

Are epiphytes important for birds in coffee plantations? An experimental assessment

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Summary

1. Coffee is produced in tropical regions of the world, largely in Latin America. Coffee cultivation techniques range from traditional systems, where coffee grows under a diverse canopy of shade trees (shade-coffee plantations), to modern systems, where coffee grows without any type of shade (sun-coffee plantations). Shade-coffee plantations provide refuge for forest fauna in otherwise deforested landscapes. The conservation value of these agro-ecosystems depends upon their structural and floristic diversity.

2. The way coffee producers manage the vegetation, including the epiphytic component, may profoundly affect the value of plantations for conserving biological diversity. Shade-coffee certification programmes have emerged to verify that coffee advertised as ‘shade grown’ is actually grown on highly biodiverse plantations. Although these programmes universally encourage epiphyte protection from pruning (a common practice), there has been no experimental evaluation of the importance of epiphytes in supporting faunal diversity. We report the effect of experimentally removing epiphytes on the bird assemblage in a shade-coffee farm near Coatepec, Veracruz, Mexico.

3. We established two matching pairs of epiphyte removal and control plots. We compared bird diversity and abundance, based on daily censuses during the breeding and non-breeding season. We used existing information on the way in which birds use epiphytes as foraging and nesting substrates to explain the presence of different species in plots with epiphytes.

4. Plots without epiphytes tended to be less diverse than plots with epiphytes, but rarefaction analysis and ANOVA showed no significant differences in species richness between treatments in any of the seasons. Mean bird abundance was significantly higher in plots with epiphytes during both seasons, and a multidimensional scaling analysis showed that bird community structure differed between the two treatments.

5. Eighteen forest bird species were significantly more abundant in plots with epiphytes. Three non-forest species were more common in plots without epiphytes. Resident bird species that used epiphytes as a nesting substrate were significantly more abundant in plots with epiphytes.

6. When epiphytes are removed, canopy cover, foraging substrates, nest sites and nest materials are eliminated and microclimatic conditions change. This could increase predation on adult birds and nests, increase intra- and interspecific competition, and decrease individual survivorship.

7. *Synthesis and applications.* This is the first experimental assessment of the importance of epiphytes for birds. Shade-coffee plantations with epiphytes maintain higher abundance and diversity of the inhabitant bird fauna than plantations without epiphytes. This study reinforces the value of positive epiphyte management as an important factor in shade-grown coffee certification, where the goal is to promote biodiversity conservation.

Key-words: biodiversity, birds, community structure, shade coffee management, vascular epiphytes

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Introduction

Coffee cultivation techniques range from traditional systems, where coffee grows under a diverse canopy of shade trees (shade-coffee plantations), to a modern monoculture, where coffee grows without any type of shade (sun-coffee plantations). Shaded coffee plantations provide refuge for forest birds in otherwise deforested landscapes in the tropics (Aguilar-Ortiz 1982; Wunderle & Waide 1993; Warkentin, Greenberg & Salgado-Ortiz 1995; Perfecto *et al.* 1996; Wunderle & Latta 1996), especially in Latin America, where coffee production for export is one of the most important agricultural activities (Perfecto & Armbrrecht 2002). High levels of structural diversity in the canopy of coffee plantations are critical for maintaining high bird diversity and abundance (Greenberg *et al.* 1997; Greenberg, Bichier & Sterling 1997; Johnson 2000). However, while emphasis has been placed on the presence or absence of trees that form an arboreal canopy (Perfecto *et al.* 1996), epiphytes might also play a critical role in supporting avian biodiversity (Greenberg *et al.* 1997; Mas 1999; Johnson 2000; Mas & Dietsch 2003).

Planted shade trees such as *Inga* spp. are colonized by epiphytes that have dispersed as seeds from nearby forest or remnant forest trees (Solis 2002). Epiphytes increase the structural complexity of forests by creating a variety of supplementary microhabitats and by adding considerable biomass and surface area to the tree crowns (Remsen 1985; Gentry & Dodson 1987; Sillett 1996; Nadkarni, Merwin & Nieder 2001). Furthermore, epiphytes can provide birds with nest sites, nest materials and food in the form of flower nectar, fruit, water, small vertebrates and invertebrates that inhabit them (Dean, Milton & Siegfried 1990; Richter 1998; A. Cruz-Angón, personal observations).

The few studies that have assessed the importance of epiphyte flora for bird communities in the tropics have focused on the use of epiphytes by foraging birds during just one part of the annual cycle (Remsen 1985; Nadkarni & Matelson 1989; Sillett 1996; Sillett, James & Sillett 1997). This approach cannot detect all of the influences that the presence of epiphytes might have on bird distribution, particularly indirect effects such as changes in microclimate. Only experimental removal of epiphytes can fully assess bird dependence on them.

In this study, we took advantage of a common management practice (epiphyte removal) in shaded plantations throughout Latin America (Jones *et al.* 2000; A. Cruz-Angón, personal observation) to assess the importance of epiphytes for birds in these habitats. There is no clear reason why coffee plantation managers remove epiphytes from shade trees in their plantations, although some managers believe that all epiphytes are parasites that will harm or even kill trees. Many farmers assume that greater canopy openness and ambient light levels will increase coffee yields, but this has never been demonstrated as a direct result of epiphyte removal. It is clear, however, that epiphyte elimination

results in the structural simplification of coffee plantation canopies, which could affect the structure and dynamics of avian communities in these habitats (Greenberg *et al.* 1997).

In recent years, shade-coffee certification programmes have emerged to promote ecologically sound management among coffee growers and to verify that coffee marketed as 'shade grown' is truly grown on farms with high structural diversity and adequate resources to support a diverse associated fauna (Mas & Dietsch 2003). Correlative evidence supports the hypothesis that epiphytes might be important for canopy faunas (Greenberg *et al.* 1997; Mas 1999; Johnson 2000; Stuntz 2001). All the certification programmes consider the presence of epiphytes to be an important factor contributing to biodiversity, and these programmes require positive management to promote epiphyte growth (Mas 1999; Mas & Dietsch 2003). The need to conduct experimental studies of the value of epiphytes is clear. Here, we present the first experimental evaluation of epiphyte influence on bird communities.

Materials and methods

STUDY SITE

Our study site was a 35-year-old, 200-ha shaded coffee plantation located in Coatepec, Veracruz, Mexico (19°28'03"N, 96°55'58"W; 1224 m a.s.l.). We selected a single large coffee plantation rather than several small coffee farms in order to control for interregional variation (e.g. weather and altitude). Slope and topography were uniform throughout the site.

The study farm was a commercial polyculture, the prevalent management type of coffee plantation in central Veracruz (Moguel & Toledo 1999). Forest trees are completely removed, and shade trees, usually nitrogen-fixing fast-growing legumes such as *Inga* spp., and other commercial plant species, such as *Citrus* spp. and *Musa* spp., are planted over coffee (Moguel & Toledo 1999). In central Veracruz, the original forest cover is tropical montane cloud forest, which since the beginning of the last century has been replaced by coffee plantations, cattle pastures, sugarcane, cornfields, secondary vegetation and human settlements (Williams-Linera 2002; Williams-Linera, Manson & Isunza 2002). Although up to 35 trees species could be found in our study site, shade was dominated by trees of the genus *Inga*. Epiphytes were abundant in the plantation and included bromeliads such as *Tillandsia schiedeana* Steud., *Tillandsia heterophylla* E. Morren, and *Tillandsia juncea* (Ruiz & Pav.) Poir. as the most common species. The cactus *Rhipsalis baccifera* (Mill.) Stearn and the aroid *Anthurium scandens* (Aubl.) Engl. were also common. Plantation management included herbicide applications (once a year) and mechanical elimination of weeds (by machete). Shade trees were pruned every 2 years to keep shade cover around 60%. Before 1999, epiphytes were removed from coffee shrubs every 2 years, but

Table 1. Descriptive statistics of vegetation surveys done in four experimental plots (treatments) in a coffee plantation in Coatepec, Mexico. Data are mean values ± 1 SE (in parentheses), based on estimates made at five 625-m² quadrats per plot. Epiphyte richness surveys were based on 15 *Inga jinicuil* trees per plot, before workers removed all epiphytes from shade trees in one of two plots at each site (north and south). Treatment: with epiphytes (E+); without epiphytes (E-). Significant differences are shown with superscript letter ($P < 0.0001$). NA, information not available

Site	Treatment	Canopy cover (%)	Tree ha ⁻¹	Tree		Coffee		<i>Inga jinicuil</i> dominance (%)	Epiphyte richness
				Species	Height (m)	Height (m)	Density (%)		
North	E-	21.9 (2.6) ^a	230.4 (62.7)	3.8 (0.2)	7.7 (0.7)	2.1 (0.2)	76.0 (4.0)	56.1 (12.0)	15.9 (0.6)
North	E+	38.7 (5.7) ^b	262.4 (36.7)	4.2 (0.8)	8.1 (0.8)	1.9 (0.2)	64.0 (4.0)	48.3 (13.9)	15.9 (0.7)
South	E-	29.0 (2.3) ^{ac}	172.8 (15.5)	3.2 (0.6)	8.7 (1.0)	2.8 (0.3)	60.0 (5.5)	77.7 (6.9)	NA
South	E+	65.3 (1.2) ^d	195.2 (13.8)	1.8 (0.2)	9.0 (1.0)	2.5 (0.1)	79.0 (4.6)	58.7 (1.7)	14.8 (0.8)

during the dry seasons of 1999 and 2000 coffee managers began to remove epiphytes from shade trees. For this study plantation managers removed the epiphytes in accordance with our experimental design.

EXPERIMENTAL DESIGN

In 1999 and 2000 we established two experimental sites located approximately 1 km apart at opposite sides of the plantation (hereafter site: N, north; S, south). Each site was divided into two 3-ha plots surrounded by a matrix of shaded coffee with epiphytes. Plantation workers removed all epiphytes from shade trees in one of the two plots at each site (hereafter treatment: E+, with epiphytes; E-, without epiphytes). Epiphyte removal involved climbing on branches, which could be done safely only during the dry season (February–May) when epiphyte mats were not holding great amounts of water. Workers tossed the removed epiphytes to the ground and stacked them into small piles, where they decomposed.

Vegetation surveys

Canopy management was not uniform throughout the plantation, so variation among plots was expected. To assess variation in vegetation variables among plots, we randomly choose five 625-m² (25 × 25-m) quadrats per plot and measured shade cover with a spherical densiometer (Lemmon 1957). We counted the number of tree species and tree individuals (> 10 cm d.b.h.), and calculated tree height per species. We measured coffee shrub density as a percentage of ground cover in the quadrat and we calculated mean coffee shrub height.

The dominant shade tree species in the plantation was *Inga jinicuil* Schltdl. & Cham. Ex G. Don (Table 1), which supported a typical vascular epiphyte community (A. Cruz-Angón, unpublished data). We randomly selected and measured 15 *I. jinicuil* trees (> 10 cm d.b.h.) in each plot and identified all vascular epiphytes present in each tree. Observations were made with binoculars from the ground (Shaw & Bergstrom 1997). We established epiphyte richness on three plots; the southern plot without epiphytes (SE-) had no epiphytes before the start of the study.

Shade cover was the only significantly different variable between plots ($F_{1,16} = 24.98$, $P = 0.001$; Table 1) as result of epiphyte removal. We recorded 40 species of vascular epiphytes in the experimental plots out of a total of 57 canopy dwelling species found on the farm. Mean epiphyte richness per tree among plots did not differ ($F_{2,42} = 0.88$, $P = 0.42$) but bird pollinated bromeliads were the most dominant epiphyte group.

Bird diversity and abundance

After a 3-month training period, bird surveys were conducted in each plot by two observers. The results presented in this paper cover observations taken from 1 August 2001 to 23 March 2002, which included the last part of the breeding season (seven observation days per plot) and most of the non-breeding season (16 observation days per plot). We alternated survey days between sites and plots, covering one plot each day. Each day one observer zig-zagged forwards through the entire plot at a constant rate for 3.5 h (07:00–10:30). All birds seen or heard at a distance within 25 m of each side of the observer were recorded. To minimize double-counting we did not record birds that were behind the observer or further than 25 m away. Species were classified according to migratory status: (i) neotropical migrants, species that breed in the nearctic region and winter in the neotropics; (ii) resident breeders, species that breed in the coffee plantation; (iii) resident non-breeders, Veracruz resident species only seen in coffee plantations during the non-breeding season; and (iv) residents, species seen all year in the area but not observed breeding in coffee plantations. Common and Latin names of bird species follow the American Ornithologists' Union (1998) and are presented in the Appendix.

Epiphyte use by birds

Birds were classified according to their use of epiphytes as (i) foraging substrate and (ii) nesting sites and materials. We used 2629 foraging observations gathered in the same plantation from 1995 to 1998, and in addition conducted 130 days of foraging observations ($n = 2403$) on the experimental plots from May 2001 to March

Table 2. Bird species richness observed and expected for two pairs of experimental plots in a coffee plantation in Coatepec, Mexico. Mean expected species richness is based on rarefaction of 200 individuals for the breeding season and 900 individuals for the non-breeding season. Total numbers of individuals observed are shown in parentheses after the observed species richness per season. Treatment, with epiphytes (E+), without epiphytes (E-)

Site	Treatment	Species richness per season				Total richness
		Breeding		Non-breeding		
		Observed	Estimated (SD)	Observed	Estimated (SD)	
North	E+	26 (280)	24.5 (1.0)	54 (1227)	51.7 (1.3)	60
North	E-	35 (249)	33.0 (1.2)	50 (1042)	48.6 (1.1)	62
South	E+	40 (378)	33.9 (1.9)	54 (1238)	51.9 (1.3)	65
South	E-	33 (201)	32.9 (0.04)	48 (977)	47.3 (0.8)	57

2002. We recorded one foraging observation per individual to maximize sample independence. We collected data on bird species, height of the bird in the tree when foraging, manoeuvre type, foraging substrate, tree species and type of food obtained (nectar, arthropods, fruit) (methods based on Remsen & Robinson 1990; modified by Greenberg *et al.* 1999). When an individual bird obtained a food item from an epiphyte, we identified the family and species of epiphyte whenever possible.

We observed nesting behaviours in the coffee plantation during the summers of 1995–99. Where we were able to find and describe nests we calculated the percentage of nests built in epiphyte substrates from the total number of nests found per species.

DATA ANALYSIS

We analysed seasons separately, because bird diversity and abundance are much higher during the non-breeding season when neotropical migrants are present.

Bird diversity and abundance

To assess the reliability of our surveys for recording bird species richness, we carried out a rarefaction analysis (Hurlbert 1971; James & Ratburn 1981) using EcoSim v. 7 (Gottelli & Entsminger 2004). We set a maximum number of individuals for the breeding season to 200 and for the wintering season to 900, taking into account the plot with the least number of individuals observed (Table 2). To examine the effect of epiphyte removal on bird abundance and species richness, we conducted an ANOVA for a split-plot design where observation day was considered a random block that contained the site split into smaller experimental plots (treatment). This allowed us to maximize the power of test for the factor (treatment) in which we were most interested (Sahai & Ageel 2000). Following tests for normality and homoscedasticity we square-root transformed the data (Zar 1999).

To quantify the similarity of community composition among plots, we generated a similarity matrix with the Bray–Curtis coefficient. This index is calculated as:

$$C_N = \frac{2N_j}{Na + Nb}$$

where Na is the total number of individuals in site A, Nb is the total number of individuals in site B, and N_j is the sum of the lower of the two abundances recorded for species found in both sites. The index ranges from 1, when communities are identical, to 0, when they are entirely dissimilar (Magurran 1988). We then used a multidimensional scaling algorithm (NMDS; Gauch, Whittaker & Singer 1981; Gauch 1982; StatSoft Inc. 2000) to examine for clustering by community composition. We plotted the values obtained through this procedure in a scatter plot, where the proximity of the sites is proportional to the degree of similarity. This allowed us to detect meaningful underlying dimensions and explain the observed similarities among the investigated plots. The degree of correspondence between the distances among points implied by the NMDS plot and our similarity matrix is measured (inversely) by a stress function. Finally, we carried out a Mantel's test (Mantel 1967) to calculate the probability of acquiring a given level of clustering by chance (Quinn & Keough 2002).

We conducted a Wilcoxon signed test to assess the overall association of species within a treatment type. The null hypothesis was that the signs (+ and -) and the magnitude of the differences were equally distributed (Zar 1999). We conducted a comparison of proportions using chi-square tests to determine if the number of individuals of a given species was significantly more abundant in any of the treatments (with or without epiphytes). The null hypothesis was that individuals were evenly distributed in both treatments. We performed tests only for those species whose frequencies fulfilled the test assumptions (Zar 1999). We assigned species to one of three categories based on whether they were significantly more abundant in either of the treatments: (i) species more abundant on E- plots; (ii) species evenly distributed among treatments (E- and E+); and (iii) species significantly more abundant on E+. Significance levels of the chi-square tests were corrected with the Bonferroni method to counteract for the number of simultaneous tests.

Epiphyte use by birds

For those bird species where we had at least 20 foraging observations ($n = 33$), we calculated the percentage of foraging incidents that occurred on epiphytes. We correlated this percentage with the percentage of individuals of each of those species found in the E+ plots. With nesting observation data, we used a Kruskal–Wallis test to determine if species that use epiphytes as nest sites were significantly more abundant in E+ plots than those not using epiphytes for nesting (Zar 1999).

Results**BIRD DIVERSITY AND ABUNDANCE**

We recorded 91 bird species, of which 46 were neotropical migrants and 45 were residents. Among the residents, 29 were confirmed breeders in the study site and 11 were year-round residents for which we had no evidence of on-site breeding. The remaining five resident species did not spend the breeding season in the area (see the Appendix).

Total species richness was similar among plots and ranged from 57 to 65. No one plot contained all 91 species. During the breeding season, the NE+ plot had the lowest richness (26 species) and the SE+ the highest (40 species). During the non-breeding season, with-epiphyte plots (NE+ and SE+) had more species than without-epiphyte plots (NE– and SE–). Estimated species richness, as determined by rarefaction analysis, confirmed this pattern for both seasons (Table 2). We present rarefaction curves at three points of individual resampling: 50, 100 and 200 individuals for the breeding season, and 300, 600 and 900 individuals for the non-breeding season (Fig. 1). Confidence intervals at 95% overlapped widely among plots in both seasons, with the exception of the NE+ plot, which remained the lowest species diversity during the breeding season.

The ANOVA showed no significant differences in the mean number of species observed within treatment in any of the seasons (breeding season: $F_{1,6} = 2.13$, $P = 0.19$; non-breeding season: $F_{1,15} = 3.64$, $P = 0.07$). The site was not a significant factor during the breeding season ($F_{1,6} = 2.00$, $P = 0.20$). During the non-breeding season, however, mean species richness was significantly greater ($F_{1,15} = 6.67$, $P = 0.02$) in northern plots (NE+ and NE–). None the less, E– plots tended to have fewer species than their E+ counterparts. There was no significant site \times treatment effects for either season (all $P > 0.05$). The mean number of individuals observed was significantly higher in E+ plots than in E– plots in both seasons (breeding season: $F_{1,6} = 43.61$, $P < 0.001$; non-breeding season: $F_{1,15} = 8.52$, $P < 0.05$). Neither site nor site \times treatment effects were significant factors for either season ($P > 0.05$; Fig. 2).

Even though rarefaction analysis and ANOVA for species richness showed somewhat unexpected results between treatments, the multidimensional scaling (NMDS)

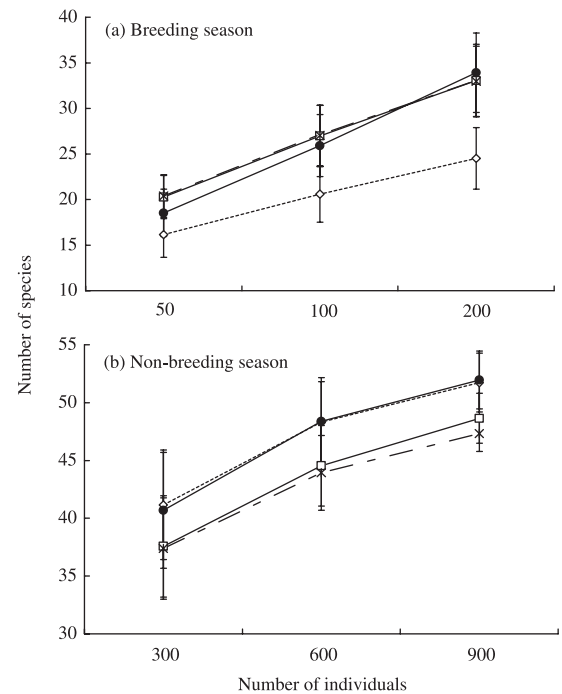


Fig. 1. Rarefaction curves for the number of bird species recorded in experimental plots in a coffee plantation in Coatepec, Mexico. Mean species richness is shown at three points of individual resampling: (a) 50, 100 and 200 individuals for the breeding season; and (b) 300, 600 and 900 individuals for the non-breeding season. Data points are mean expected richness, bars are 95% confidence intervals. Experimental plots: north with epiphytes (diamonds), north without epiphytes (squares), south with epiphytes (circles), south without epiphytes (crosses).

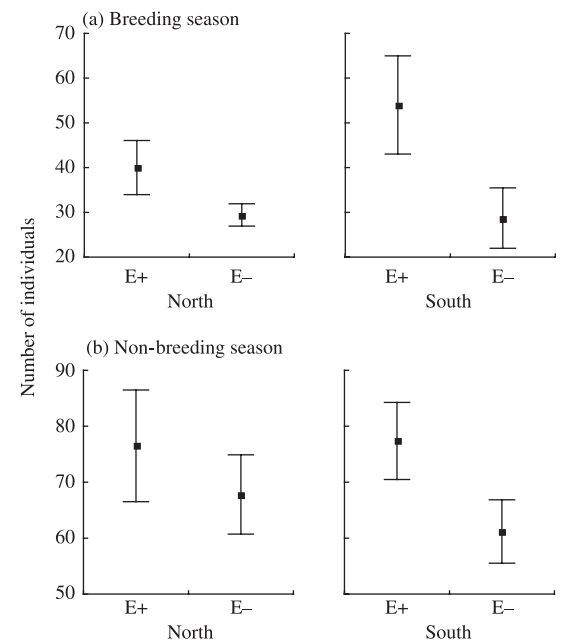


Fig. 2. Abundance of birds observed in four experimental plots in a coffee plantation in Coatepec, Mexico, during the (a) breeding season and (b) non-breeding season. Sites: north and south. Treatments: with epiphytes (E+); without epiphytes (E–). Data points represent mean number of individuals observed, and whiskers are 95% confidence intervals.

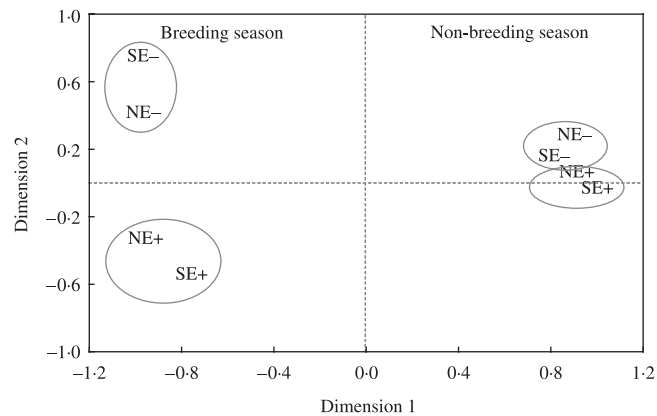


Fig. 3. Ordination of two matched pairs of experimental plots, based on a multidimensional scaling analysis used to compare the similarities of the studied plots during the breeding and non-breeding seasons (2001–02) in a coffee plantation in central Veracruz, Mexico. Plots: north with epiphytes (NE+), north without epiphytes (NE-), south with epiphytes (SE+), south without epiphytes (SE-). Stress = 0.006.

procedure showed a more consistent pattern. Two dimensions were obtained (stress = 0.006): dimension 1 grouped plots according to the season (breeding vs. non-breeding), and could be explained by the presence of neotropical migrants that modify the structure of tropical communities during the non-breeding season; dimension 2 grouped plots according to the treatment (with- or without-epiphytes). This pattern was more evident for the breeding season, whereas during the non-breeding season community structure was very similar among plots; however, equal treatments remained closer to each other, which implied that plots with the same treatment had similar bird community structures (Fig. 3). The Mantel's test showed a significant correlation ($r = 0.39$, $P < 0.01$) between the similarity matrix and the matrix produced by the NMDS procedure. These results indicate that the grouping observed was not due to chance.

We found an overall tendency for bird species to occur more commonly in E+ plots ($Z = 2.76$, $P = 0.006$). Eighteen bird species were significantly more common in E+ plots, while only three were more common in E- plots. Seven migrant species were significantly more abundant in E+ plots (χ^2 , d.f. = 1, $P < 0.05$). Among residents, 11 species were significantly more abundant in E+ plots (χ^2 , d.f. = 1, $P < 0.05$): two hummingbirds, four breeding tanagers, three understory breeding birds and two non-breeding flycatchers. Only two migrants (both granivores) and one breeding resident were more abundant in E- plots (χ^2 , d.f. = 1, $P < 0.05$). When Bonferroni correction was conducted, 11 of the 18 species that were more abundant in E+ plots remained significant ($P < 0.005$), and only two of the three species that were more abundant in E- plots remained significant (see the Appendix).

EPIPHYTE USE BY BIRDS

Foraging

We recorded 33 species (15 migrants and 18 residents) using epiphytes as a foraging substrate (observed for-

aging incidents per species; $n = 20$). The percentage use among species ranged from 3% to 74%. For example, yellow-throated euphonias and the band-backed wrens foraged on epiphytes in 74% of the observations. Wedge-tailed sabrewings, grey catbirds and black-and-white warblers were observed using epiphytes in about 50% of foraging observations. Common bush-tanagers, the most common resident in the plantation and the most common species in the plots with epiphytes, foraged in epiphytes around 30% of the time. Foraging guilds using epiphytes included omnivores, insectivores and nectarivores. We did not observe any granivorous species foraging in epiphytes. The correlation between the proportion of individuals found in with-epiphyte plots and the percentage use of epiphytes as foraging substrate was not significant (Fig. 4; $r = 0.19$, $P = 0.07$).

Nesting

Overall, species that used epiphytes as a nesting site or for nesting materials were significantly more abundant in E+ plots than those species that did not nest in epiphytes ($H_{1,26} = 3.42$, $P = 0.03$). Among the 29 confirmed breeders, seven species used epiphytes as nesting sites: band-backed wren, blue bunting, common bush-tanager, squirrel cuckoo, tropical parula, white-winged tanager and yellow-throated euphonia. The birds usually built their nests inside epiphyte clumps, most commonly bromeliads. The percentage use varied from 38% to 100%. Three of the four breeding tanagers were particularly dependent upon epiphyte clumps as nesting sites, using them for 84–100% of their nests (see the Appendix). The wedge-tailed hummingbirds and the azure-crowned hummingbird used epiphytic lichens and mosses to 'decorate' their nest. Band-backed wrens used *Tillandsia* spp. with plumose seeds as a lining material for their nests.

Discussion

Our data suggest that the presence of epiphytes may have direct and indirect effects not only on the canopy

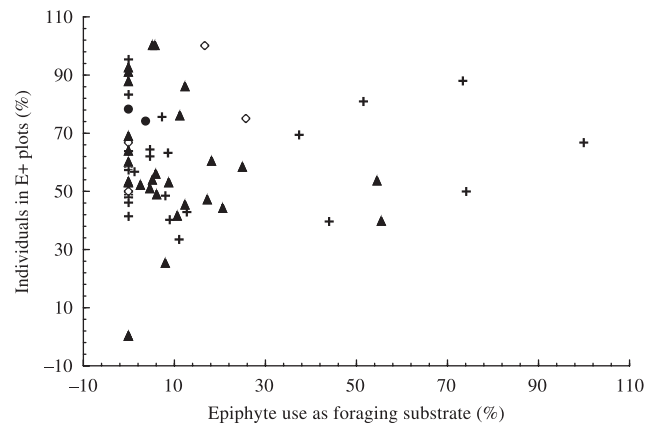


Fig. 4. Correlation between the percentage use of epiphytes as a foraging substrate and the proportion of individuals observed in the experimental plots with epiphytes (E+) in a coffee plantation in Central Veracruz, Mexico. Resident breeders (crosses), residents with unknown breeding status (diamonds), residents non-breeders (circles), and neotropical migrants (triangles). $r = 0.19$, $P = 0.07$.

avifauna but on the understorey birds as well. The four experimental plots differed only in the treatment applied. This was confirmed by the vegetation surveys where canopy cover, determined by epiphyte density, was the only variable where plots differed significantly. We did not find significant differences between treatments in total species richness or mean number of bird species observed, but there was an overall tendency for bird species to occur in larger numbers in E+ plots. The use of complementary biodiversity measurements, such as similarity coefficients that take into account both species richness and abundance, may reflect ecological patterns in a more integral manner. Thus, we were able to detect differences in bird abundance in a number of forest-dependent taxa, which in turn had a strong influence on overall community structure.

Focusing only on patterns of species presence and absence may be too restricted when assessing diversity in avian communities; changes in individual numbers may be the first indication of local extinction (Ferraz *et al.* 2003). The presence of a species does not imply that a viable population is supported (Martin 1992; Donovan *et al.* 1995; Robinson *et al.* 1995; Mas & Dietsch 2003). Even abundance measures do not address this concern and further research is required to explore the demographic consequences of management actions such as epiphyte removal.

As we would expect, species more strongly associated with epiphytes were less abundant in without-epiphyte plots, which in turn may influence the structure of the entire avian assemblage. For example, common bush-tanagers were significantly more abundant in with-epiphyte plots, as were all tanager species recorded in our study site. Common bush-tanagers used epiphytes as forage (30% of the time) and as a nesting substrate (80% of the time). The use of epiphyte resources by this species has been described previously (Powell 1979; Isler & Isler 1987; Nadkarni & Matelson 1989; Sillett 1996; Richter 1998); however, this study confirms the direct dependence and the importance of epiphyte

resources for these tanager species. Bush-tanagers play an important role in mixed species flock structure and function (Valburg 1992), hence their decline due to the removal of epiphytes might affect the behaviour of many other species.

Epiphytes may play a key role in reducing phenological gaps in resources. In floristically impoverished plantations such as commercial polycultures in the central region of Veracruz, tree species of the genus *Inga* comprise up to 70% of the shade trees. In this type of plantation, epiphytes may become a critically important food resource when tree hosts are not flowering or fruiting (Williams-Linera 1997). Epiphytes such as *Anthurium scandens* and *Rhipsalis baccifera* produce large quantities of fruits that are regularly consumed by resident tanagers and euphonias (i.e. common bush-tanager, white-winged tanager and yellow-throated euphonia; Snow 1981). Fruit production of these epiphytes coincides with the birds' breeding season (April–September). Breeding requires high levels of energy that can be obtained quickly and easily from the epiphyte fruits (Greenberg 1981; Denslow, Moermond & Levey 1986). In addition, the sequential flowering of several bird-pollinated *Tillandsia* occurring in the with-epiphyte plots at our study site guarantees a year-round nectar supply for nectarivores such as wedge-tailed hummingbirds (García-Franco, Martínez-Burgoa & Pérez 2001).

Interestingly, we did not find a significant correlation between the percentage use of epiphytes as a foraging substrate and the proportion of individuals per species in the with-epiphyte plots. This suggests that the use of epiphytes as foraging substrate may not be the most important factor explaining the presence of birds in the with-epiphyte plots. None the less, the removal of epiphytes modifies the canopy's vertical structure by decreasing foliage surface and biomass (Hoefstede, Wolf & Benzig 1993). These changes may influence encounter rates with prey, prey accessibility and energetic costs of attacking and capturing prey (Gradwhol

& Greenberg 1980; Robinson & Holmes 1982; Schmidt 1998; Whelan 2001). Furthermore, the removal of epiphytes might disrupt the life cycle of arthropods predated by birds, thus further limiting food availability (Kitching *et al.* 1997).

The significant relationship between the species that use epiphytes as a nesting site and their greater abundance in plots with epiphytes confirms the close dependence of resident species upon epiphyte resources. The use of epiphytes as a nesting site may give additional concealment against potential predators. On the other hand, some species that were more abundant in the E+ plots did not utilize epiphytes directly. This was particularly true for migrant species such as olive-sided flycatchers, solitary vireos, summer tanagers and Tennessee warblers, which did not forage on epiphytes but were more abundant in the E+ plots. Some species may have preferred E+ plots because they use epiphytes as a simple cue to assess appropriate (forest) habitat (Lack 1933).

In addition, some understorey resident breeders (golden-crowned warbler, spot-breasted wren and rusty sparrow), which neither forage nor nest in epiphytes, were more abundant in the E+ plots. Epiphytes may play an indirect role in maintaining the abundance of many species. Such indirect effects would be undetectable from observational studies on the use of epiphytes by birds, for example epiphyte influence on microclimate. Lorr (2001), working on our experimental plots, found that, as a consequence of epiphyte removal, canopy cover and soil moisture were reduced while stemflow and rain through-fall increased. Thus, more water reached the ground in less time but evaporated faster. During the breeding season, increases in running water could flood nests and affect ground nesters such as golden-crowned warblers and rusty sparrows. Moreover, unexpected changes in the microclimate could influence the abundance and diversity of arthropods, not only in the canopy but in the understorey arthropod fauna as well, and important prey species may become less abundant and less accessible (Stuntz 2001; A. Cruz-Angón & Greenberg, unpublished data). In addition, greater canopy openness due to epiphyte removal may increase birds' detection by potential predators. Several authors have demonstrated that individual fitness can be affected by environmental factors such as extreme temperature, food shortage and predation (Calder 1984; Peters 1986; Nager & Zandt 1994; Carrascal *et al.* 1998).

As a consequence of increased canopy openness and greater light incidence in the without-epiphyte plots, weeds might proliferate. This could explain the significantly higher abundance of weed-dependent granivores such as indigo buntings and painted buntings in without-epiphyte plots. However, weeds are an ephemeral resource in coffee plantations because they are regularly removed from the understorey. The only resident species that was significantly more abundant in the without-epiphyte plot was the golden-fronted

woodpecker, which paradoxically used epiphytes as a foraging substrate about 50% of the time. The higher abundance of this species could be due to epiphyte removal increasing woodpecker accessibility to tree bark. This might be advantageous for a primary cavity nesting species as epiphyte-free trees would improve tree selection.

CONCLUSION

This study has provided experimental evidence of the importance of epiphytes in supporting bird abundance and diversity in coffee plantations, particularly forest-dependent species. Although focused on coffee plantations, these findings might also indicate the ecological importance of epiphytes for birds in other ecosystems, such as tropical montane cloud forests. Our results support the use of the positive epiphyte management and validate the use of this criterion to certify shade-grown coffee. Epiphytes are an important resource for birds, not only because they provide critical resources such as food and nest materials, but also because epiphytes mediate in microclimate regulation, and may offer refuge and cover to the birds. The long-term effects of epiphyte removal still need to be assessed. Although coffee plantations where epiphyte removal is practised provide a unique opportunity to research direct and indirect effects of this practice, the management should not be promoted. Given the negative impacts of this technique on birds it should be actively discouraged. The shade-grown coffee certification scheme provides a practical means of achieving this.

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE983/JPE983sm.htm>.

Appendix. Abundance and epiphyte use by bird species recorded in experimental plots in a coffee plantation in Coatepec, Mexico.

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