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Epiphyte Biodiversity in the Coffee Agricultural Matrix: Canopy Stratification and Distance from Forest Fragments

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Abstract: *Quality of the agricultural matrix profoundly affects biodiversity and dispersal in agricultural areas. Vegetatively complex coffee agroecosystems maintain species richness at larger distances from the forest. Epiphytes colonize canopy trees and provide resources for birds and insects and thus effects of agricultural production on epiphytes may affect other species. We compared diversity, composition, and vertical stratification of epiphytes in a forest fragment and in two coffee farms differing in management intensity in southern Mexico. We also examined spatial distribution of epiphytes with respect to the forest fragment to examine quality of the two agricultural matrix types for epiphyte conservation. We sampled vascular epiphytes in a forest fragment, a shade polyculture farm, and a shade monoculture farm at 100 m, 200 m, and 400 m from the forest. Epiphyte and orchid richness was greater in the forest than in the monoculture but richness was similar in the forest and polyculture farm. Epiphyte species composition differed with habitat type, but not with distance from the forest. In the forest, epiphytes were distributed throughout tree canopies, but in the farms, epiphytes were primarily found on trunks and larger branches. Epiphyte richness and species similarity to forest species declined with distance from the forest fragment in the monoculture, but richness and similarity to forest species did not decline with distance from forest in the polyculture. This suggests polyculture coffee has greater conservation value. In contrast, monoculture coffee is likely a sink habitat for epiphytes dispersing from forests into coffee. Coffee farms differ from forests in terms of the habitat they provide and species composition, thus protecting forest fragments is essential for epiphyte conservation. Nonetheless, in agricultural landscapes, vegetatively complex coffee farms may contribute to conservation of epiphytes more than other agricultural land uses.*

Keywords: agricultural matrix quality, bromeliad, Chiapas, coffee, dispersal, distance from forest, fern, Mexico, orchid

Biodiversidad de Epífitas en la Matriz Agrícola de Café: Estratificación del Dosel y Distancia a los Fragmentos de Bosque

Resumen: *La calidad de la matriz agrícola afecta profundamente a la biodiversidad y la dispersión en áreas agrícolas. Los agroecosistemas cafetaleros con una vegetación compleja mantienen riqueza de especies a mayores distancias del bosque. Las epífitas colonizan el dosel de árboles y proporcionan recursos para aves e insectos y, por lo tanto, los efectos de la producción agrícola sobre las epífitas pueden afectar a otras especies. Comparamos la diversidad, composición, diversidad y estratificación vertical de epífitas en un fragmento de bosque y en dos fincas cafetaleras con diferente intensidad de manejo en el sur de México. También examinamos la distribución espacial de epífitas respecto al fragmento de bosque para evaluar la calidad de los dos tipos de matriz para la conservación de epífitas. Muestreamos las epífitas vasculares en un fragmento de bosque, una finca con sombra policultivo y una con sombre monocultivo a 100 m, 200 m y 400 m del*

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bosque. La riqueza de epífitas y orquídeas fue mayor en el bosque que en el bosque que el monocultivo pero la riqueza fue similar en el bosque y el policultivo. La composición de especies de epífitas difirió con el tipo de hábitat, pero no con la distancia al bosque. En el bosque, las epífitas se distribuyeron en el dosel de los árboles, pero en las fincas se distribuyeron principalmente sobre los troncos y ramas mayores. La riqueza y similitud de especies de epífitas disminuyeron con la distancia al fragmento de bosque en el monocultivo, pero la riqueza y la similitud con las especies de bosque no declinaron con la distancia al bosque en el policultivo. Esto sugiere que el café policultivo tiene un mayor valor de conservación. En contraste, el café monocultivo probablemente es un hábitat vertedero para epífitas en dispersión desde los bosques. Las fincas cafetaleras difieren de los bosques en términos del hábitat que proporcionan y la composición de especies, por lo tanto la protección de fragmentos de bosque es esencial para la conservación de epífitas. Sin embargo, las fincas cafetaleras con vegetación compleja pueden contribuir a la conservación de epífitas mejor que otros usos de suelo en los paisajes agrícolas.

Palabras Clave: bromelia, café, calidad de la matriz agrícola, Chiapas, dispersión, distancia del bosque, helecho, México, orquídea

Introduction

The quality of agricultural matrix has important implications for species richness, dispersal, and ecosystem services. Much recent work has compared biodiversity in different types of agricultural systems (e.g., shade and sun coffee, cacao, pasture), and results of these studies show that areas with vegetation more closely mimicking nearby forest fragments generally have higher species richness (e.g., Luck & Daily 2003; Perfecto et al. 2007; Philpott et al. 2008). Several researchers have specifically examined how diversity of animals, primarily, declines with distance from forest fragments (Ricketts et al. 2001; Klein et al. 2006), which has negative implications for ecosystem services such as pollination (Ricketts 2004). Nevertheless, high-quality agricultural matrices can, better than low-quality matrices, buffer species losses that occur in patches that are far from forest (Perfecto & Vandermeer 2002; Armbrecht & Perfecto 2003). Furthermore, high-quality agricultural matrices can increase dispersal between forest fragments (Fahrig 2001; Vandermeer & Carvajal 2001; Castellon & Sieving 2006).

Coffee was traditionally cultivated in agroecosystems with diverse and dense tree canopies, but recently, coffee production has been intensified, resulting in systems with fewer shade trees (Perfecto et al. 1996). Changes in coffee management and in microclimate conditions on farms due to reduction and elimination of shade trees have had severe negative consequences for biodiversity of birds, insects, and mammals (Perfecto et al. 2007; Philpott et al. 2008). Furthermore, biodiversity and ecosystem services in coffee farms often decline with increasing distance from forest because dispersal and survival rates are lower in the lower-quality agricultural habitats and in areas that differ substantially from natural areas in terms of canopy cover and microclimate (Perfecto & Vandermeer 2002; Ricketts 2004). Despite the recent proliferation of information on biodiversity in coffee agroecosystems, there has been little work on the diversity and abundance of plants (besides trees) within the coffee agricultural matrix relative to the distance from forest.

Epiphytes are important components of tropical forests and may be negatively affected by poor-quality agricultural matrix. Epiphytes—such as orchids, bromeliads, and ferns—are abundant in tropical forest canopies and can account for up to half of forest-plant richness (Benzing 1990). In tropical habitats, epiphytes may act as keystone species providing resources for thousands of arthropod species and habitat and nesting material for tropical birds (Benzing 1990; Nadkarni 1994; Cruz-Angón & Greenberg 2005). For example, trees in agricultural sites from which epiphytes have been experimentally removed support 90% fewer insect individuals and 22% fewer insect species than those with naturally occurring epiphytes (Cruz-Angón et al. 2009). Epiphytes naturally grow abundantly in tropical forests, but with loss of suitable habitat due to agriculture, abundance and diversity may be altered. Epiphyte diversity and abundance is lower in traditional shaded coffee farms and home gardens than in nearby forests and is positively correlated with increased tree size (Hietz 2005; Hylander & Nemomissa 2008, 2009). Nevertheless, the spatial patterns of biodiversity loss of epiphytes across coffee landscapes—namely how epiphyte abundance and diversity change with distance from forest fragments—has not been investigated. Furthermore, in natural forests, epiphytes fill the entire canopy, with different species occupying different areas of the canopy. This vertical stratification can be highly affected by changes in microclimatic conditions, which in turn affects epiphyte richness generally (e.g., Hietz-Seifert et al. 1996; Sillett & Bailey 2003).

Most epiphyte species are wind dispersed; thus, most species should be able to disperse far from sources such as forest fragments (Madison 1977; Winkler et al. 2005*a*,*b*, but see Cascante-Marín et al. 2006; Laube & Zotz 2006). If the quality of the agricultural matrix surrounding forest fragments is low, however, epiphytes may experience limited establishment and thus have lower diversity, abundance, and significant changes in species composition in such matrices. We investigated the following questions to examine, which, if any, system of coffee management provides a higher-quality agricultural matrix for epiphyte biodiversity: Is species richness and species composition of epiphytes (overall and for certain groups of epiphytes) different in forest and coffee agroecosystems that differ in management intensity? Is the vertical stratification of epiphytes different in forest and coffee habitats that differ in management intensity? Do changes in particular vegetation characteristics correlate with epiphyte richness? And does epiphyte richness, composition, and similarity between agricultural and forest species change at increasing distances from the forest in the two coffee management systems?

Methods

Field Sites and Sampling

We worked in two coffee farms and a forest fragment in the Soconusco region of Chiapas, Mexico. Finca Irlanda (15°11′N, 92°20′W) is a 280-ha organic coffee farm that maintains a high density and diversity of shade trees (approximately 25 species/ha) and roughly 50–75% canopy cover. Finca Hamburgo (15°10′N, 92°19′W) is a 300-ha farm under conventional management with lower density and diversity of trees (approximately 10 species/ha) and relatively low levels of canopy cover (10–30%). Each farm maintains approximately 1200–2500 coffee plants/ha. The two farms differ significantly in management practices and in quality of agricultural matrix (Perfecto & Vandermeer 2002). Management at Finca Irlanda is a cross between a traditional and commercial polyculture (hereafter polyculture), and Finca Hamburgo is a shade monoculture (hereafter monoculture) (Moguel & Toledo 1999; Philpott et al. 2008). In both farms the majority of trees were planted when the coffee farms were established. Between the two farms is a small, relatively linear 15-ha biological reserve (La Montañita) with some large trees (>25 m height) and patches of secondary tree growth. All habitats are between 800–1200 m asl and receive approximately 4500 mm rain/year.

We established five 400-m transects in the polyculture and six 400-m transects in the monoculture that extended perpendicularly away from the forest reserve. Along each transect, we marked three 20 × 20 m plots at 100 m, 200 m, and 400 m from the forest fragment. Each transect was separated by approximately 100 m. We also established three 20 × 20 m plots in the forest, each separated by at least 100 m.

Within each plot we counted and identified each tree, measured tree heights with a range finder (Bushnell, Overland Park, Kansas), and measured tree diameter at breast height. We recoded canopy cover at the four corners and in the center of each plot with a concave SpectroDensiometer (Forestry Suppliers, Jackson, Mississippi). We counted the number of coffee plants per plot and estimated mean coffee height. We calculated stand basal area (the sum of the cross sectional area of all trees in the plot scaled to square meter per hectare) for each plot with diameter data. Wind speed and direction may influence epiphyte diaspore dispersal (Madison 1977; Winkler et al. 2005*a*,*b*); however, we recorded no data on wind. The forest fragment, however, was in a river valley, with the two farms on either side; thus, wind through the valley likely flowed parallel to the farms. Finally, we collected hourly temperature and relative humidity data with Hobo Pro Series data loggers (Onset Computer, Bourne, Massachusetts).

We recorded the presence, location, and identity of all epiphytes in each tree in each plot. We divided trees into five vertical zones (Johansson 1974): the main trunk, from the ground up to 2 m; from 2 m above ground to the first main branch; primary branches; secondary branches; and tertiary and beyond branches. We sampled epiphytes primarily from the ground with high-quality binoculars and high-zoom photographs. We climbed some trees to confirm identifications. Epiphytes were grouped by taxa (e.g., bromeliad, orchid, fern) and assigned to morphospecies according to distinguishable traits. Juvenile bromeliads, difficult to identify to species (Hietz 2005), were identified only to genus and were not included as separate species in the analyses. Because it was difficult to distinguish individuals of some epiphytic plants, we noted presence or absence of each morphospecies within each zone on each tree as a proxy for total frequency of occurrence (Hietz 2005; Hylander & Nemomissa 2008).

Statistical Analyses

To examine differences in vegetation characteristics in the three habitat types and at different distances from the forest, we ran multivariate analyses of variance (MANOVA) with different vegetation factors as the dependent variables and habitat type (polyculture, monoculture, and forest) or distance (100 m, 200 m, and 400 m) as the independent variables. Each plot was considered a replicate. Percent cover data were arcsin transformed and other variables were log transformed.

To examine whether total epiphyte richness or richness of orchids, bromeliads, and ferns differed among habitats or at different distances from the forest, we created species accumulation curves for observed richness with EstimateS (Colwell 2005). We tested for significant differences among habitat types or distances by examining overlap in 95% confidence intervals (CIs).

To examine for differences in species composition of epiphytes we used three methods. First, we examined the fraction of epiphyte occurrences and species accounted for by the major epiphyte groups (bromeliads, orchids, ferns, and other) and compared observed values with expected values with χ^2 in Vassar Stats (http://faculty.vassar.edu/lowry/newcs.html). Second, we used nonmetric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM) with PAST (Hammer et al. 2001) to visually and statistically compare species composition of epiphytes. For both analyses we considered each plot a replicate and used the Bray-Curtis similarity index. The ANOSIM produces a global p value that indicates differences in species composition and reports pairwise comparisons between particular sites. Third, we examined species similarity between the forest and coffee plots at different distances from the forest. We computed the Bray-Curtis similarity values for each coffee-forest plot pair and examined differences in forest similarity at different distances with analysis of variance (ANOVA).

To examine the vertical distribution of epiphytes in the three habitat types, we examined differences in the fraction of occurrences and the fraction of total species occurrences in the different zones with χ^2 in Vassar Stats (http://faculty.vassar.edu/lowry/newcs.html).

Finally, we examined correlations between epiphyte richness and vegetation characteristics with multiple stepwise regressions with backward selection with each plot as a replicate. Vegetation variables included tree richness, number of tree individuals, mean percent canopy cover, mean tree height, mean coffee height, number of coffee individuals, and stand basal area. All variables, including epiphyte richness, were log transformed to meet conditions of normality (canopy cover was arcsin transformed).

Results

Site Characteristics

Vegetation characteristics differed in each habitat ($F_{10,56} = 7.71, p < 0.001$) (Table 1). There were generally higher levels of canopy cover ($F_{2,31} = 29.62, p < 0.001$) tree richness ($F_{2,31} = 16.02, p < 0.001$), number of trees ($F_{2,31} = 24.25, p < 0.001$), mean tree height ($F_{2,31} = 11.55, p < 0.001$), and stand basal area ($F_{2,31} = 33.03, p < 0.001$) in the forest than in either coffee habitat, and the two coffee habitats differed for all factors except tree richness and number of trees (Table 1). Nevertheless, there were no significant differences in vegetation at different distances from the forest within the polyculture coffee ($F_{10,14} = 0.53, p = 0.844$) or the monoculture ($F_{10,24} = 1.57, p = 0.167$). Sites also differed in relative humidity and temperature. Forests had higher relative humidity (100.4% [SE 0.09]) than polyculture (96.38 [0.19]) or monoculture coffee (92.5% [0.42]) ($F_{2,1251} = 48196, p < 0.001$). The monoculture was warmer (21.41 °C [0.16]) than polyculture (20.44 °C [0.08]) and forests (19.85 °C [0.05]) ($F_{2,2294} = 19150000, p < 0.001$).

Comparison of Epiphytes among Habitat Types

The forest had higher epiphyte species density than either coffee habitat, and species density was greater in the polyculture than in the monoculture farm (Fig. 1a). Overall, we encountered 58 species (961 occurrences) in the forest, 44 species (997 occurrences) in the polyculture, and only 26 species (355 occurrences) in the monoculture farm. Bromeliad species density was higher in the forest than in polyculture and higher in the polyculture than in the monoculture farm (Fig. 1b). Species density of orchids was similar in the forest and polyculture and lower in the monoculture farm (Fig. 1c). Fern species density was greater in the forest than in the farms but did not differ with type of farm management (Fig. 1d). For epiphyte richness, only stand basal area ($t = 8.56, p < 0.001$) was a significant factor in the best model ($r^2 = 0.696$).

There were large differences in the distribution of epiphytes in tree canopies in the forest and in the coffee agroecosystems, but the two agroecosystems had a similar vertical distribution of epiphytes. The abundance of epiphytes differed across the zones with generally fewer epiphytes on the main trunk and more epiphytes in canopy branches in the forest than in the polyculture ($\chi^2 = 575.17$, df $= 4, p < 0.001$) and monoculture ($\chi^2 = 349.52$, df $= 4, p < 0.001$), but no differences in abundance in the two coffee habitats ($\chi^2 = 1.57$, df $= 4$, $p = 0.814$) (Fig. 2a). Similarly, there were more species of epiphytes in the outer branches and fewer species on the trunk in the forest than in the polyculture ($\chi^2 = 36.62$, df $= 4, p < 0.001$) and monoculture farms ($\chi^2 = 35.79$, df $= 4$, $p < 0.001$), but there was no difference in the vertical distribution of species richness in the two coffee habitats ($\chi^2 = 2.55$, df $= 4, p = 0.636$) (Fig. 2b).

Epiphyte species composition differed among habitat types. At a broad taxonomic level, the percentage of

Table 1. Vegetation characteristics of a forest fragment and two shaded coffee farms in the Soconusco region of Chiapas, Mexico.*

Site	*Number of trees (> 10 cm circumference)*	*Number of tree species*	*Tree height (m)*	*Percent canopy cover*	*Stand basal area (m^2/ha)*
Forest	32.67 (0.33)a	14.33 (1.86)a	15.39 (1.54)a	92.30 (2.45)a	77.68 (35.1)a
Polyculture	11.93 (0.94)b	4.87 (0.44)b	11.28 (0.69)a	72.75 (5.74)b	34.1 (2.86)b
Monoculture	8.44 (0.68)b	4.0 (0.37)b	7.55 (1.19)b	30.56 (4.20)c	12.23 (1.09)c

**Numbers are means (SE). Small letters represent significant differences (*p < 0.05*) across different habitat types.*

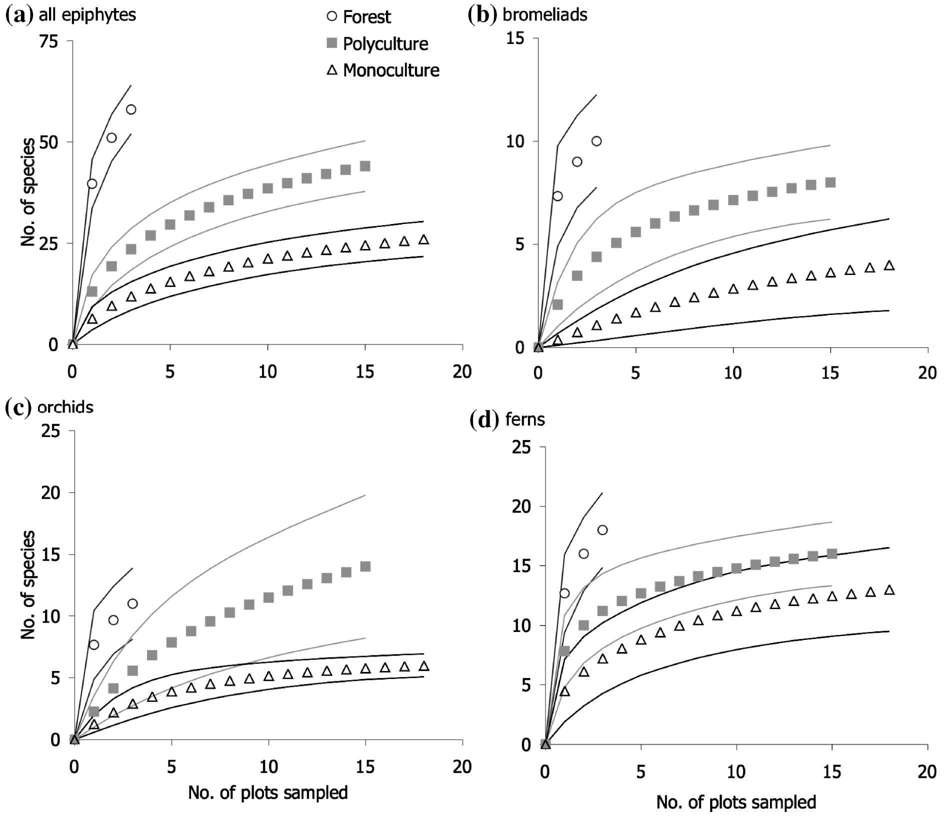

Figure 1. Species accumulation curves for observed species density of all (a) epiphytes, (b) bromeliads, (c) orchids, and (d) ferns in one forest fragment and two coffee farms with different types of management intensity (shade polyculture and monoculture) in Chiapas, Mexico. The lines show 95% confidence intervals around the site with the same colored symbol.

species and of occurrences accounted for by the four main epiphytes groups (orchids, bromeliads, ferns, and all other species) differed in the three habitats (Fig. 2c). Ferns were most abundant in the farms accounting for >82% of all occurrences, a significantly greater fraction both in the polyculture ($\chi^2 = 713.55$, df = 3, $p < 0.001$) and monoculture ($\chi^2 = 393.81$, df = 3, $p < 0.001$) than in the forest. Generally the fraction of occurrences of

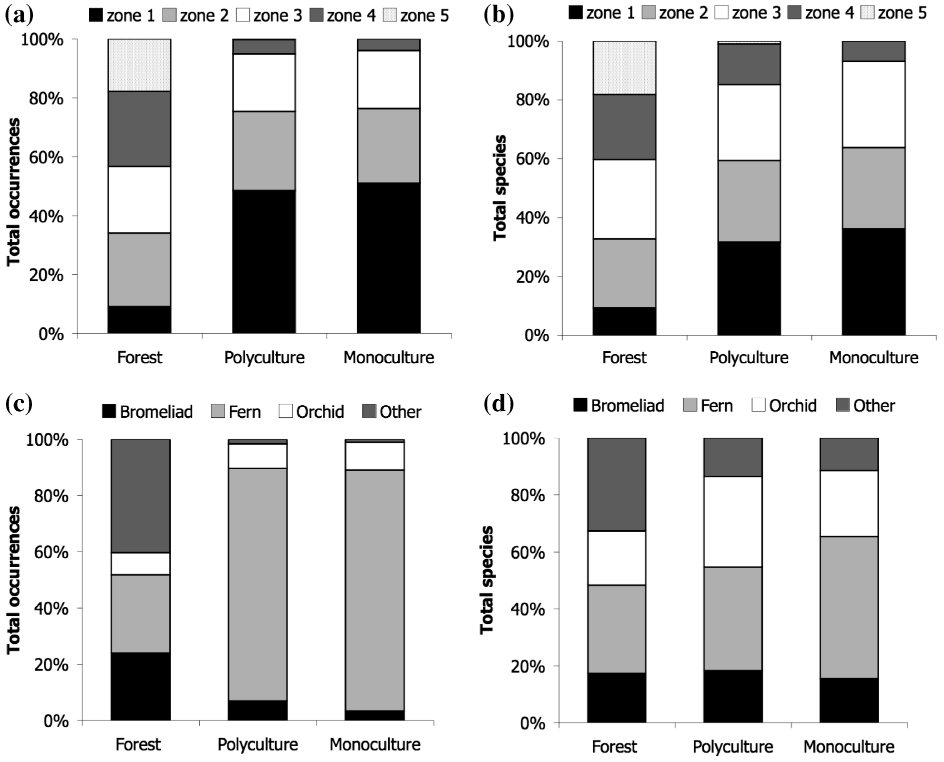

Figure 2. Composition of the epiphyte assemblage in the shade-polyculture coffee farm (Irlanda), the monoculture farm (Hamburgo), and a forest fragment in Chiapas, Mexico: (a) percentage of occurrences within each zone, (b) percentage of species found in each zone, (c) percentage of occurrences according to epiphyte type, and (d) percentage of species according to epiphyte type. Zones were as follows: 1, the main trunk, from the ground up to 2 m; 2, from 2 m above ground to the first main branch; 3, primary branches; 4, secondary branches; and 5, tertiary and beyond branches.

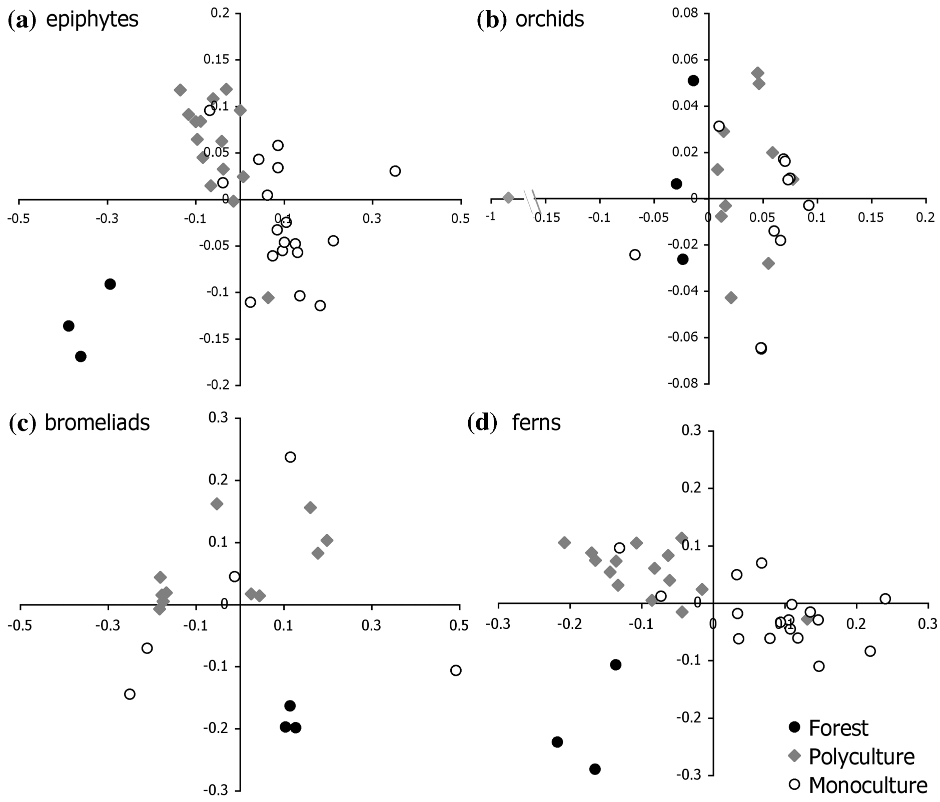

Figure 3. Results of nonmetric multidimensional scaling analysis comparing species composition of (a) all epiphytes, (b) orchids, (c) bromeliads, and (d) ferns in one forest fragment and two coffee farms managed under different intensities (shade polyculture and monoculture).

different groups in the two farms did not differ ($\chi^2 = 6.52$, df $= 3$, $p = 0.089$). There were more species in the "other" group (consisting primarily of Araceae, Cactaceae, Piperaceae) in the forest (35.9% of species encountered) than coffee farms, but these differences were not significant for the polyculture ($\chi^2 = 5.64$, df $= 3$, $p = 0.131$) or monoculture ($\chi^2 = 5.02$, df $= 3$, $p = 0.170$), and there were no differences in the percentage of "other" species between the coffee habitats ($\chi^2 = 1.3$, df $= 3$, $p = 0.729$) (Fig. 2d). The two most common species in farms were the ferns *Pleopeltis astrolepis* (35% of occurrences in polyculture and 47% in the monoculture) and *Polypodium trisereale* (18% of occurrences in polyculture and 13% in the monoculture). In the forest, the two most common taxa were *Tillandsia* spp. (Bromeliaceae) (primarily *T. flabellate* and *T. schiedeana*) and two unidentified *Peperomia* spp. (Piperaceae) that accounted for 25% and 34% percent of occurrences, respectively.

The NMDS plot showed significant differences in species composition of epiphytes, orchids, bromeliads, and ferns in the three types of sites, but patterns differed slightly for each group (Fig. 3). Overall epiphyte composition differed in the types of sites (global $R = 0.693$, $p < 0.001$; all pairwise comparisons $p \leq 0.001$, Fig. 3a). Similarly, fern composition differed between forest and the polyculture ($p = 0.003$) and monoculture ($p = 0.001$) and between the two coffee habitats ($p < 0.001$) (global $R = 0.578$, $p < 0.001$, Fig. 3d). Orchid composition differed between the forest and monoculture ($p = 0.002$) and between the two coffee habitats ($p = 0.013$), but did not differ between the forest and polyculture farm ($p = 0.251$) (global $R = 0.239$, $p < 0.001$, Fig. 3b). Finally, bromeliad composition was similar in the forest and monoculture farm ($p = 0.139$) and similar in the two coffee habitats ($p = 0.142$), but bromeliad composition differed between the forest and polyculture ($p = 0.004$) (global $R = 0.2955$, $p = 0.013$, Fig. 3c).

Epiphyte Comparison between Coffee Habitats at Increasing Distance from Forest

In both farms epiphyte richness was lowest at the farthest measured distance from the forest; however, this decline in species richness was only significant for the monoculture (Fig. 4a). In the polyculture, species richness was highest 200 m from the forest (37 species, 1226 occurrences), and in the monoculture species richness was highest 100 m from the forest (22 species, 323 occurrences) (Fig. 4). There was no significant change in observed richness at different distances from the forest in the polyculture (Fig. 4a). There was, however, a significant decline in species richness in the monoculture at 400 m from the forest fragment (Fig. 4a).

The epiphyte species composition in the polyculture was more similar to epiphyte composition in the forest fragment than the monoculture farm, and similarity to forest species of epiphytes declined with increasing distance to forest, but only for the monoculture coffee (Fig. 4b). According to Bray-Curtis values, polyculture epiphytes were much more similar to

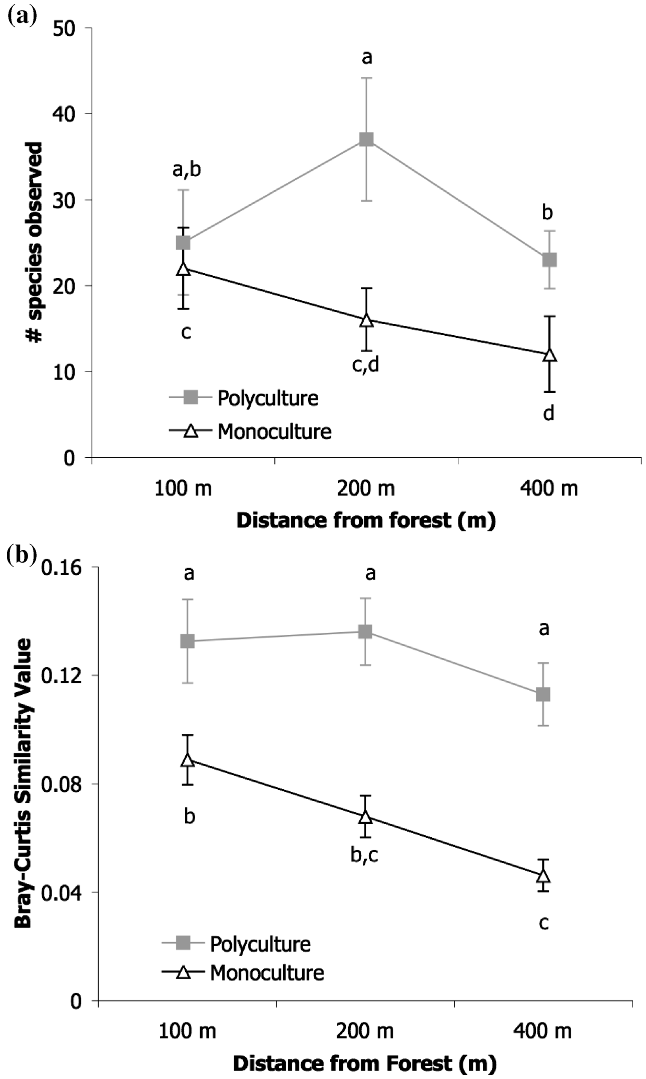

Figure 4. Observed species richness and species similarity between coffee and forest epiphytes within a polyculture and a monoculture coffee farm. Error bars for richness are 95% CIs and for similarity are SE. Different lowercase letters indicate significant differences between treatments within each farm.

forest epiphytes than were monoculture epiphytes to forest epiphytes (Fig. 4b, $F_{1,97} = 45.45$, $p < 0.001$). In the polyculture sites, similarity to forest epiphytes did not differ with increasing distance from the forest ($F_{2,42} = 0.892$, $p = 0.417$). In contrast, in the monoculture site, similarity to forest species significantly declined with increasing distance from forest ($F_{2,51} = 7.63$, $p = 0.001$). According to the NMDS, within the polyculture farm, species composition in 100 m, 200 m, and 400 m plots did not differ (global $R = 0.027$, $p = 0.336$), and there were no significant pairwise comparisons ($p > 0.189$). Similarly, there were no differences in species composition at different distances from forest within the monoculture coffee (global $R = -0.005$, $p = 0.488$), and there were no significant pairwise comparisons ($p > 0.110$).

Discussion

Epiphyte richness was greater in the forest fragment than in either coffee farm, but richness did not differ between the polyculture and monoculture farms. Additionally, there were very significant differences in epiphyte species composition in the three habitat types. Stand basal area and richness of epiphytes were significantly correlated, which demonstrates that plots with larger trees likely support higher richness and abundance. These results are somewhat consistent with those of studies in which epiphytes in different coffee habitats were examined, but we did find important differences. Other comparisons of epiphytes in forests and coffee agroecosystems show that forests generally maintain higher richness and abundance than coffee agroecosystems, but that traditional coffee farms (Mexico) and traditional home gardens (Ethiopia) harbor more epiphytes than intensive farms or exotic tree plantations (Hietz 2005; Hylander & Nemomissa 2008, 2009). Likewise, in coffee farms and disturbed habitats in Mexico, epiphyte richness positively correlates with tree size (Hietz-Seifert et al. 1996; Hietz 2005). Differences in species composition between forest and disturbed sites are common (Barthlott et al. 2001; Hylander & Nemomissa 2009), but the patterns others have found differ somewhat from those we identified. For example, Barthlott et al. (2001) found fewer ferns and orchids in disturbed sites (tree plantations, secondary vegetation) in the Venezuelan Andes relative to primary forests. We found that ferns comprised a much greater fraction of total occurrences in the disturbed sites (coffee) relative to forests. We also found that orchids and ferns were equally as rich in the polyculture coffee as in the forest and that orchid composition did not differ in the forest and polyculture. This is a potentially important result that shows that polyculture coffee may be important for orchid conservation, especially compared with other land-use choices.

There are several reasons why epiphyte richness and composition may differ in different habitats. Site differences in microclimatic conditions, a lack of suitable microsites, and increased impacts of wind may affect epiphytes. Epiphytes depend on suitable microsites for germination, including appropriate humidity conditions, temperature, and suitable substrate (Winkler et al. 2005*a*,*b*). Because of changes in conditions relative to forests, disturbed sites may tend to contain drought-tolerant species (Flores-Palacios & García-Franco 2004). Greater relative humidity in the forest compared with the polyculture and monoculture may have influenced differences in composition. Furthermore, temperature extremes tend to be greater in a monoculture farm than in a polyculture (Lin 2007). These changes in microclimate in the coffee habitats may prevent the survival of forest species. It is likely that several species found in the coffee habitats are better adapted to survive and reproduce in the drier, warmer climate of these sites than in the native forest. For example, the most common species in both the coffee sites, *Pleopeltis astrolepis*, a desiccant-tolerant species, is also found commonly in remnant trees in pastures (Hietz-Seifert et al. 1996). Thus, the coffee farm conditions may actually promote some species that do not thrive as well in forested habitats.

Selection and management of shade trees may also affect epiphyte composition. Tree composition in forest and coffee differs greatly, and factors such as bark architecture and pH may also restrict colonization and survival of forest epiphytes in these more open areas (e.g., Winkler et al. 2005*a*,*b*). Furthermore, farmers often prune epiphytes from trees because they believe epiphytes may lower coffee yields or because farms with epiphytes are perceived as unmanaged or undesirable from a visual standpoint (Hietz 2005). Epiphyte removal is not a common management practice in our study sites, but tree pruning is common; shade trees are normally pruned every other year. Such frequent cutting of outer branches would prevent colonization and survival of some epiphytes in the canopy. Epiphytes can also be dislodged from their substrate by wind and falling branches, and coffee plantations are generally far windier than forests (Winkler et al. 2007).

Our study is unique because we not only compared richness in the different habitats, but also looked at the spatial distribution of epiphytes within coffee plantations in terms of vertical stratification (zones) and in terms of occurrence in the coffee plantation at increasing distance from forest. There were highly significant differences in the vertical stratification of the epiphytes in the forest and in coffee farms, but there were no differences in vertical stratification in the polyculture versus the monoculture. In the forest fragment, epiphytes were distributed relatively evenly throughout the entire tree canopy from the trunk to the smaller branches. But in the coffee farms, epiphytes were concentrated near the trunk and major branches with few if any epiphytes in the outer branches. In forests and pastures in Xalapa, Mexico, Hietz-Seifert et al. (1996) found similar patterns. They attributed differences between more open and forested habitats to epiphyte needs for light and protection from extreme conditions. In pastures, epiphytes were concentrated on branches closer to the trunk, on the trunk, and farther from outer braches because of light penetration to the ground and more exposure to wind and heat closer to the canopy (Hietz-Seifert et al. 1996). Thus, many of the same reasons invoked to explain differences in habitats apply similarly to differences within the canopy. Pruning should tend to affect epiphytes on outer branches more than those on the trunk, whereas extreme temperatures and low humidity should tend to affect those epiphytes that need more shade and frequently occur on tree trunks in the forest (Acebey et al. 2003). Furthermore, several species of epiphytes are more abundant in particular tree zones (Hietz-Seifert et al. 1996), so species loss may not be random with conversion to coffee.

Perhaps the most striking and interesting result in the study is that epiphyte richness and floristic similarity of coffee epiphytes to forest epiphytes decreased with increasing distance from the forest in the monoculture farm but not in the polyculture farm. Several researchers have found similar patterns for species richness of ants and moths (Ricketts et al. 2001; Perfecto & Vandermeer 2002; Armbrecht & Perfecto 2003) and for epiphytes in other types of disturbed habitats (Hietz-Seifert et al. 1996). Köster et al. (2009), however, did not find a decline in epiphyte richness with increasing distance to forest in a number of disturbed habitats (e.g., pastures, secondary forests) in the Ecuadorian Andes. We are the first to document declines in epiphyte species richness at increasing distances from the forest in intensive, but not in highly shaded coffee agroecosystems.

There are several probable reasons for the decline in species richness in the more intensive farm. For example, some attribute the decline in richness primarily to lack of seed dispersal. Generally, seed dispersal from forests into disturbed habitats, such as coffee farms, can be low, and seeds may have lower survival or germination rates due to higher predation rates or differences in conditions (Cubiña & Aide 2001). In contrast Cascante-Marín et al. (2009) found that epiphyte seed traps collect a significantly higher number of fruiting individuals and seeds at forest edges and in pastures than in forest interiors, although germination rates inside of forests are greater. Although they found a few examples of long-distance dispersal, they generally concluded that forest epiphytes are dispersal-limited. In the context of this study, we assume that epiphytes are dispersing from the forest and arriving in the coffee habitats, where they will either survive or likely perish because of a lack of suitable substrate. This would have important implications for population dynamics within coffee agroecosystems. We found fertile individuals of several species in each epiphyte group in all habitats, but did not complete a rigorous analysis of the size of epiphytes encountered or the dispersal and survival of epiphytes in coffee agroecosystems. These are important areas for future research.

Epiphytes are extremely important components of tropical systems because they provide habitat for arthropods and birds; thus, decreases in epiphyte species richness and abundance may have cascading effects in agroecosystems and may affect ecosystem services. We found that diversity of epiphytes was greatest in native forests, but diversity was also high in polyculture coffee farms relative to monoculture farms. Furthermore, diversity of epiphytes and similarity of coffee epiphytes to forest epiphytes was higher in the polyculture farm even at greater (400 m) distances from the forest fragment. We also found that orchid richness and composition did not differ significantly between forest and polyculture: thus, more vegetatively complex coffee farms may be important for epiphyte conservation.

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