Vascular Epiphyte Communities in the Inner-Crown of *Hyeronima alchorneoides* and *Lecythis ampla* at La Selva Biological Station, Costa Rica

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ABSTRACT

The community composition and percent cover of vascular epiphytes were examined in relation to photosynthetic photon flux density (PFD), temperature, vapor pressure, and tree characteristics in the inner-crown of two emergent tree species, *Hyeronima alchorneoides* and *Lecythis ampla,* at La Selva Biological Station, Costa Rica. A total of 53 species were found in a total sampled branch area of 32 m^2 in eight trees—four trees per species. Community composition varied both among individuals of the same tree species and between tree species. However, percent cover patterns of vascular epiphytes were significantly different between the two tree species; *Hyeronima* had a significantly greater percent cover of epiphytes than *Lecythis*. The higher percent light transmittance as well as lower humidity in *Lecythis* are likely causes of its lower percent cover of epiphytes.

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

Key words: epiphyte community; forest canopy; *Hyeronima*; *Lecythis;* species richness.

THE RAIN FOREST CANOPY IS HOST TO A LARGE PROPORTION OF THE BIODIVERSITY in tropical wet forests (Ellwood & Foster 2004), including 25 percent of the vascular plant flora in tropical systems (Nieder *et al.* 2001). Yet the factors that drive the distribution of epiphytes within tree crowns remain unclear. Of specific interest is the degree to which tree characteristics, microclimate and chance, determine epiphyte species distributions. There are often distinct plant assemblages distributed throughout the canopy (Pittendrigh 1948; Cardelús & Watkins 1998; Hietz & Briones 1998, 2001; Watkins *et al.* 2006), with light-demanding, drought tolerant species in the outer-crown and shade-adapted and less drought tolerant species in the inner-crown (Pittendrigh 1948). The distribution of vascular epiphytes may be influenced by tree characteristics such as branch diameter (Zimmerman & Olmstead 1992, Hietz & Ausserer 1998), branch height (Zotz 1997, Lyons *et al.* 2000, McCune *et al.* 2000), bark water holding capacity (Callaway *et al.* 2001), and bark mineral content (Hauck *et al.* 2001).

Microclimate has been invoked as a possible determinant of epiphyte species distributions (Pittendrigh 1948). Microenvironmental gradients exist from the trunk to the twig, with microsites in the exposed outer crown often brighter and drier than the inner-crown with a progression of environments in-between (Thompson & Hinckley 1977, Freiberg 1996). However, little quantitative work has been done to link epiphyte communities with microclimate. Tree characteristics such as leaf phenology, leaf size, and the arrangement of branches act in concert to shape within canopy microclimate, potentially making microclimate a host tree species-specific character. This in turn may directly affect epiphyte species distributions (Cardelús & Chazdon 2005).

Although several studies have shown that there are distinct vertical and horizontal epiphyte communities or assemblages at the spatial scale of the entire canopy, it is unclear whether communities within a given canopy zone are stochastically organized or whether microclimate and tree characteristics play a role in their grouping. In this study, I explore the species richness and percent cover of epiphytes in the inner-crown within two tree species with known differences in microclimate and tree characteristics (Cardelús & Chazdon 2005). The inner-crown is considered the oldest and most stable part of the crown and is thought to be the zone that is latest in succession (Freiberg 1996, Rudolph *et al.* 1998). As a result, I would predict that the most stable plant community would be found in the inner-crown.

In previous work examining the microenvironment of the inner-crown, Cardelús and Chazdon (2005) found that there was no microclimatic gradient within the first four meters of the inner-crown. Yet, the study did find that microenvironment varied significantly among the two tree species studied, particularly with respect to light transmittance and humidity on major limbs. *Hyeronima alchorneoides* (an evergreen species) averaged 5.8 percent light transmittance and 93 percent relative humidity year-round while *Lecythis ampla* (deciduous for 2 mo during the wet season) averaged 12.3 percent light transmittance and 86.5 percent relative humidity. The significant differences among microenvironments between the two tree species may lead to differences in epiphyte species composition or percent cover.

METHODS

STUDY SITE.—Field work was conducted in the Atlantic lowlands of northeastern Costa Rica at La Selva Biological Station (Sarapiquí, Heredia Province). La Selva receives 4000 mm/year of rainfall and is classified as a Tropical Wet Forest under the Holdridge system

(Hartshorn & Peralta 1988). Rainfall occurs throughout the year with a noticeable drier period from January to April and from September to October, with no month receiving less than 100 mm (McDade *et al.* 1994).

STUDY TREE SPECIES.—Two emergent canopy tree species were chosen for this study: *Hyeronima alchorneoides* Allemao (Euphorbiaceae) and *Lecythis ampla* Miers (Lecythidaceae). Both canopy trees can grow large, with main branch diameters >50 cm and variable branch angles of 40–90° from the vertical. The main differences between *Hyeronima* and *Lecythis* are leaf size, display, phenology, and bark texture. *Hyeronima* leaves are evergreen, simple, large (278 cm^2), and whorled with orthotropic (vertical), whorled branches, producing a multilayered effect (Horn 1971, Menalled & Kelty 2001). *Hyeronima* bark is fibrous, spongy and absorbs much water when wetted while *Lecythis* bark is rough, longitudinally fissured (1 cm) and absorbs little water when wetted. *Lecythis* has small (20 cm^2), simple leaves, which are displayed plagiotropically (in all directions diverting) on orthotropic branches to produce a monolayered effect (Horn 1971). *Lecythis* is deciduous for 2 mo at the beginning of the 9-mo wet season. The onset of the deciduous phase of *Lecythis* is rapid with all leaves shed in the course of 48 h (pers. obs.).

SAMPLING AND MICROCLIMATE MEASUREMENTS.—I sampled the two lowest branches (average height above the ground ∼22 m) in the inner-crown of four individuals of each *Hyeronima* and *Lecythis* where vascular epiphyte composition and distribution were recorded. Measurements were done, *sensu* Cardelús and Chazdon (2005), *in situ* using single rope climbing techniques (Perry 1978). On each of the sampled branches, a transect was established, measuring 4.0 × 0.5 m. The transect was subdivided into eight 0.5 × 0.5 m quadrats. A total of 4.0 m^2 of branch space was studied per individual for a total branch area of 32 m^2. Microclimatic measurements of photosynthetic PFD, temperature (°C), and vapor pressure were measured approximately 7 cm above the branch at the center of each 0.5 × 0.5 m quadrat. Branch characteristics including angle, azimuth, height, diameter, and soil depth were also recorded.

To measure percent cover of each species within each quadrat, quadrats were further divided into sixteen 12.5 × 12.5 cm subplots. Subplots were used to improve accuracy in assessing percent cover of small individuals such as members of the Hymenophyllaceae. Percent cover of each epiphyte was scored to the nearest five percent within each subplot. For each species, a mean percent cover value was calculated. Total epiphyte percent cover per quadrat was then calculated as the sum of all species percent covers per quadrat. Total epiphyte cover within each quadrat was calculated by summing values for all species. To compare relative percent cover of epiphytes between *Hyeronima* and *Lecythis*, I summed the percent cover of each taxon within each host tree species separately and divided by the total taxon percent cover sampled in both tree species.

Identification of plant species was done non-destructively to maintain integrity of quadrats and, when possible, specimens directly outside of quadrat were collected for identification. Juveniles were not distinguished from adults when recorded. Collections were pressed, dried, and identified at the La Selva Biological Station

herbarium or in San Jose at the Instituto Nacional de Biodiversidad herbarium (INBio) or at the Museo Nacional de Costa Rica herbarium (MNCR). Voucher specimens were deposited at INBio and MNCR. All species composition and distribution data were input into the relational database Biota (Colwell 1996–2000).

DATA ANALYSIS.—To estimate the species richness from the samples, two non-parametric incidence coverage-based estimators were computed as samples were accumulated: ICE, incidence-based estimator, and Chao2 (Chazdon *et al.* 1998). The difference in epiphyte species richness between tree species was tested using rarefaction curves and confidence intervals generated in EstimateS (Colwell 2005). To determine differences in vascular epiphyte cover between *Hyeronima* and *Lecythis,* as well as differences in cover of certain groups within the two tree species, a *t*-test was run on the percent cover within each tree ($N = 4$ trees/species) (SAS 1999). Using the species richness data, I calculated the Chao-Sorensen Similarity Index (Chao *et al.* 2005, Colwell 2005) to determine the overall floristic similarity among individuals of a species and between tree species.

Direct gradient analyses with Canonical Correspondence Analysis (CCA; Digby & Kempton 1987, Jongman *et al.* 1997) were run on the epiphyte species composition and the microenvironmental (dry and wet season and leafless phase percent transmittance, temperature and vapor pressure) and tree characteristics (angle, azimuth, soil depth diameter, height, and distance from trunk) data per quadrat for all individuals of both tree species. Environmental variables were standardized to data taken simultaneously at the micrometeorological station at La Selva Biological Station to eliminate daily variations of weather (Cardelús & Chazdon 2005). All 16 variables were used when all epiphyte species in both tree species were analyzed. *Hyeronima* does not have a deciduous phase, but the deciduous phase of *Lecythis* occurs in the wet season (lasting 2 mo of the 9-mo wet season). To adjust for this asymmetry, wet season data of *Hyeronima* were duplicated for the deciduous season data for *Hyeronima* in the environmental matrix. Two CCA analyses were performed: one on all observed epiphyte species on *Hyeronima* and *Lecythis* and another only on species occurring on both *Hyeronima* and *Lecythis* to determine if there were particular communities that formed within a set of generalist species. All species matrices were composed of species percent cover that were arcsine square root transformed for percent cover data (McCune & Grace 2002).

All non-parametric analyses were run using PC-ORD (McCune & Mefford 1999). CCA row and column scores were standardized by centering and normalizing, ordinations were optimized by species, and *post-hoc* Monte Carlo and Pearson Correlation tests were performed. The Monte Carlo test was run with a random seed number 100 times. Eigenvalues > 0.50 indicated a good separation of species (Jongman *et al.* 1997). All parametric analyses were done with SAS 8.2 (1999).

RESULTS

SPECIES RICHNESS AND PERCENT COVER.—I observed a total of 53 vascular epiphyte species in the eight trees examined with a range of 18–21 vascular epiphyte species within the inner-crown study

area of each tree (4.0 m^2). In the *Hyeronima* transects, 1474 individuals were examined from 43 species, 25 genera, and 16 families, while in the *Lecythis* transects 941 individuals were examined from 38 species, 22 genera, and 16 families. Seventeen of the species were found only in *Hyeronima* inner-crowns, while ten species were found only in *Lecythis*. The families with the greatest number of species were the Araceae with 19 spp., Bromeliaceae with 6 spp., and Elaphoglossaceae with 5 spp. (Table 1). If all fern species are lumped, they represent the second most species-rich group with 15 species. The rank order of groups changed when epiphyte cover was examined. Four of the five most abundant groups were ferns with Araceae representing the third greatest percent cover in all plots (Table 1). When all of the ferns were grouped together, they represented 64 percent of the total percent cover followed by the Araceae with 19 percent and the Cyclanthaceae with six percent (Table 1).

Average epiphyte cover within *Hyeronima* individuals was almost twice that of *Lecythis* quadrats, 51.3 percent (± 7.5 SE) and 27.2 percent (± 2.1 SE), respectively. Average relative epiphyte cover per individual host tree was significantly higher in *Hyeronima* (15.3 ± 3.1% SE) than *Lecythis* (9.7 ± 1.0% SE; $t = 2.16$, $P = 0.037$), with 61 percent total epiphyte cover in *Hyeronima* inner-crowns compared to 39 percent epiphyte cover in *Lecythis* (Table 1). The ferns averaged twice the relative percent cover in *Hyeronima* than *Lecythis* individuals (10.5 ± 0.14 SE vs. 5.1 ± 0.93 SE);
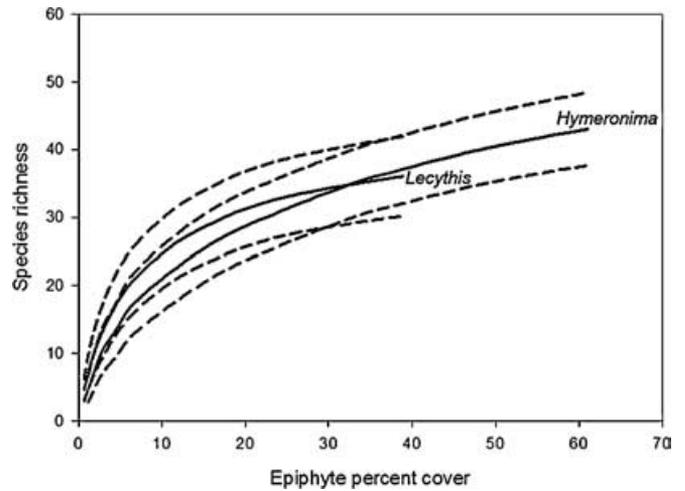
FIGURE 1.   Sample-based rarefaction curves and 95% CI for epiphyte species found in four individuals each of *Hyeronima* and *Lecythis* at La Selva Biological Station, Costa Rica.

however, this difference was only marginally statistically different ($t = 1.64$, $P = 0.08$).

Chao2 and ICE species richness estimators estimated a higher than observed richness for both tree species combined, 77 and 73 species, respectively. Species richness between the two tree species, corrected for density, was not significantly different as seen by the overlap of confidence intervals in their rarefaction curves (Fig. 1). Similarity of epiphytes among individuals within a tree species was lower than that between species as demonstrated by the Chao-Sørensen incidence-based index (Chao *et al.* 2005; Table 2).

TABLE 1.   *Total number of epiphyte species found within both* Hyeronima *and* Lecythis *inner-crowns as well as the total number found only within each tree species; total percent cover of each family and the relative percent cover of each family found only within* Hyeronima *and* Lecythis.

Family	Total species	*Hyeronima* species	*Lecythis* species	Total % cover	*Hyeronima* % cover	*Lecythis* % cover
Araceae	19	13	11	19	10	8
Bromeliaceae	6	5	5	5	2	3
Elaphoglossaceae	5	5	5	26	17	9
Hymenophyllaceae	3	3	2	18	8	10
Cactaceae	3	3	1	1	0	1
Orchidaceae	3	2	2	0.7	0	0
Vittariaceae	2	1	2	6	4	2
Polypodiaceae	2	2	1	2	2	0
Clusiaceae	2	2	2	1	0	1
Dryopteridaceae	1	1	1	12	12	0
Cyclanthaceae	1	1	1	6	3	3
Gesneriaceae	1	1	1	2	2	0
Ericaceae	1	1	1	0.8	0	0
Aspleniaceae	1	1	1	0.1	0	0
Grammatidaceae	1	1	1	0.1	0	0
Melastomaceae	1	0	1	0	0	0
Piperaceae	1	1	0	0	0	0
Total	53	43	38	100	61	39
Pteridophytes	15	14	13	64	43	21

TABLE 2.   *(a) Chao-Sorensen Estimate of similarity between individuals of* Hyeronima alchorneoides *lower left, (b) between individuals of* Lecythis ampla, *and (c) between tree species. a–b upper right, number of species shared between individuals. Bold numbers are the number of species found in each individual.*

a.	*Hyeronima1*	*Hyeronima2*	*Hyeronima3*	*Hyeronima4*
Hyeronima1	**11**	8	5	6
Hyeronima2	0.53	**19**	10	8
Hyeronima3	0.32	0.51	**20**	6
Hyeronima4	0.39	0.41	0.3	**20**

b.	*Lecythis1*	*Lecythis2*	*Lecythis3*	*Lecythis4*
Lecythis1	**20**	12	10	10
Lecythis2	0.51	**22**	9	10
Lecythis3	0.65	0.39	**17**	7
Lecythis4	0.5	0.54	0.36	**15**

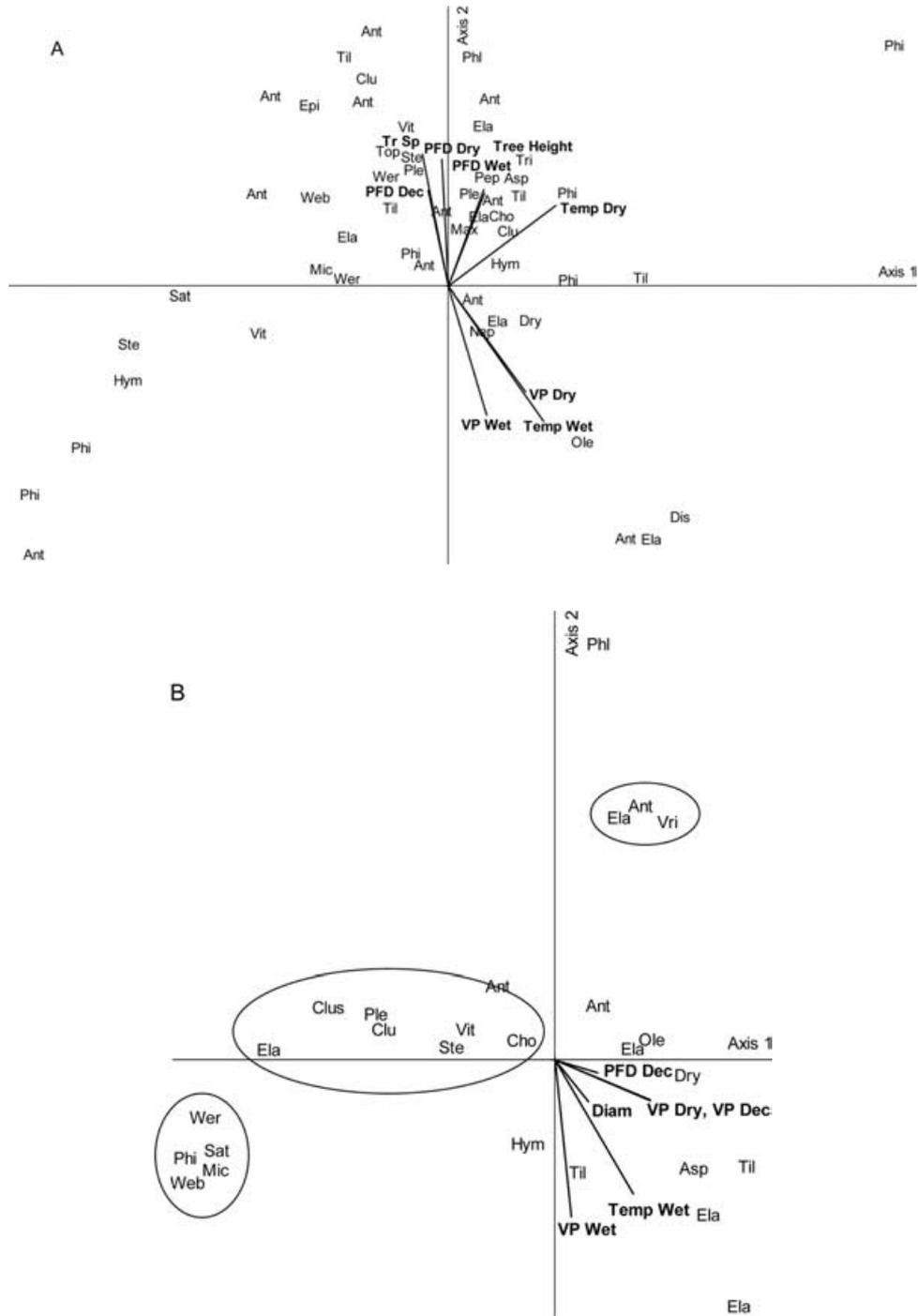| c.	*Hyeronima*
Lecythis	0.64

FIGURE 2.   Bi-plot of canonical correspondence analysis for two vascular epiphyte species datasets: A. all species found in both *Hyeronima* and *Lecythis* inner-crowns (N = 53), B. shared species between *Hyeronima* and *Lecythis* (N = 27). Each three letter code represents a genus which in turn represents a species. The diagonal lines indicate the microclimatic variable or branch characteristic associated with axis 1 and axis 2. The circled genera show some association with the microclimate and tree characteristics. The epiphyte family and associated genera are: Araceae: *Anthurium, Philodendron, Stenospermation*; Aspleniaceae: *Asplenium;* Bromeliaceae: *Tillandsia, Werauhia*; Cactaceae: *Disocactus, Epiphyllum, Weberocereus;* Clusiaceae: *Clusia, Clusiella*; Cyclanthaceae: *Chorigyne;* Dryopteridaceae: *Oleandra;* Elaphoglossaceae: *Elaphoglossum*; Ericaceae: *Satyria;* Gesneriaceae: *Drymonia;* Grammatidaceae: *Microgramma;* Hymenophyllaceae: *Hymenophyllum, Trichomanes;* Melastomaceae: *Topobea;* Orchidaceae: *Maxillaria, Pleurothalis*; Piperaceae: *Peperomia*; Polypodiaceae: *Nephrolepis, Phlebodium;* Vittariaceae: *Vittaria.*

EPIPHYTE DISTRIBUTION.—The CCA for all 53 epiphyte species with all 16 environmental and tree characteristic variables accounted for 13.8 percent of the variance. The Pearson Correlation test, which examines the relationship between the species scores and the environmental matrix scores, was high for axes 1–3: 0.935, 0.906, and 0.876, respectively. Monte-Carlo permutation tests were significant for all axes ($P < 0.01$). Both axis 1 and 2 had a good separation of species (Eigenvalue > 0.5). Axis 1 was correlated positively with dry season vapor pressure and wet and dry season temperature while negatively correlated with distance along branch. Although some minor associations of species were apparent in ordination space, these associations were in the periphery/corner of the axes and therefore likely an artifact of rarity and not true groupings (Fig. 2A) (Jongman *et al.* 1997).

The CCA for only shared epiphyte species between *Hyeronima* and *Lecythis* explained more of the total variance (19.8%) than with all species combined (13.8%). The Pearson Correlation was high for all three axes: 0.919, 0.909, and 0.826. The Monte Carlo Permutation Tests showed significance for all axes (axis 1 and 2, $P = < 0.001$; axis 3, $P = 0.02$). Axis 1, the only axis with an Eigenvalue > 0.50, was positively correlated with dry and wet season temperature, dry and leafless wet season vapor pressure, and quadrat height. There was some association among species in bi-plots of axis 1 and axis 2 (Fig. 2B). The three associations among species did not appear to fall along morphological or taxonomic lines. The group associated strongly with axis 2 (Fig. 2B) was composed of an erect aroid (*Anthurium ramonense*), a tank bromeliad (*Werauhia kupperiana*) and an erect, succulent fern (*Elaphoglossum* sp. 2).

DISCUSSION

The overwhelming diversity of vascular epiphytes in tropical rain forests is a remarkable phenomenon (Madison 1977; Gentry & Dodson 1987a, 1987b; Nieder *et al.* 2001). In this study, a total branch area of 32 m^2 maintained 53 species of vascular epiphytes— 12 percent of the epiphytes found at La Selva Biological Station. About 20 epiphyte species per tree were found in the 4 m^2 sampled on major limbs. The high species richness found within the inner-crown did not show distinct communities or assemblages for either study tree species. The dominance in species richness of aroids, ferns, bromeliads, and orchids in this study follows a common pattern reported in other neotropical epiphyte diversity studies (Madison 1977, Gentry & Dodson 1987a, Wolf 1994, Cardelús *et al.* 2006). However, orchid species richness is often the highest in other studies while it was the lowest of the dominant groups in this study (Table 1). The limitation of this study to the inner-crown likely contributes to the lower diversity of orchids compared to other studies because orchids appear to be more common in the outer-crown than the inner-crown at La Selva Biological Station (pers. obs.).

The percent cover differences between tree species are probably due to differences in inner-crown microclimate. *Hyeronima* had a more homogeneous inner-crown with respect to PFD, temperature,

and vapor pressure compared to *Lecythis* (Cardelús & Chazdon 2005). *Hyeronima* had significantly lower percent light transmittance and less variable vapor pressure, humidity, and temperature than *Lecythis*, in part due to *Lecythis'* leaflessness in the wet season. While there was complete species overlap of epiphytes between the two tree species, these microclimatic differences could result in the significant differences in epiphyte cover seen between tree species. Ferns might be more abundant in *Hyeronima* than *Lecythis* (43% vs. 21%, Table 1), because the interiors of *Hyeronima* crowns were more humid. The higher percent light transmittance and lower humidity in *Lecythis* provides a hotter and drier habitat and hosts a greater cover of more drought tolerant species such as the Bromeliaceae and Cactaceae, although not necessarily more species of these groups. The differences in microclimate within the inner-crown between tree species do not appear great enough to completely exclude epiphyte groups from either tree species, but they appear sufficiently great to cause differences in epiphyte cover between tree species.

The sampled epiphyte stands in the inner-crown of *Hyeronima* and *Lecythis* at La Selva reveal extensive overlap of epiphyte species among sampled trees and a lack of predictable community structure based on microclimate and tree characteristics. At the spatial scale of the entire canopy, more community structure may be apparent (Kernan & Fowler 1995, Cardelús & Watkins 1998, Hietz & Briones 1998); however, at the small spatial scale of the inner-crown, chance seems to govern community dynamics.

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LITERATURE CITED

CALLAWAY, R. M., K. O. REINHART, S. C. TUCKER, AND S. C. PENNINGS. 2001. Effects of epiphytic lichens on host preference of the vascular epiphyte *Tillandsia usneoides*. Oikos 94: 433–441.

CARDELÚS, C., AND R. L. CHAZDON. 2005. Inner-crown microenvironments of two emergent tree species in a lowland wet forest. Biotropica 37: 238–244.

CARDELÚS, C., AND J. E. WATKINS JR. 1998. Epiphytic fern diversity and stratification on trunks of *Hyeronima alchorneoides* (Euphorbiaceae) at La Selva Biological Station, Costa Rica. Selbyana 19: 270.

CARDELÚS, C., R. K. COLWELL, AND J. WATKINS. 2006. Vascular epiphyte distribution patterns: Explaining the mid-elevation richness peak. J. Ecol. 94: 144–156.

CHAO, A., R. L. CHAZDON, R. K. COLWELL, AND T.- J. SHEN. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol. Lett. 8: 148–159.

CHAZDON, R. L., R. K. COLWELL, J. S. DENSLOW, AND M. R. GUARIGUATA. 1998. Statistical estimation of species richness of woody regeneration in primary and secondary rainforests of NE Costa Rica. *In* F. Dallmeier and J. Comisky (Eds.). Forest biodiversity in North, Central, and South America and the Caribbean: Research and monitoring, pp. 285–309. Parthenon Press, Paris, France.

COLWELL, R. K. 1996–2000. Biota: The biodiversity database manager. Sinauer Associates. Sunderland, Massachusetts.

COLWELL, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates. [Persistent URL: http://purl.oclc.org/estimates.].

DIGBY, P. G. N., AND R. A. KEMPTON. 1987. Multivariate analysis of ecological communities. Chapman Hall, London, UK.

ELLWOOD, M. D. F., AND W. A. FOSTER. 2004. Doubling the estimate of invertebrate biomass in a rainforest canopy. Nature 429: 549–551.

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

GENTRY, A. H., AND C. H. DODSON. 1987a. Diversity and biogeography of neotropical vascular epiphytes. Ann. Mo. Bot. Gard. 74: 205–233.

GENTRY, A. H., AND C. DODSON. 1987b. Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19: 149–156.

HARTSHORN, G., AND R. PERALTA. 1988. Preliminary description of primary forests along the La Selva-Volcán Barva altitudinal transect, Costa Rica. *In* F. Almeda and C. M. Pringle (Eds.). Tropical rainforests: Diversity and conservation, pp. 281–306. California Academy of Sciences and Pacific Division, American Association for the Advancement of Science, San Francisco, California.

HAUCK, M., R. JUNG, AND M. RUNGE. 2001. Relevance of element content of bark for the distribution of epiphytic lichens in a montane spruce forest affected by forest dieback. Environ. Pollut. 112: 221–227.

HIETZ, P., AND J. AUSSERER. 1998. Population dynamics and growth of epiphytes in a humid montane forest in Mexico. Selbyana 19: 281.

HIETZ, P., AND O. BRIONES. 1998. Correlation between water relations and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. Oecologia 114: 305–316.

HIETZ, P., AND O. BRIONES. 2001. Photosynthesis, chlorophyll fluorescence and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. Plant Biol. 3: 279–287.

HORN, H. 1971. The adaptive geometry of trees. Princeton University Press, Princeton, New Jersey.

JONGMAN, R. H. G., C. J. F. T. BRAAK, AND O. F. R. V. TONGEREN. (Eds.). 1997. Data analysis in community and landscape ecology. 299. Cambridge University Press, Cambridge, UK.

KERNAN, C., AND N. FOWLER. 1995. Differential substrate use by epiphytes in Corcovado National Park, Costa Rica: A source guild structure. J. Ecol. 83: 65–73.

LYONS, B., N. M. NADKARNI, AND M. P. NORTH. 2000. Spatial distribution and succession of epiphytes on *Tsuga heterophylla* (western hemlock) in an old-growth Douglas-fir forest. Can. J. Bot. 78: 957–968.

MADISON, M. 1977. Vascular epiphytes: Their systematic occurrence and salient features. Selbyana 2: 1–13.

MCCUNE, B., AND J. B. GRACE. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

MCCUNE, B., AND M. J. MEFFORD. 1999. PC-ORD. Multivariate analysis of ecological data. MjM Software Design. Gleneden Beach, Oregon.

MCCUNE, B., R. ROSENTRETER, M. PONZETTI JEANNE, AND C. SHAW DAVID. 2000. Epiphyte habitats in an old conifer forest in Western Washington, U.S.A. Bryologist 103: 417–427.

MCDADE, L. A., K. S. BAWA, H. A. HESPENHEIDE, AND G. S. HARTSHORN. (Eds.). 1994. La Selva: Ecology and natural history of a neotropical rain forest. Chicago University Press, Chicago, Illinois.

MENALLED, F. D., AND M. J. KELTY. 2001. Crown structure and biomass allocation strategies of three juvenile tropical tree species. Plant Ecol. 152: 1–11.

NIEDER, J., J. PROSPERÍ, AND G. MICHALOUD. 2001. Epiphytes and their contribution to canopy diversity. Plant Ecol. 153: 51–63.

PERRY, D. R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10: 155–157.

PITTENDRIGH, C. S. 1948. The bromeliad-*Anopheles*-malaria complex in Trinidad. I-The bromeliad flora. Evolution 2: 58–89.

RUDOLPH, D., G. RAUER, J. NIEDER, AND W. BARTHLOTT. 1998. Distributional patterns of epiphytes in the canopy and phorophyte characteristics in a Western Andean rain forest in Western Ecuador. Selbyana 19: 27–33.

SAS. 1999. The SAS system for Windows. SAS Institute Inc. Cary, North Carolina.

THOMPSON, D. R., AND T. M. HINCKLEY. 1977. Effect of vertical and temporal variations in stand microclimate and soil moisture on water status of several species in an oak-hickory forest. Am. Midl. Nat. 97: 373–380.

WATKINS, JR., J. E., C. L. CARDELÚS, AND R. K. COLWELL. 2006. Species richness and distribution of ferns along an elevational gradient in Costa Rica. Am. J. Bot. 93: 73–83.

WOLF, J. H. D. 1994. Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. Vegetatio 112: 15–28.

ZIMMERMAN, J. K., AND I. C. OLMSTEAD. 1992. Host tree utilization by vascular epiphytes in a seasonally inundated forest (Tintal) in Mexico. Biotropica 24: 402–407.

ZOTZ, G. 1997. Substrate use of three epiphytic bromeliads. Ecography 20: 264–270.