island and plantation plots (Fig. 3a). Planted tree species consistently had higher epiphyte richness than naturally recruited trees (Fig. 3b), even after taking into account that planted trees were 1.5 times larger on average than naturally recruited trees ($t = 9.9$, $P < 0.0001$; Appendices S4 and S5). Additionally, planted restoration plots had 1.6–4.0 times more trees available for epiphyte colonization than natural regeneration plots (Table 1).

The landscape context around restoration plots also influenced epiphyte recovery. Landscape forest cover effects were strongest when forest cover was measured within 100–150 m buffers around restoration plots (Fig. 4a). Trees embedded in landscapes with higher forest cover within 100 m harboured more epiphyte species (Fig 4b); two families and three genera were found only at one site that was adjacent to a large forest fragment (Las Cruces Biological Reserve). Moreover, trees in two restoration sites above 1300 m elevation were twice as rich in epiphytes as trees at lower elevation sites (1060–1290 m; Fig 4c); these higher-elevation sites also contained two families and 14 genera found nowhere else.

Both local restoration effects and landscape effects were sensitive to epiphyte composition. When we re-ran models using taxonomic subsets, we found that restoration strategy effects were not significant when ferns were excluded (Fig. 5a), whereas elevation and landscape forest cover effects were not significant without angiosperms (Fig. 5b, c). These sensitivities were not attributable to any particular family (Appendix S6).

## Discussion

Our results show that restoration tree plantings enriched vascular epiphyte colonization during the first decade of succession on recovering, agricultural lands in southern Costa Rica. Restoration plantings increased epiphyte richness at tree and plot scales because trees in planted forests were larger, older and more abundant than in naturally regenerating forests. Promisingly, 17% of recorded species were regionally endemic, supporting the notion that tree planting for ecological restoration can improve the plant conservation outlook in secondary tropical forests.

### Tree planting

Tree size and age are two principal drivers of epiphyte colonization; they typically co-vary but represent distinct
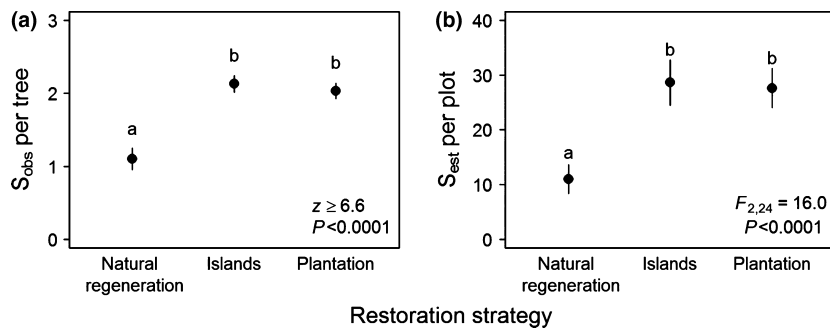
**Fig. 1.** Effect of restoration strategy on epiphyte species richness at the scale of (**a**) individual trees and (**b**) all trees within 0.25-ha plots. $S_{obs}$ is observed species richness; $S_{est}$ is estimated species richness. Error bars show 1 SE. Pai-rwise comparisons for individual trees (a) are from contrasts within GLMER (Appendix S3). Comparisons at the plot scale (b) are from Tukey HSD *post-hoc* tests on a two-way ANOVA.
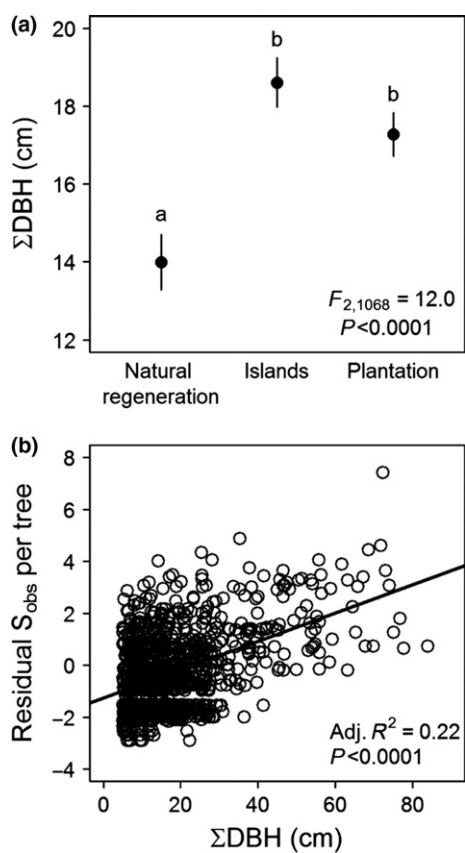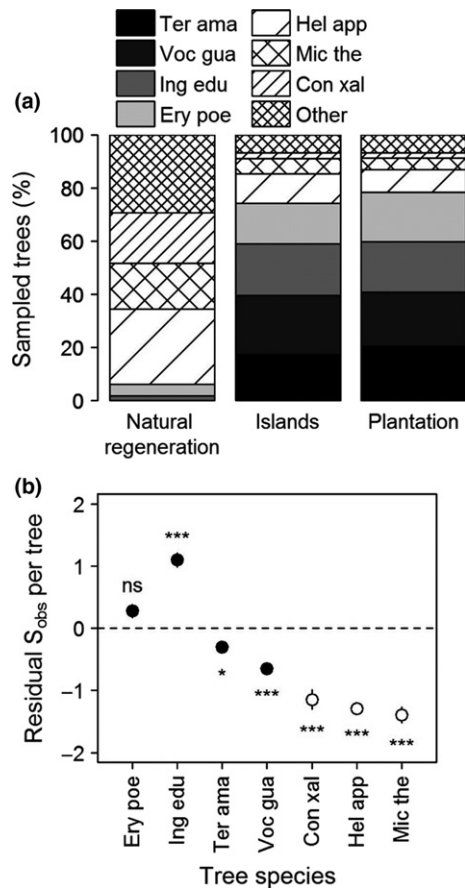


**Fig. 2.** Differences in tree size between restoration strategies (**a**) and their effect on epiphyte richness (**b**). ΣDBH is the sum of stem diameters for all tree stems with diameter ≥5 cm (range: 1–3 stems). Error bars are 1 SE. (a) Lowercase letters denote significant differences in Tukey HSD pair-wise comparisons on a two-way ANOVA (both $P < 0.0001$). (b) Residual epiphyte species richness ($S_{obs}$) was from a GLMER using site elevation and landscape forest cover with a random intercept for site. Slopes did not vary between restoration strategies (GLM, $P \geq 0.15$).

processes (Yeaton & Gladstone 1982). Older trees accumulate opportunities for rare colonization events, whereas larger trees provide bigger 'targets' (Taylor & Burns 2015).

Our planted trees were about 1.5 times larger and, due to our initial site maintenance, they were also at least 3 yrs older than natural recruits. This age difference can be significant; for comparison, bromeliad biomass was 5–46 times higher in 8-yr-old trees than 4-yr-old trees in plantations in northeastern Costa Rica (Merwin et al. 2003). These results suggest that through tree planting, restorationists can increase both the time and area available for epiphyte colonization.

After accounting for age and size, some tree species were still more 'epiphyte friendly' than others. For example, a common pioneer, *Heliocarpus appendiculatus*, hosted fewer epiphyte species per trunk than several other naturally recruiting species of similar size, and among planted species, *I. edulis* and, to a lesser degree, *E. poeppigiana*, hosted more epiphytes than *V. guatemalensis* or *T. amazonia*. Given that all tree species grew in close proximity at each site, we expect that host preferences were primarily due to tree species' characteristics that affect epiphyte establishment and survival rather than tree characteristics that could influence propagule arrival. Wagner et al. (2015) reviewed epiphyte host preferences in more than 200 studies, and identified three commonly invoked groups of hypotheses relating to physical bark characteristics, leaf and bark chemistry and architecture. High epiphyte richness on *Inga* is most likely explained by architecture; its multiple low-angled stems may facilitate establishment by accumulating organic debris (Nadkarni & Matelson 1991), increasing water availability through stem flow (Park & Cameron 2008) and reducing the danger of epiphyte detachment. Another possibility is that that N-fixing trees (including *Inga* and *Erythrina*) release N to epiphytes through canopy soil enrichment (Cardelús et al. 2009). Further research identifying 'epiphyte friendly' tree qualities would help restorationists choose appropriate species.

Tree planting effects were an order of magnitude stronger for ferns than for angiosperms. This pattern is consistent with a land-use study in northern Ecuador, where remnant

**Fig. 3.** Differences in tree composition between restoration strategies (**a**) and their effect on epiphyte species richness (**b**). Species planted as seedlings in islands ($N = 457$) and plantations ($N = 510$) are shaded grey; naturally recruited seedlings that dominated the natural regeneration ($N = 116$) are shaded white with cross-hatching. A few 'planted' tree species individuals established naturally in natural regeneration plots. (b) Residual epiphyte species richness ($S_{obs}$) was from a GLMER using site elevation and landscape forest cover with a random intercept for site. Points above the dotted line represent species with a positive effect on epiphyte species richness. Black points are planted tree species; white points are naturally recruited tree species. Error bars are 1 SE. Stars denote significant differences from zero based on two-sided $t$-tests with Bonferroni correction (*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$, n.s. $P > 0.05$). Species codes: Ter ama = *Terminalia amazonia*; Voc gua = *Vochysia guatemalensis*; Ing edu = *Inga edulis*; Ery poe = *Erythrina poeppigiana*; Hel app = *Heliocarpus appendiculatus*; Mic the = *Miconia theaezans*; Con xal = *Conostegia xalapensis*.

trees in areas recently cleared for cattle pasture were depauperate in fern diversity compared to remnants in closed-canopy forest (Larrea & Werner 2010). The authors attributed local fern extirpation to excess light and desiccation stress on pasture trees, and these filters may also explain poor fern colonization on young trees growing in naturally regenerating areas with incomplete canopy closure. Alternatively, ferns and angiosperms may eventually be benefited by tree planting to similar degrees, but ferns may have responded more rapidly because of their relatively long-distance spore dispersal (Wolf et al. 2001), allowing them to colonize new suitable habitats faster than dispersal-limited angiosperms. Indeed, angiosperms in our study were more strongly influenced by landscape forest cover.

Epiphyte richness at both the tree and plot level were similar in plots restored using island and plantation planting strategies, despite the fact that there were significantly more trees per plot in the plantations. These findings are consistent with previous island/plantation comparisons for tree seedling recruitment (Zahawi et al. 2013) and seed dispersal (Reid et al. 2015), and they support the practical recommendation that planting smaller clusters of tree seedlings is a cost-effective strategy for restoring biodiversity (Rey Benayas et al. 2008).

## Landscape context

Our results show that epiphyte colonization is affected by the landscape context. Specifically, trees embedded in higher forest cover landscapes had more epiphyte species than trees in deforested landscapes, a pattern that was driven by angiosperms. The landscape forest cover effect was strongest when measured at scales of 100–150 m around restoration plots. These distances are considerably further than documented dispersal kernels for wind-dispersed bromeliads ($\leq$15 m; Mondragón et al. 2006; Paggi et al. 2010) and may better reflect longer distance dispersal by dust-like orchid seeds (Trapnell & Hamrick 2004), bat-dispersed seeds (e.g. hemiepiphytic figs; August 1981) and bird-dispersed seeds (e.g. Araceae, Gesneriaceae; Sheldon & Nadkarni 2013). In practice, our results suggest that restored sites nearer existing forests will have larger capacity for spontaneous vascular epiphyte recolonization, as has been shown for other taxa (de Souza Leite et al. 2013),

**Table 1.** Large tree (DBH $\geq$5 cm) density (trees/0.25 ha) in three restoration strategies in southern Costa Rica. Lowercase letters denote significant differences in Tukey *post-hoc* tests ($P < 0.05$).

|  | Natural Regeneration | Islands | Plantation | $F_{df}$ ($P$) |
|---|---|---|---|---|
| Planted Trees | 0 ± 0 | 45 ± 5[a] | 201 ± 12[b] | 365.2[1,12] (<0.0001) |
| Naturally Recruited Trees | 58 ± 21 | 45 ± 8 | 33 ± 17 | 2.5[2,24] (0.0995) |
| Total | 58 ± 21[a] | 90 ± 10[b] | 234 ± 21[c] | 40.8[2,24] (<0.0001) |
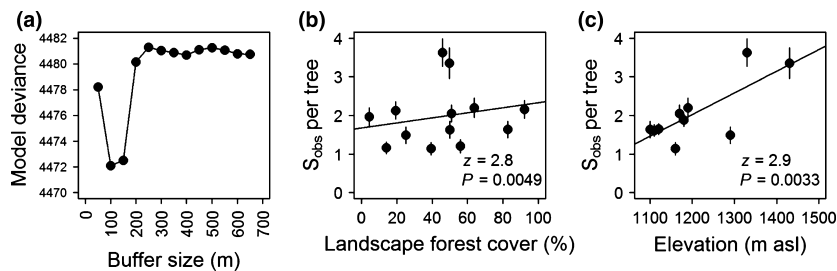
**Fig. 4.** Effects of landscape context on epiphyte species richness ($S_{obs}$) per tree. Error bars show 1 SE. (**a**) Scaling of landscape forest cover effects on $S_{obs}$. Deviances were calculated for fully specified GLMERs where landscape forest cover was measured within differently sized concentric rings around each restoration plot. Statistics in (**b**) and (**c**) are from a GLMER using elevation, forest cover and restoration strategy with a random intercept for site. Landscape forest cover in (b) was measured within a 100-m buffer of each restoration plot. This effect was significant with ($P = 0.0049$) or without ($P = 0.0211$) the two sites with mean $S_{obs} > 3$.
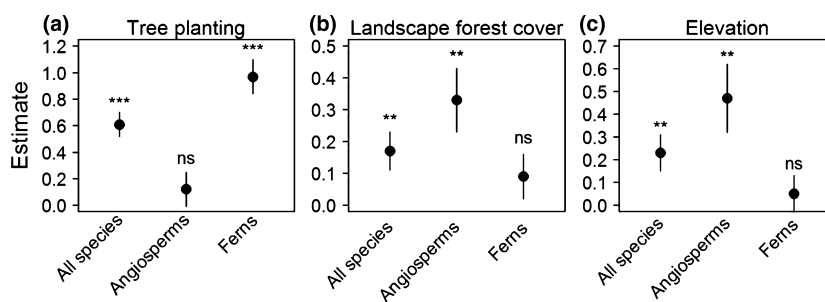


**Fig. 5.** Epiphyte composition effects on model estimates for (**a**) restoration strategy, (**b**) landscape forest cover and (**c**) elevation. Error bars are 1 SE. Stars denote model estimates that were significantly different from zero in GLMERs using different taxonomic subsets (*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$, n.s. $P > 0.05$). For example, tree planting had a significant positive effect (when compared to natural regeneration) on epiphyte species richness using the entire data set (All species) and ferns only, but not for angiosperms.

whereas more isolated sites could benefit from epiphyte reintroductions. We found that local restoration strategies were more important than landscape forest cover for predicting epiphyte species richness, but landscape forest cover effects may be stronger if future studies can account for surrounding forest age, since older remnant trees are particularly important propagule sources (Nadkarni & Haber 2009).

Not surprisingly, elevation was also an important determinant of epiphyte species richness (Cardelús et al. 2006). We found that trees at two restoration sites on a humid mountain ridge hosted particularly diverse epiphyte communities. Differentiating among the debated mechanisms for epiphyte elevational diversity patterns is beyond the scope of this study; suffice it to say that the angiosperms driving our observed elevation gradient comprised species at both the low and high ends of their elevational distributions, and high humidity on this foggy ridge seemed to allow for profuse epiphyte growth (Rahbek 1995), even on fence posts and power lines (pers obs). In turn, these plants probably contributed to increased propagule availability in restoration sites.

## Conclusions

This study represents a snapshot of epiphyte community development after a decade of forest recovery, but restoration dynamics are likely to shift over time as trees mature and tree composition changes. Whereas epiphytes on the young trees in this study were concentrated on the lower trunks, full-tree surveys will be useful in the future and might be accomplished during thinning operations or, as self-thinning becomes more frequent, by monitoring canopy communities based on individuals that have fallen to the forest floor (Cabral et al. 2015).

Ecological restoration is an incremental process of observing barriers to ecosystem recovery and identifying solutions to overcome them. Previous studies observed that vascular epiphytes recover slowly in naturally regenerating tropical forests; here we showed that conventional and applied nucleation tree plantings could accelerate epiphyte recovery in suitable landscapes. Where budgets allow, it may be worthwhile to transplant dispersal-limited epiphyte species to unlock additional species interactions.

## Acknowledgements

## References

August, P.V. 1981. Fig fruit consumption and seed dispersal by *Artibeus jamaicensis* in the llanos of Venezuela. *Biotropica* 13: 70–76.

Bare, M. & Tello, O. 2010. Restoration of tropical forest: the orchid and botanical garden of Puyo, Ecuador. *Ecological Restoration* 28: 81–85.

Barthlott, W., Schmit-Neuerburg, V., Nieder, J. & Engwald, S. 2001. Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. *Plant Ecology* 152: 145–156.

Bennett, B.C. 1986. Patchiness, diversity, and abundance relationships of vascular epiphytes. *Selbyana* 9: 70–75.

Cabral, J.S., Petter, G., Mendieta-Leiva, G., Wagner, K., Zotz, G. & Kreft, H. 2015. Branchfall as a demographic filter for epiphyte communities: lessons from forest floor-based sampling. *PLoS ONE* 10: e0128019.

Cardelús, C.L., Colwell, R.K. & Watkins, J.E. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology* 94: 144–156.

Cardelús, C.L., Mack, M.C., Woods, C., DeMarco, J. & Treseder, K.K. 2009. The influence of tree species on canopy soil nutrient status in a tropical lowland wet forest in Costa Rica. *Plant and Soil* 318: 47–61.

Cascante-Marín, A., Wolf, J.H.D., Oostermeijer, J.G.B. & Den Nijs, J.C.M. 2008. Establishment of epiphytic bromeliads in successional tropical premontane forests in Costa Rica. *Biotropica* 40: 441–448.

Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E. & Miller, S.E. 2009. The potential for species conservation in tropical secondary forests. *Conservation Biology* 23: 1406–1417.

Clark, K.L., Nadkarni, N.M., Schaefer, D. & Gholz, H.L. 1998. Atmospheric deposition and net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica. *Journal of Tropical Ecology* 14: 27–45.

Corbin, J.D. & Holl, K.D. 2012. Applied nucleation as a forest restoration strategy. *Forest Ecology and Management* 265: 37–46.

de Souza Leite, M., Tambosi, L.R., Romitelli, I. & Metzger, J.P. 2013. Landscape ecology perspective in restoration projects for biodiversity conservation: a review. *Natureza & Conservação* 11: 108–118.

Duellman, W.E. 1988. Patterns of species diversity in anuran amphibians in the American tropics. *Annals of the Missouri Botanical Garden* 75: 79–104.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography* 40: 1649–1663.

Flores-Palacios, A. & García-Franco, J. 2001. Sampling methods for vascular epiphytes: their effectiveness in recording species richness and frequency. *Selbyana* 22: 181–191.

Flores-Palacios, A. & García-Franco, J.G. 2006. The relationship between tree size and epiphyte species richness: testing four different hypotheses. *Journal of Biogeography* 33: 323–330.

Freiberg, M. 1996. Spatial distribution of vascular epiphytes on three emergent canopy trees in French Guiana. *Biotropica* 28: 345–355.

Gentry, A.H. & Dodson, C.H. 1987. Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden* 74: 205–233.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E. & Sodhi, N.S. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478: 378–381.

Gradstein, S.R., Nadkarni, N.M., Krömer, T., Holz, I. & Nöske, N. 2003. A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. *Selbyana* 24: 105–111.

Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liany, T. & Tosi, J.A. Jr 1971. *Forest environments in tropical life zones*. Pergamon Press, New York, NY, US.

Holl, K.D., Zahawi, R.A., Cole, R.J., Ostertag, R. & Cordell, S. 2011. Planting seedlings in tree islands versus plantations as a large-scale tropical forest restoration strategy. *Restoration Ecology* 19: 470–479.

Holl, K.D., Stout, V.M., Reid, J.L. & Zahawi, R.A. 2013. Testing heterogeneity-diversity relationships in tropical forest restoration. *Oecologia* 173: 569–578.

Jackson, S.T. & Sax, D.F. 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution* 25: 153–160.

Johansson, D. 1974. Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeographica Suecica* 59: 1–136.

Kanowski, J., Catterall, C., Wardell-Johnson, G., Proctor, H. & Reis, T. 2003. Development of forest structure on cleared rainforest land in eastern Australia under different styles of reforestation. *Forest Ecology and Management* 183: 265–280.

Larrea, M.L. & Werner, F.A. 2010. Response of vascular epiphyte diversity to different land-use intensities in a neotropical montane wet forest. *Forest Ecology and Management* 260: 1950–1955.

Lindell, C.A., Reid, J.L. & Cole, R.J. 2013. Planting design effects on avian seed dispersers in a tropical forest restoration experiment. *Restoration Ecology* 21: 515–522.

Lisboa, P.L.B., Maciel, U.N. & Prance, G.T. 1991. Some effects of colonization on the tropical flora of Amazonia: a case study from Rondônia. *Kew Bulletin* 46: 187–204.

Lowman, M.D. & Schowalter, T.D. 2012. Plant science in forest canopies – the first 30 years of advances and challenges (1980–2010). *New Phytologist* 194: 12–27.

Martin, P.A., Newton, A.C. & Bullock, J.M. 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proceedings of the Royal Society B: Biological Sciences* 281: 20140303.

Martínez-Garza, C. & Howe, H.F. 2003. Restoring tropical diversity: beating the time tax on species loss. *Journal of Applied Ecology* 40: 423–429.

Mehltreter, K., Flores-Palacios, A. & García-Franco, J.G. 2005. Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. *Journal of Tropical Ecology* 21: 651–660.

Meli, P. & Dirzo, R. 2013. Effects of grasses on sapling establishment and the role of transplanted saplings on the light environment of pastures: implications for tropical forest restoration. *Applied Vegetation Science* 16: 296–308.

Mendenhall, C.D., Sekercioglu, C.H., Brenes, F.O., Ehrlich, P.R. & Daily, G.C. 2011. Predictive model for sustaining biodiversity in tropical countryside. *Proceedings of the National Academy of Sciences of the United States of America* 108: 16313–16316.

Mendieta-Leiva, G. & Zotz, G. 2015. A conceptual framework for the analysis of vascular epiphyte assemblages. *Perspectives in Plant Ecology, Evolution and Systematics* 17: 510–521.

Merwin, M.C., Rentmeester, S.A. & Nadkarni, N.M. 2003. The influence of host tree species on the distribution of epiphytic bromeliads in experimental monospecific plantations, La Selva, Costa Rica. *Biotropica* 35: 37–47.

Mondragón, D., Maria Calvo-Irabien, L. & Wester, D. 2006. Seed dispersal and germination of the epiphyte *Tillandsia brachy-caulos* (Bromeliaceae) in a tropical dry forest, Mexico. *The Southwestern Naturalist* 51: 462–470.

Moran, R.C., Klimas, S. & Carlsen, M. 2003. Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. *Biotropica* 35: 48–56.

Nadkarni, N.M. & Haber, W.A. 2009. Canopy seed banks as time capsules of biodiversity in pasture-remnant tree crowns. *Conservation Biology* 23: 1117–1126.

Nadkarni, N.M. & Matelson, T.J. 1989. Bird use of epiphyte resources in neotropical trees. *Condor* 91: 891–907.

Nadkarni, N.M. & Matelson, T.J. 1991. Fine litter dynamics within the tree canopy of a tropical cloud forest. *Ecology* 72: 2071–2082.

Paggi, G.M., Sampaio, J.A.T., Bruxel, M., Zanella, C.M., Göetze, M., Büttow, M.V., Palma-Silva, C. & Bered, F. 2010. Seed dispersal and population structure in *Vriesea gigantea*, a bromeliad from the Brazilian Atlantic Rainforest. *Botanical Journal of the Linnean Society* 164: 317–325.

Park, A. & Cameron, J.L. 2008. The influence of canopy traits on throughfall and stemflow in five tropical trees growing in a Panamanian plantation. *Forest Ecology and Management* 255: 1915–1925.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18: 200–205.

Reid, J.L., Holl, K.D. & Zahawi, R.A. 2015. Seed dispersal limitations shift over time in tropical forest restoration. *Ecological Applications* 25: 1072–1082.

Rey Benayas, J.M., Bullock, J.M. & Newton, A.C. 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and the Environment* 6: 329–336.

Robinson, G.R. & Handel, S.N. 2000. Directing spatial patterns of recruitment during an experimental urban woodland reclamation. *Ecological Applications* 10: 174–188.

Scheffers, B.R., Brunner, R.M., Ramirez, S.D., Shoo, L.P., Diesmos, A. & Williams, S.E. 2013. Thermal buffering of microhabitats is a critical factor mediating warming vulnerability of frogs in the Philippine biodiversity hotspot. *Biotropica* 45: 628–635.

Sheldon, K.S. & Nadkarni, N.M. 2013. Spatial and temporal variation of seed rain in the canopy and on the ground of a tropical cloud forest. *Biotropica* 45: 549–556.

Taylor, A. & Burns, K. 2015. Epiphyte community development throughout tree ontogeny: an island ontogeny framework. *Journal of Vegetation Science* 26: 902–910.

Trapnell, D.W. & Hamrick, J.L. 2004. Partitioning nuclear and chloroplast variation at multiple spatial scales in the neotropical epiphytic orchid, *Laelia rubescens*. *Molecular Ecology* 13: 2655–2666.

Vellend, M. 2003. Habitat loss inhibits recovery of plant diversity as forests regrow. *Ecology* 84: 1158–1164.

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Calster, H.V., Peterken, G. & Hermy, M. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 87: 542–548.

Wagner, K., Mendieta-Leiva, G. & Zotz, G. 2015. Host specificity in vascular epiphytes: a review of methodology, empirical evidence and potential mechanisms. *AoB Plants* 7: plu092.

Werner, F. & Gradstein, S.R. 2008. Seedling establishment of vascular epiphytes on isolated and enclosed forest trees in an Andean landscape, Ecuador. *Biodiversity and Conservation* 17: 3195–3207.

Wolf, P.G., Schneider, H. & Ranker, T.A. 2001. Geographic distributions of homosporous ferns: does dispersal obscure evidence of vicariance? *Journal of Biogeography* 28: 263–270.

Wolf, J.H.D., Gradstein, S.R. & Nadkarni, N.M. 2009. A protocol for sampling vascular epiphyte richness and abundance. *Journal of Tropical Ecology* 25: 107–121.

Woods, C.L. & DeWalt, S.J. 2013. The conservation value of secondary forests for vascular epiphytes in central Panama. *Biotropica* 45: 119–127.

Woods, C.L., Cardelús, C.L. & DeWalt, S.J. 2015. Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. *Journal of Ecology* 103: 421–430.

Yeaton, R.I. & Gladstone, D.E. 1982. The pattern of colonization of epiphytes on calabash trees (*Crescentia alata* HBK.) in Guanacaste Province, Costa Rica. *Biotropica* 14: 137–140.

Zahawi, R.A., Holl, K.D., Cole, R.J. & Reid, J.L. 2013. Testing applied nucleation as a strategy to facilitate tropical forest recovery. *Journal of Applied Ecology* 50: 88–96.

Zahawi, R.A., Dandois, J.P., Holl, K.D., Nadwodny, D., Reid, J.L. & Ellis, E.C. 2015a. Using lightweight unmanned aerial vehicles to monitor tropical forest recovery. *Biological Conservation* 186: 287–295.

Zahawi, R.A., Duran, G. & Kormann, U. 2015b. Sixty-seven years of land-use change in southern Costa Rica. *PLoS ONE* 10: e0143554.

Zotz, G. & Vollrath, B. 2003. The epiphyte vegetation of the palm *Socratea exorrhiza*: correlations with tree size, tree age and bryophyte cover. *Journal of Tropical Ecology* 19: 81–90.

## Supporting Information

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

**Appendix S1.** Experimental design.
**Appendix S2.** Epiphyte species and higher taxa recorded in thirteen restoration sites in southern Costa Rica.
**Appendix S3.** GLMER results: effects of restoration strategy and landscape context on epiphyte richness.
**Appendix S4.** Trees sampled for vascular epiphytes.
**Appendix S5.** Residual effects of tree size and composition on epiphyte species richness.
**Appendix S6.** Sensitivity of GLMER results to epiphyte composition.