

Primary ecological succession in vascular epiphytes: The species accumulation model

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ABSTRACT

Epiphytes are integral to tropical forests yet little is understood about how succession proceeds in these communities. As trees increase in size they create microhabitats for late-colonizing species in both small and large branches while maintaining small tree microhabitats for early colonizing species in the small and young branches. Thus, epiphyte succession may follow different models depending on the scale: at the scale of the entire tree, epiphytes may follow a species accumulation model where species are continuously added to the tree as trees increase in size but at the scale of one zone on a branch (*e.g.*, inner crown: 0–2 m from the trunk), they may follow the replacement model of succession seen in terrestrial ecosystems. Assuming tree size as an indicator of tree age, I surveyed 61 *Virola koschnyi* trees of varying size (2.5–103.3 cm diameter at breast height) in lowland wet tropical forest in Costa Rica to examine how epiphyte communities change through succession. Epiphyte communities in small trees were nested subsets of those in large trees and epiphyte communities became more similar to the largest trees as trees increased in size. Furthermore, epiphyte species in small trees were replaced by mid- and late-successional species in the oldest parts of the tree crown but dispersed toward the younger branches as trees increased in size. Thus, epiphyte succession followed a replacement model in particular zones within treecrowns but a species accumulation model at the scale of the entire tree crown.

Abstract in Spanish is available with online material.

Key words: community composition; Costa Rica; La Selva Biological Research Station; microhabitat heterogeneity; nestedness; niche differentiation; *Virola koschnyi*.

PRIMARY ECOLOGICAL SUCCESSION FOR TERRESTRIAL PLANTS IN A GIVEN AREA TYPICALLY FOLLOWS A REPLACEMENT SEQUENCE, whereby species composition changes through time as a few species dominate along a continuum of different strategies at each successional stage (Cooper 1923, Oosting 1942). Species turnover during succession is thought to be driven by differences in environmental conditions, such as the availability of light, water, and nutrients at each successional stage that alter conditions for germination and establishment for different species (Clements 1916, Yarranton & Morrison 1974) as well as stochastic factors such as dispersal (Gleason 1926, Hubbell 2001). Diversity patterns in forests may be unimodal if the climax community is reached or logarithmic if there are levels of disturbance that maintain the community in a non-equilibrium state (Connell 1978, Chazdon 2003).

While research on primary ecological succession in terrestrial communities has been ongoing for over 90 yr, little is known about how succession proceeds in epiphyte communities, plants that grow on other plants, often on the trunks and branches of trees. Epiphytes are a conspicuous and integral component of tropical and temperate rain forests (McCune 1993, Lyons *et al.* 2000, Nieder *et al.* 2001, Zotz & Schultz 2008). Epiphytes contribute to floristic diversity (Gentry & Dodson 1987), create habitats for countless invertebrate and vertebrate species (Maser *et al.* 1985, Nadkarni & Matelson 1989, Ellwood *et al.* 2002) and also

contribute to nutrient cycling and microclimates within treecrowns (Pike 1978, Stuntz *et al.* 2002, Nadkarni 2004, Woods *et al.* 2012). Research on epiphyte communities has focused on their distribution within large trees (*e.g.*, Schimper 1888, Johansson 1974, Hietz & Briones 1998, Cardelús 2006, Woods *et al.* 2015), and successional patterns of epiphyte communities have been inferred by chronosequence studies in different-aged forest stands (Uliczka & Angelstam 1999, Barthlott *et al.* 2001, Benavides *et al.* 2006, Chao *et al.* 2006, Hilmo *et al.* 2009, Woods & DeWalt 2013). Only one study attempted to examine epiphyte succession in a single tree species by stripping large branches of the epiphyte community and examining recovery over time in montane tropical forests (Nadkarni 2000). However, recovery on old branches is a measure of secondary succession for epiphytes following a disturbance. A more direct measure of primary succession would be to examine how epiphyte communities change with tree size in one tree species, which has yet to be investigated.

For epiphytes, primary succession may adhere to replacement models built for terrestrial plants in a given area of the tree crown. For example, the inner crown (0–2 m from the trunk) of emergent tropical trees (*i.e.*, those that grow above the canopy) undergoes changes in light, substrate, and microclimate with tree size that likely influence and drive epiphyte succession. In small tropical trees in the understory of old growth forest, the inner crown has small, bare branches, low light, and high relative humidity (Woods *et al.* 2015). As the tree increases in size, the inner crown changes; its diameter increases, light levels increase

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and relative humidity decreases as it increases its height and emerges above the canopy (Woods *et al.* 2015). Once emergent, the inner crown changes again; light availability is low and relative humidity is high, which is likely due to a boundary effect created by the many epiphytes that inhabit the large branches along with the many canopy layers above it (Woods *et al.* 2015). Furthermore, the inner crown often develops canopy humus, which is formed from the decomposition of plant material (Nadkarni 1984, Cardelús *et al.* 2009, Woods *et al.* 2015). The outer crown (>5 m from the trunk) also undergoes changes with tree size; while maintaining bare branches in both small and large trees, it has low light and high relative humidity in small trees when in the understory but is very exposed with high light and low relative humidity when emergent above the canopy. In temperate trees, the lower crown changes with tree size; in small trees it is exposed, dry, and has high light while in larger trees it is wet and has less light (McCune 1993, Sillett & Neitlich 1996). These changes in environmental conditions with tree size, such as the availability of light and water, likely drive epiphyte succession.

While succession in some parts of the tree crown may adhere to replacement models built for terrestrial plants (*i.e.*, the inner crown in tropical trees and the lower crown in temperate trees), the entire tree crown is often considered the community in many epiphyte studies (*e.g.*, Johansson 1974, Hietz & Briones 1998, Zotz & Schultz 2008). Thus, a different model is needed to explain succession in epiphyte communities at the scale of the entire tree. A widely documented pattern in epiphyte studies is that of increasing epiphyte diversity with increasing tree size (McCune 1993, Lyons *et al.* 2000, Zotz & Vollrath 2003, Woods *et al.* 2015). This is due to increasing time for colonization, increasing area upon which to establish, and increasing microhabitat heterogeneity that enables more species with specialized habitat requirements to colonize the tree crown. For example, within large host trees, many epiphytes show distribution patterns, such that particular species are adapted to particular microhabitats

created by gradients in environmental conditions (Johansson 1974, McCune 1993, Hietz & Briones 1998, Lyons *et al.* 2000, Antoine & McCune 2004, Woods *et al.* 2015). As a result of increasing microhabitat heterogeneity with tree size, in both tropical and temperate trees, many epiphytic species that are replaced in the inner or lower crown as trees increase in size are still found in large trees but in the outer or upper crown (McCune 1993, Woods *et al.* 2015). Thus, at the scale of the entire crown I propose a new model of succession: the species accumulation model in which new species are added to new microhabitats that are created in all parts of the tree crown as trees increase in size without replacing existing species (Fig. 1). This could be thought of as simply due to an area effect where old growth trees have both early- and late-stages of succession (equivalent to increasing area on land such that early- and late-successional forests are included as area increases); however, increasing area alone does not explain the presence of many outer or upper crown epiphyte species in large trees not being found in small trees. The outer and upper crowns of large trees in tropical and temperate forests, respectively, are new microhabitats for some species because the environmental conditions are different from those in small trees. This accumulation of species with tree size would result in a nested relationship of epiphyte species composition such that species in smaller trees are a nested subset of the species in larger trees, and similarity in species composition to the largest trees should increase with tree size. Furthermore, it could explain why the relationship of epiphyte diversity with tree size follows a linear or logarithmic model and not a unimodal relationship as seen in some terrestrial systems.

I examined whether vascular epiphyte succession occurs through a species accumulation model at the scale of the entire tree crown and one of replacement at the scale of the inner crown of a branch in lowland tropical forests in northeastern Costa Rica. If epiphyte succession follows a species accumulation model, in addition to the predictions stated above, I predicted

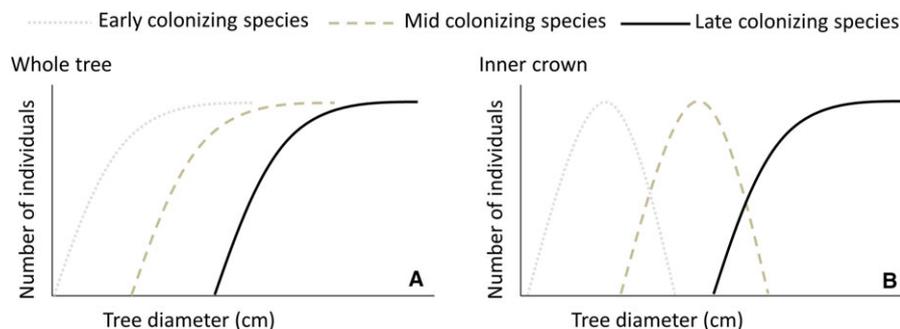


FIGURE 1. Epiphyte succession is predicted to follow a species accumulation model for the whole tree whereby new species are added to the tree as new microhabitats are formed with increasing tree size (A) and a replacement model of succession in the inner crown of tropical trees (0–2 m from the trunk), whereby early colonizing species are replaced by mid colonizing and eventually late colonizing species (B). In the entire tree crown, early colonizing species are followed by mid colonizing species and finally late colonizing species, such that all species stay within the tree crown as the trees increase in size. In the inner crown, early colonizing species are replaced by mid colonizing species, which are then replaced by late colonizing species, which follows the replacement model of succession. Species turnover in the inner crown is akin to primary succession in terrestrial environments. Because the epiphyte community includes the entire tree crown, the species accumulation model is better suited to examine changes in epiphyte communities with tree size than terrestrial-based models.

that the species composition of the smallest trees would be more similar to the outer crown of the largest trees than to the inner crown of the largest trees.

METHODS

STUDY AREA.—This study was conducted at La Selva Biological Research Station (84°00'12" W, 10°25'52" N, 40 m asl) located in northeastern Costa Rica. The station includes 1600 ha of lowland wet tropical forest (Holdridge 1967) and receives approximately 4000 mm of annual precipitation, predominantly during the wet season, May–January, with an average monthly precipitation of 382 mm. The drier season, February–April, receives an average monthly precipitation of 172 mm. Average monthly temperature is $25.8 \pm 0.2^\circ\text{C}$ and varies little throughout the year (McDade *et al.* 1994).

EPIPHYTE SURVEY.—To determine how epiphyte communities change through succession, I surveyed vascular epiphyte communities within the crowns of 61 individual *Virola koschnyi* trees (Myristicaceae) that ranged in diameter at breast height (dbh) from 2.5 to 103.3 cm within 1300 ha of the La Selva old-growth forest. I assumed a space-for-time substitution, such that small trees were assumed to be younger than large trees. All trees were >5 m from the main trails, and the largest trees (>70 cm dbh; $N = 5$) were chosen from the 17 available in the TREES database (D. B. Clark and D. A. Clark, personal communication) that were healthy and safe to climb. I chose different-sized trees of one tree species in order to control for host characteristics that could influence colonization patterns of epiphytes as well as to control for changing environmental conditions as trees increase in size, such as bark characteristics, canopy humus chemistry, life history (*e.g.*, deciduous vs. evergreen) and foliar leaching (Callaway *et al.* 2002, Cardelús & Chazdon 2005, Cardelús *et al.* 2009). I also chose one tree species to directly examine epiphyte succession. I chose *Virola* because of their consistent branch sizes, their little variation in branch angle from the tree crown, the abundance of individuals of varying size classes at La Selva (density of trees ≥ 10 cm dbh is 4.1 individuals/ha, D.B. Clark and D.A. Clark, unpublished data), and its robust epiphyte community that is confined to the crown alone. My study, therefore, examined epiphyte succession within tree crowns only and not on the trunk.

To survey epiphytes within each tree crown, I climbed the trees using single-rope climbing techniques (Perry 1978) and conducted within-tree surveys. Epiphytes were surveyed on five to six branches in each tree every 1 m from the bole to the branch tips. It was logistically impossible to reach and properly survey the higher two to three branches in many trees, which confined my study to the first five to six branches. For trees whose crowns were visible from the ground (most trees <70 cm dbh) I surveyed epiphytes using ground-based surveys with binoculars. I tested whether or not a ground-based survey could adequately capture the epiphyte community by surveying some trees <70 cm dbh from the ground and from the canopy of other trees (*i.e.*,

hanging beside the tree). I identified and counted approximately 89 percent of the epiphyte community with ground-based surveys, which is similar to that found in other studies (*e.g.*, 90% in Burns 2007). The ground-based surveys missed small individuals (leaves <10 cm). Thus, small individuals not identified to genus or species (*e.g.*, many bromeliads and aroids) were not included in the survey as this could have overestimated species composition similarity among small trees and differences between small and large trees.

STATISTICAL ANALYSIS.—I used R v. 3.2.1 for all statistical analyses (R Development Core Team 2009). I classified trees into size classes based on changes in epiphyte community structure (*i.e.*, richness and abundance) using multivariate regression trees (MRT), which is a cluster analysis that minimizes the dissimilarity of groups within each cluster with the *mvpart* package in R (De'Ath 2002). I used a Bray–Curtis dissimilarity matrix on epiphyte abundance and species richness. The MRT analysis resulted in four tree size classes: 15 cm ($N = 25$): 2.5–15.0 cm dbh; 30 cm ($N = 16$): 15.1–30.0 cm dbh; 70 cm ($N = 15$): 30.1–70.0 cm dbh; and >70 cm dbh ($N = 5$). I confirmed the results of the MRT analysis by examining how epiphyte richness and abundance varied among tree size classes using ANOVA followed by Tukey's HSD tests. Both richness and abundance were square root transformed to meet normality assumptions. I examined whether Bray–Curtis similarity in epiphyte species composition differed among tree size classes using ANOSIM in the *vegan* package for R (Oksanen *et al.* 2010). To examine patterns in dominance in epiphyte communities among tree size classes, I used rank abundance curves for each size class.

To examine whether the log-linear relationship found between epiphyte species richness with tree size at the scale of the entire tree (Woods *et al.* 2015) was also found for just the inner crown of the tree (0–2 m from the trunk), I used regression to test whether epiphyte species richness followed a linear, log-linear, or quadratic relationship with tree size. The model with the lowest order Akaike information criterion that controls for small sample size (AICc) was deemed the best fit model. I also tested whether the relationship followed a unimodal distribution using Hardigan's *diptest* in the *diptest* package in R (Maechler 2014).

To examine whether epiphyte communities found in the outer crown of the largest trees would be compositionally more similar to those found in small trees crowns than to the inner crown of the same large trees, I broke up the largest trees into three crown zones as was done in previous studies (Johansson 1974, Woods *et al.* 2015): inner crown (0–2 m from the trunk), mid crown (2–5 m from the trunk), and outer crown (>5 m from the trunk).

To examine if epiphyte communities in smaller trees were nested within the largest trees, a nestedness analysis was conducted using the Nestedness metric based on Overlap and Decreasing Fill (NODF) index using presence–absence data for epiphyte species with at least two individuals ($N = 60$; Almeida-Neto & Ulrich 2010). To examine how epiphyte composition

changed with tree size and among crown zones, I used non-metric multidimensional scaling (NMS) using a Bray–Curtis distance metric implemented with the metaMDS function in the vegan package in R (Oksanen *et al.* 2010). I used ellipses to denote variance in species composition among the tree size classes and among crown zones in the largest trees (*i.e.*, >70 cm dbh). To examine if species composition became more similar to the largest trees with tree size, I used regression of similarity of each tree to the largest trees with tree size. For each tree <70 cm dbh, I calculated the pairwise Bray–Curtis similarity index to each of the five trees >70 cm dbh and then averaged them.

RESULTS

Across 61 *Virola koschnyi* crowns, I documented a total of 6250 individual epiphytes from 97 species, 51 genera, and 15 families, which represented 30 percent of the known epiphyte species at La Selva Biological Research Station (McDade *et al.* 1994). The number of epiphyte species in a single tree crown ranged from 0 in small trees (<5 cm dbh) to 65 in large trees (>70 cm dbh), and the number of trees with only one epiphyte species was 29. Bromeliaceae made up the most individuals (64%) followed by Orchidaceae (7%).

Species richness differed significantly among all tree size classes with the largest tree size class having the greatest richness (Table 1, $F_{3,60} = 81.1$, $P < 0.001$). Epiphyte abundance was significantly different among tree size classes except between the 15 and 30 cm size classes (Table 1, $F_{3,60} = 142.5$, $P < 0.001$). Epiphyte abundance was highest in the largest tree size class (Table 1). These results confirm those of the MRT analysis that separated the trees into size classes based on richness and abundance (Woods *et al.* 2015) and are presented as a table rather than an MRT to facilitate interpretation.

Species richness in the inner crown increased significantly with tree size. The model that best fit the relationship of inner

crown species richness with tree size was the log-linear model (AICc = 0.29; $F_{1,59} = 137.1$, $P < 0.001$, $R^2 = 0.70$; $\log(\text{species richness}) = 0.01 \times \text{Diameter} + 0.02$) compared to the linear model (AICc = 273.5, $R^2 = 0.84$) or the quadratic model (AICc = 275.0, $R^2 = 0.84$). The relationship of inner crown species richness with tree size was significantly different from a unimodal distribution according to a Hartigan's dip test ($D = 0.82$, $P < 0.01$).

Of the species that exhibited a significant association with a particular microhabitat as determined previously (Woods *et al.* 2015), early colonizing species that dominated small trees included *Microgramma reptans* (Polypodiaceae) and *Peperomia rotundifolia* (Piperaceae; Fig. 2). Mid colonizing species included orchids, such as *Nidema boothii* (Orchidaceae; Fig. 2). Species that colonized the largest trees were numerous and included many fern species, such as *Elaphoglossum latifolium* (Dryopteridaceae) and *E. bermineri* (Dryopteridaceae) and cyclanths, such as *Sphaeradenia acutitelpela* (Cyclanthaceae) and *Chorizyne pendula* (Dryopteridaceae; Fig. 2). Bromeliads, which are a dominant group in the canopy, were found as mid and late colonizing species and showed few associations with any particular tree size with a few notable exceptions. *Tillandsia bulbosa* (Bromeliaceae), an atmospheric bromeliad, and *Vriesea vittata* (Bromeliaceae), which has an atmospheric juvenile and small tank adult, were found predominantly in the outer crown of large trees. *Tillandsia monadelphba* (Bromeliaceae), a medium tanked bromeliad, was found predominantly in the inner crown. These results are supported by the rank abundance curves, which showed dominance by a few species in small tree size classes (*i.e.*, steep lines) and more evenness in large tree size class (*i.e.*, less steep lines, Fig. 3).

Bray–Curtis similarity in species composition was significantly different among all tree size classes and the largest trees had the highest degree of similarity (Table 1, ANOSIM statistic $R = 0.41$, $P = 0.001$). The differences in similarity in species composition among tree size classes can be seen in the NMS that showed large variation in species composition in the 15, 30 and 70 cm size classes but small variation in species composition in the >70 cm size class (Fig. 4A).

The species composition of small tree size classes was significantly nested within the species composition of the largest tree size classes (NODF: $Z = -2.79$, $P = 0.003$) with only 10.3 percent of the species found in small trees not found in large trees. Nestedness in species composition was driven by the species found in the outer crown of the largest trees as they were also found in smaller tree size classes, which can be seen in the NMS—the outer crown cluster is closer to the 30 cm and 70 cm tree size classes than the inner crown cluster (Fig. 4B). Similarity in species composition of the smaller tree size classes to the largest tree size class increased significantly with tree size (Fig. 5).

DISCUSSION

Epiphyte succession within *V. koschnyi* trees at the scale of the tree crown followed the predictions of the species accumulation model. As trees increased in size, epiphyte richness and

TABLE 1. Mean (\pm SE) species richness, abundance, and Bray–Curtis similarity of vascular epiphyte communities within different tree size classes of 61 *Virola koschnyi* trees at La Selva Biological Research Station, Costa Rica showed higher species richness, abundance, and similarity in species composition in large trees relative to small trees.

Diameter class (cm)	Species richness	Abundance	Similarity
15	1 \pm 0.3 ^a	3 \pm 0.8 ^a	0.37 \pm 0.04 ^a
30	3 \pm 0.5 ^b	20 \pm 7.9 ^a	0.41 \pm 0.02 ^b
70	9 \pm 2.0 ^c	72 \pm 19.9 ^b	0.39 \pm 0.01 ^{ab}
>70	52 \pm 3.7 ^d	955 \pm 117.0 ^c	0.71 \pm 0.03 ^c

Multivariate regression trees were used to delineate tree size classes based on epiphyte richness and abundance (15 cm = 2.5–15.0 cm dbh; 30 cm = 15.1–30.0 cm; 70 cm = 30.1–70 cm; >70 cm) and were tested with ANOVA. Values for species richness and abundance with different letters are significantly different among diameter classes according to a Tukey's HSD test ($P < 0.05$) and values for similarity with different letters are significantly different according to an analysis of similarity (ANOSIM, $P < 0.05$).

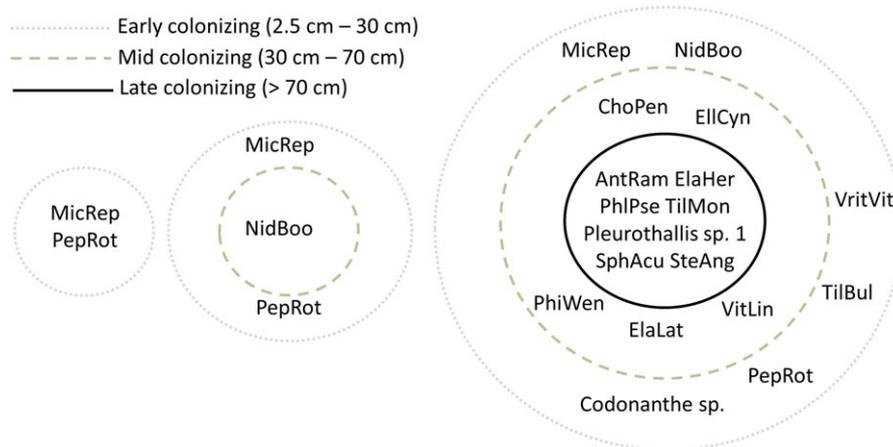


FIGURE 2. The colonization patterns of epiphyte species showed support for the species accumulation model at the scale of the entire tree as early colonizing species dominated small trees and more species were added to the tree crown as the trees increased in size. Support for the replacement model was found in the inner crown as the early colonizing species were found in the entire crown of small trees and were replaced by mid-colonizing and finally late colonizing species as the trees increased in size. These patterns are of epiphyte species that showed a significant association with a particular tree size or crown zone within the largest tree size class as determined by a previous study (Woods *et al.* 2015). The epiphyte species found in the small trees were nested subsets of larger trees as the early colonizing species were not excluded from the community as trees increased in size but dispersed toward the outer crown through succession. Araceae: AntRam, *Anthurium ramonense*, PhiWen, *Philodendron wendlandii*; SteAng, *Stenospermation angustifolium*; Bromeliaceae: TilBul, *Tillandsia bulbosa*; TilMon, *Tillandsia monadelphae*; VriVit, *Vriesea vittata*; Cyrtanthaceae: ChoPen, *Chorizyne pendula*; SphAcu, *Sphaeradenia acutitepala*; Dryopteridaceae: ElaHer, *Elaphoglossum herminieri*; ElaLat, *Elaphoglossum latifolium*; Orchidaceae: EilCyn, *Elleanthus cynarcephalus*; NidBoo, *Nidema boothii*; Piperaceae: PepRot, *Peperomia rotundifolia*; Polypodiaceae: MicRep, *Microgramma reptans*; PhiPse, *Phlebodium pseudoaureum*; Pteridaceae: VitLin, *Vittaria lineata*.

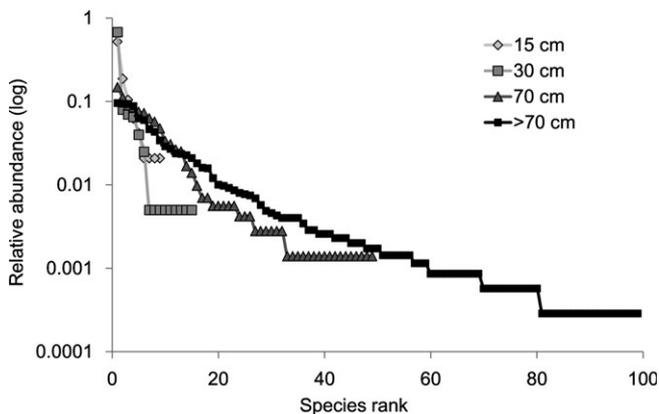


FIGURE 3. Epiphyte communities in different-sized trees showed a pattern from dominance by a few species in small trees to more evenness in large trees as evidenced by the change in steepness of the rank abundance curves for epiphyte communities within the canopies of *Virola koschnyi* trees from lowland wet rain forest in Costa Rica from each of four size classes defined by multivariate regression trees: light gray diamonds = 15 cm dbh; medium gray squares = 30 cm dbh; dark gray triangles = 70 cm dbh; black rectangles = >70 cm dbh.

abundance increased as species were added to the epiphyte community through succession (Woods *et al.* 2015). The epiphyte communities in small trees were nested subsets of the epiphyte communities in large trees and only 10 of the 97 epiphyte species were found only in small trees (*i.e.*, 10.3%). Furthermore, the

similarity in epiphyte species composition to the largest trees increased with tree size. These patterns were driven by the early colonizing epiphyte species that dominated small trees being replaced by mid and then late colonizing species in the inner crown but dispersing to the outer crown in large trees. Thus, epiphyte species composition of small trees was more similar to that of the outer than the inner crown of large trees. This study was restricted to examining epiphyte succession within one tree species, but the findings are likely generalizable. For example, similar to what was found in this study, in submontane rainforests in Indonesia, species composition of epiphytic bryophytes in understory trees was similar to the composition of the outer crowns of canopy trees, but the composition of the inner crowns in small and large trees were very different (Sporn *et al.* 2010). Also, many of the epiphyte species found in the inner crown of the oldest *V. koschnyi* trees are also found in the inner crown of large trees of other tree species (*e.g.*, *Hyeronima alchorneoides* and *Lecythis ampla*) at La Selva (Cardelús 2006). Given the varying environmental conditions in small trees and the outer crown of large trees, early colonizing species must be able to tolerate a wide range of environmental conditions. The results also show that the accumulation of epiphyte species with tree size was not simply due to an area effect. The outer crown of large trees is a novel microhabitat that enabled the colonization of species that were only found in that microhabitat and not in small trees, such as atmospheric bromeliads. Many atmospheric bromeliads are intolerant of high relative humidity (Benzing *et al.* 1978), which may explain their inability to colonize small trees.

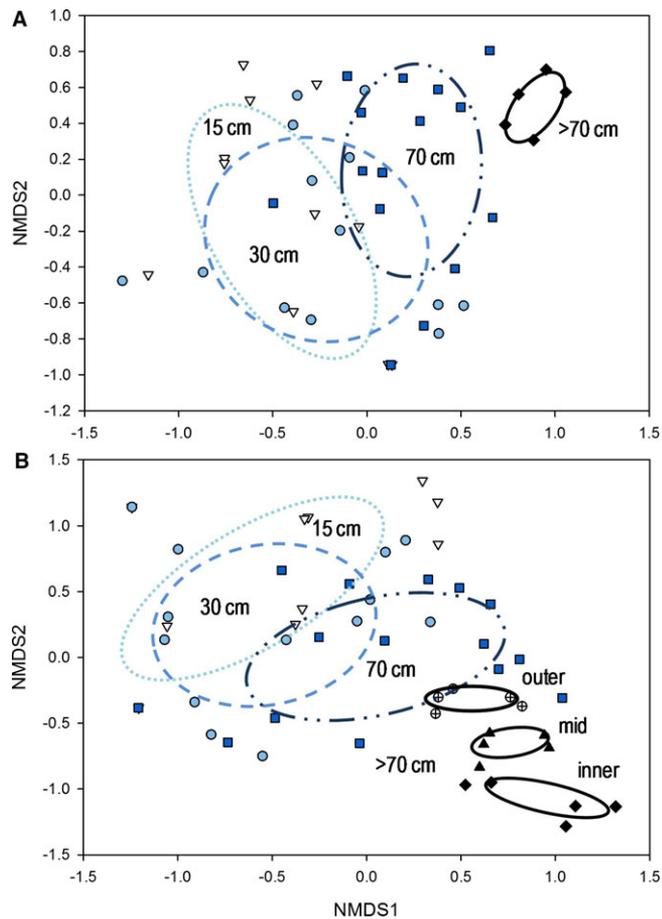


FIGURE 4. Non-metric multidimensional scaling (NMS) ordination of epiphyte community composition within the canopies of 5–25 *Virola koschnyi* trees from each of four size classes from lowland wet rain forest in Costa Rica using a Bray–Curtis distance matrix on relative abundance for all trees (A) and with the largest trees separated into crown zones (B). Two-dimensional stress = 18.02 for (A), and two-dimensional stress = 15.77 for (B). Trees were classified into diameter classes: downward facing triangles = 15 cm dbh; filled circles = 30 cm dbh; filled squares = 70 cm dbh; filled diamonds (in A) = >70 cm dbh. For (B), trees >70 cm dbh were separated into crown zones: diamonds = inner crown (0–2 m); upward facing triangles = mid crown (2–5 m); circle with a cross = outer crown (>5 m). The ellipses show the covariance matrix centered on the mean of each tree size class or zone: dotted = 15 cm dbh; dashed = 30 cm dbh; dotted and dashed = 70 cm dbh; solid = >70 cm dbh. Only 45 of the 61 trees were included in the NMS analysis because trees with fewer than two epiphyte individuals were excluded from the analyses (*i.e.*, 13 trees in the 15 cm dbh size class and 3 trees in the 30 cm dbh size class were excluded). Only epiphyte species found in at least two trees were included in the analyses, which resulted in the inclusion of 68 epiphyte species (29 species were excluded because they were only found on a single tree).

Epiphyte succession at the scale of the entire crown changed from being driven mainly by dispersal to being driven by more deterministic factors. Among the smaller tree size classes, there was low similarity in species composition among individual trees and a large degree of variation in species composition (as

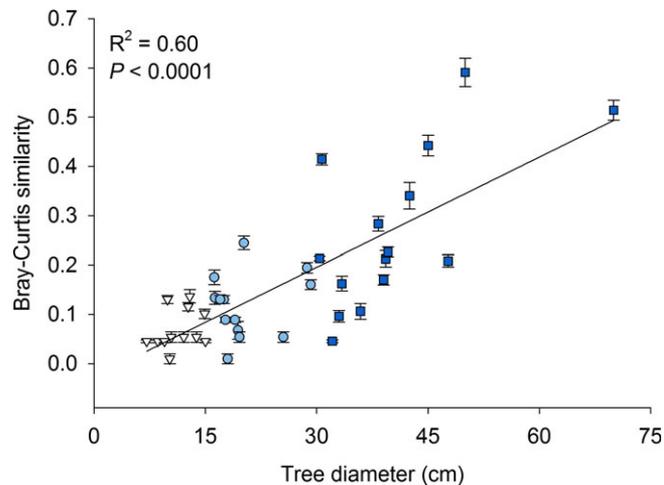


FIGURE 5. The similarity in epiphyte species composition of each of the smaller tree size classes to the largest tree size class increased with tree diameter. Points are mean \pm 1 SE Bray–Curtis similarity in epiphyte species composition between each individual *Virola koschnyi* tree \leq 70 cm dbh to each of the five trees >70 cm dbh at La Selva Biological Research Station.

evidenced by the large ellipses in the NMS in Fig. 4). The large degree of variation among small trees is likely due to dispersal limitation as there are few numbers of early colonizing species that are able to colonize small trees. The early colonizing species included creeping ferns such as *M. reptans* (Polypodiaceae) and *M. lycopodioides* (Polypodiaceae) as well as *P. rotundifolia* (Piperaceae). These species are drought-deciduous (Benzing 1990) and the gametophytes of the ferns are desiccation tolerant (Watkins *et al.* 2007), which may explain their ability to colonize the more drought-prone bare bark microhabitats within small tree crowns and the outer crowns of large trees. The distribution of epiphyte species within the crowns of the largest trees was non-random. Many aroids and large fern species such as *Elaphoglossum* spp. (Dryopteridaceae) that often root in canopy humus were only found in the inner crown of the largest trees, which was predominantly covered by humus and moss. Atmospheric bromeliads such as *T. bulbosa* (Bromeliaceae) and creeping ferns such as *Microgramma* spp. (Polypodiaceae) were only found in the outer crown, which is predominantly bare bark. Evidence of this can be seen in the lack of overlap of the inner and outer crown ellipses in the NMS, which indicates different species composition (Fig. 4B). The lack of overlap between the inner and outer crowns in the largest trees is surprising given that these microhabitats are only meters apart yet the large trees were kilometers apart and had the same epiphyte species in each microhabitat. The high similarity in species composition among the largest tree sizes suggests that epiphyte community composition is predictable at later stages of succession and influenced by deterministic factors, such as niche partitioning. These data are supported by many studies that have found the distribution of epiphytes within large tree crowns to be non-random, such that particular epiphyte species show specialization to particular microhabitats

(Johansson 1974, McCune 1993, Hietz & Briones 1998, Lyons *et al.* 2000, Woods *et al.* 2015).

At the scale of the inner crown, epiphyte succession followed a replacement model that is commonly seen in terrestrial systems. Early colonizing species dominated the inner crown in small trees but were replaced by mid and late colonizing species in larger trees. The replacement of species in the inner crown as trees increased in size could be due to autogenic changes by the early colonizing plants that make the microhabitat more suitable for mid and late colonizing species, thus following the facilitation model of succession (Connell & Slatyer 1977, Switzer *et al.* 1979, Finegan 1984). Some of these changes could include an increase in relative humidity from plant evapotranspiration as well as increased shading (Denslow 1980, Woods *et al.* 2015) or the creation of substrates to facilitate germination and seedling recruitment, such as bryophyte cover and canopy humus from the decomposition of early colonizing plants (Nadkarni 1984, 2000). The formation of canopy humus increases moisture retention in the substrate (Freiberg 1996) that likely enables germination of particular plant species. In this study, some epiphytic ferns, such as *Elaphoglossum* spp. (Dryopteridaceae) and cyclanths, were only found rooted in canopy humus, which may explain their absence in smaller trees and dependence on early colonizing species to create their required substrate. Nadkarni (2000) stripped branches of epiphyte communities in large trees in Costa Rican montane forests to examine epiphyte recolonization patterns (*i.e.*, secondary succession). Recolonization of the stripped branches was slow, and colonization by vascular epiphytes required bryophyte cover before they could re-establish on the branch (Nadkarni 2000). Epiphyte species richness with tree size in the inner crown followed a log-linear relationship and not a unimodal relationship, which indicates that epiphyte succession did not reach saturation, even on the oldest branches in the largest trees. This may be due to increasing habitat complexity in the inner crown as trees increase in size; small trees have bare branches with little microhabitat variation, whereas large trees have branches with high microhabitat variation (*e.g.*, spots with canopy humus cover or spots with bryophyte cover). This is also likely due to either a high level of disturbance or the limits of the age of *V. koschnyi* trees that prevents the epiphyte community from reaching a climax community.

A well-documented pattern in studies of epiphyte communities at the forest level is that epiphyte biomass or abundance and diversity increase during forest succession (Lesica *et al.* 1991, Benavides *et al.* 2006, Hilmo *et al.* 2009, Woods & DeWalt 2013). This pattern indicates that more species and individuals are added to the forest as the forest ages even if the area of forest examined remains the same. Research on epiphyte distributions and diversity in secondary and primary forests may be explained by the species accumulation model. In tropical forests, most early colonizing epiphyte species that dominate secondary forests are still found in old-growth forest. In montane secondary and primary rainforests in Venezuela, for example, only 13 of the 191 epiphyte species were found only in secondary forest (Barthlott *et al.* 2001) and in moist forests in Panama only 4 of the 27 epiphyte species were found only in secondary forests (Woods &

DeWalt 2013). The early colonizing epiphytes may be found on pioneer or mid-successional trees in old-growth forest or they may be found in the younger portions of old-growth trees (as suggested by the species accumulation model) or both. To disentangle whether early colonizing epiphytes that dominate secondary forests are colonizing pioneer or mid-successional trees in old-growth forest or young branches in old-growth trees, a study examining changes in epiphyte communities where tree successional stage is controlled, such as in plantations must be examined. Hilmo *et al.* (2009) found early colonizing species of epiphytic lichen in *Picea abies* forest plantations <20 yr old to also be in forest plantations >85 yr old with many species restricted to old forest. Similarly, fast colonizing lichen species were found in young managed forest stands as well as in old managed forest stands with old forest specific lichen species suggesting little competitive exclusion of early colonizing species by late colonizing species (Uliczka & Angelstam 1999). These studies support the predictions of the species accumulation model because early colonizing epiphytes were still found in old-growth plantation forests that did not have trees of varying successional stages. The predictions of the species accumulation model of epiphyte succession, such as a high degree of nestedness between small and large trees and increasing similarity of epiphyte species composition of small trees to large trees with increasing tree size as species are added and not replaced at the scale of the entire crown, will need to be tested in different temperate and tropical forests to assess the general applicability of this model. An appropriate test of the model would be comparing the distribution of epiphytes within trees of varying size of a single tree species that can be properly aged in various forest types as well as in plantations.

CONCLUSION

Primary ecological succession for terrestrial species follows a replacement model, whereby early colonizing species are replaced by mid and late colonizing species. Succession in epiphyte communities on *V. koschnyi* trees adheres to this model at the scale of a particular zone within a tree (*e.g.*, inner crown) as early colonizing species are replaced by mid and late colonizing species in the oldest parts of the tree crown. However, at the scale of the entire tree crown, epiphyte succession follows the species accumulation model as more microhabitats are formed in tree crowns as they increase in size that enable the accumulation of species without replacement. This pattern is not simply due to an increase in area because the newly formed branches in the largest trees are colonized not only by epiphyte species that colonize the smallest trees, such as creeping ferns but also by epiphyte species that only colonize bare branches in the largest trees, such as atmospheric bromeliads. While this study was confined to one tree species, the species accumulation model is likely broadly applicable as many studies have found results that support the predictions of the model, such as in increase in epiphyte diversity with tree size (McCune 1993, Zotz & Vollrath 2003, Woods *et al.* 2015), and the inner crown of small trees being more similar in species composition to the outer crowns of large trees than the inner crowns of

large trees (Sporn *et al.* 2010). However, more studies done on more tree species are needed to test the general applicability of this model. The species accumulation model might explain why the widely documented relationship of epiphyte diversity with tree size is not unimodal as would be predicted by other models of succession with low disturbance regimes where a climax community is reached (Clements 1916, 1936; Cooper 1923, Connell 1978). This study highlights the importance of heterogeneity in substrate ages in structuring epiphyte communities as well as the importance of large old growth trees for conserving epiphyte diversity given that many of the late colonizing species appear to be specialized to the oldest parts of the tree crown.

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DATA AVAILABILITY

Data deposited in the Dryad Repository: <http://doi.org/10.5061/dryad.428q1> (Woods 2017).

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