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Simplification of a coffee foliage-dwelling beetle community under low-shade management

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Abstract

Coffee agroforests may be structurally and floristically complex and may contain a significant fraction of species from biodiverse and threatened tropical montane forest biotas; hence, understanding the dynamics of tropical forest biodiversity in coffee agroecosystems has emerged as a centrally important area of tropical conservation biology research. We conducted a morphospecies analysis on foliage-dwelling beetles collected from coffee plants on four coffee farms in southern Chiapas, Mexico, to characterize variation in the abundance, species richness, and species composition of this mega-diverse taxon in relation to coffee cultivation system, spatio-temporal variation, and predator removal. We constructed thirty-two cages to exclude birds and bats on four farms, each enclosing 7–10 coffee plants and paired with an adjacent uncaged control plot, and then collected beetles from coffee foliage with D-Vac aspirators in each plot once every 3 months for one year.

We classified the 2662 beetles collected into 293 morphospecies, representing 42 families of beetles. Extrapolation and interpolation analyses revealed a very high level of species richness, with no plateau and only a slight leveling trend observed in our species accumulation curves. We found that low-shade systems contain equal or higher beetle abundance, lower species richness, more highly homogenized species composition, and higher abundance of coffee berry borer pests on coffee foliage than do high-shade systems. We observed no effect of flying vertebrate exclusion on the coffee foliage beetle assemblage, but did find significant variation in abundance, species richness, and species composition of coffee foliage beetles across seasons and study sites.

The increased beetle biodiversity of high-shade coffee cultivation systems has important implications both for the preservation of native biodiversity in coffee growing regions and for the control of agricultural pests such as the coffee berry borer.

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Zusammenfassung

Kaffee-Agrarwälder können strukturell und floristisch komplex sein und können einen signifikanten Anteil von Arten aus biodiversen und gefährdeten tropischen montanen Waldbiotopen enthalten. Deshalb hat sich das Verständnis der Dynamik der tropischen Waldbiodiversität in Kaffee-Agrarökosystemen als ein zentrales Gebiet der Forschung in der tropischen Naturschutzbiologie entwickelt. Wir führten eine Morphospezies-Untersuchung an laubbewohnenden Käfern durch, die auf Kaffeepflanzen in vier Kaffeefarmen im südlichen Chiapas, Mexiko, gesammelt wurden, um die Variation in der Abundanz, im Artenreichtum und in der Artenzusammensetzung dieses megadiversen Taxons in Bezug zu setzen zum Kaffee-Anbausystem, zur raumzeitlichen Variation und zur Entfernung der Prädatoren. Wir konstruierten 32 Käfige um Vögel und Fledermäuse auf vier Farmen auszuschließen, von denen jeder 7-10 Kaffeepflanzen enthielt, und bildeten Paare mit naheliegenden, nicht eingeschlossenen Kontrollflächen. Wir sammelten dann in jeder Fläche über ein Jahr lang einmal in drei Monaten die Käfer mit einem D-Vac-Saugapparat von den Kaffeeblättern. Wir klassifizierten die 2662 gesammelten Käfer in 293 Morphospecies, die 42 Käferfamilien repräsentierten. Extrapolations- und Intrapolationsanalysen ließen einen sehr hohen Grad des Artenreichtums erkennen, und die Artenakkumulationskurven verliefen ohne Plateau und nur mit einer leicht abfallenden Steigung. Wir fanden, dass Systeme mit wenig Schatten eine ähnliche oder höhere Käferabundanz, einen geringeren Artenreichtum, eine viel stärker homogene Artenzusammensetzung und eine höhere Abundanz von Schädlingen, die sich in Kaffeebohnen vermehren, aufweisen als Systeme mit viel Schatten. Wir fanden keine Auswirkung des Ausschlusses von fliegenden Vertebraten auf die Käferzusammensetzung auf den Kaffeeblättern. Wir fanden jedoch eine signifikante Veränderung in der Abundanz, im Artenreichtum und in der Artenzusammensetzung der Käfer auf den Kaffeeblättern mit der Jahreszeit und in den Untersuchungsgebieten. Die erhöhte Käferdiversität der schattigen Kaffeepflanzungen hat wichtige Implikationen sowohl für die Erhaltung der vorhandenen Biodiversität in Kaffeeanbauregionen, als auch für die Kontrolle von landwirtschaftlichen Schädlingen, wie dem Kaffeebohnenbohrer.
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Introduction

Coffee agroecosystems are tropical agroforests managed to produce an agricultural commodity. Understanding how tropical forest biotas respond to coffee management regimes represents a vitally important knowledge frontier in conservation biology for several reasons: (1) the tropical forested regions in which coffee is grown are high in biodiversity and endemism (Mittermeier, Meyers, Thomsen, de Fonseca, & Olivieri, 1998; Moguel & Toledo, 1999), (2) coffee agroecosystems are of great areal and economic significance worldwide in tropical regions (FAO, 2007), (3) coffee agroecosystems may contain complex forest-like vegetation structure and harbour significant biodiversity (reviewed in Donald, 2004; Perfecto & Armbrecht, 2003; Perfecto, Armbrecht, Philpott, Soto-Pinto, & Dietsch, in press; Somarriba, Harvey, Samper, Anthony, González et al., 2004).

Of particular interest is the response of biodiversity to different shade management strategies. Variation in the cultivation techniques used by coffee growers has created tremendous variation in the structure and floristic diversity of the shade stratum, or canopy layer, of coffee agroecosystems. Despite the complexity of this variation, studies of biodiversity in coffee to date allow a meaningful distinction to be made between high-shade

systems (e.g. "rustic coffee" of Moguel & Toledo, 1999, "diverse shade" of Perfecto, Vandermeer, López Bautista, Ibarra Nuñez, Greenberg et al., 2004, "bajo monte coffee" of Gordon, Manson, Sundberg, & Cruz-Angón, 2007) and low-shade systems (e.g. "sun coffee," "shaded monoculture," of Moguel & Toledo, 1999, "monodominant shade" of Perfecto et al., 2004). High-shade systems typically harbor more species than do low-shade systems for a wide variety of taxa (e.g. birds: Gordon et al., 2007; butterflies: Mas & Dietsch, 2004; spiders: Pinkus Rendón, León Cortés, & Ibarra Nuñez, 2006; but see Klein, Steffan-Dewenter, Buchori, & Tscharntke, 2002 for a counter example with trap-nesting bees and wasps). This difference has been attributed to various features of high-shade systems, including their tall canopies (Gordon et al., 2007), shade tree species richness (Philpott, Perfecto, & Vandermeer, 2006), abundant and diverse epiphytes (Hietz, 2005), and dense shade (Perfecto, Armbrecht, Philpott, Soto-Pinto, & Dietsch, in press) in relation to low-shade systems.

This study makes two principal contributions to our understanding of biodiversity in high- vs. low-shade coffee agroecosystems. First, we present an extensive and taxonomically broad study of species richness and composition patterns in a beetle assemblage from a

coffee agroecosystem. Most prior studies of beetle faunas in coffee have examined total abundance patterns from foliage-collected beetles (Philpott, Greenberg, Bichier, & Perfecto, 2004), have sampled from a few shade trees (Perfecto, Hansen, Vandermeer, & Cartín, 1997), or have included only dung and/or carrion beetles (e.g. Arellano, Favila, & Huerta, 2005; Pineda, Moreno, Escobar, & Halffter, 2005). Using beetle morphospecies analysis with pyrethrum knockdown samples from coffee plants in western Ecuador, Richter, Klein, Tscharntke, and Tylianakis (2007) found high beetle species richness near coffee plantation edges, but no difference between traditionally managed, and abandoned coffee plantations. The species richness of foliage-dwelling beetles in tropical forest communities is well-known, and high enough to have prompted order of magnitude increases in the estimates of the total species diversity of the Earth (Erwin, 1982). Perhaps related to this extreme species richness, foliage-dwelling beetles represent a wide diversity of trophic guilds and ecological roles, including many different types of predators, herbivores, and fungivores (Arnett & Thomas, 2001; Arnett, Thomas, Skelley, & Frank, 2002). Species-level data in this megadiverse group therefore provides an extremely information-rich ecological fingerprint, with potential to make significant contributions to our understanding of the dynamics of tropical forest biodiversity in coffee agroecosystems.

Second, we deepen our understanding of the ecological processes that underlie biodiversity patterns in coffee agroecosystems by analyzing beetle community variation over time, space, cultivation technique, and in response to predator removal. Previous studies have suggested that birds and/or bats can significantly depress the abundance of arthropods on the foliage of *Inga* shade trees in coffee plantations (Philpott et al., 2004), or on the foliage of the coffee bushes, themselves (Greenberg, Bichier, Cruz-Angón, MacVean, & Perez et al., 2000; Perfecto et al., 2004). Jedlicka, Greenberg, Perfecto, Philpott, and Dietsch (2006) found that flying vertebrates depressed arthropod abundance in the canopy of *Inga* shade trees but not in the coffee bushes of the understory. Herein, we add to this emerging picture of top-down effects in coffee agroecosystems by analyzing the effects of flying vertebrate exclusion on the abundance, species richness, and species composition of beetles on coffee foliage.

Methods

Study sites

This study was conducted on four coffee farms in the Soconusco region of the state of Chiapas in southern Mexico: Belen high-shade (15°15′N, 99°22′W); Belen low-

shade (15°15′N, 92°19′W); Irlanda (15°11′N, 92°20′W); and Hamburgo (15°10′N, 92°19′W). These four farms collectively represent two pairs of adjacent farms. The pairs are separated by approximately 10 km, and each pair contains one farm under high-shade cultivation and one farm under low-shade cultivation. No coffee berry borer control techniques were being practiced on any of the farms during the period of this study. Detailed characterizations of the vegetation structure, floristics, and management of these four farms can be found in Mas and Dietsch (2003), Philpott et al. (2006), Philpott, Perfecto, and Vandermeer (in press) Belen high- and low-shade farms are located within the municipality of Huixtla, are described as traditional and commercial polycultures (Moguel & Toledo, 1999), respectively, by Philpott et al. (in press), and are hereafter referred to as Huixtla high-shade and Huixtla low-shade. The other two farms, Irlanda (high-shade) and Hamburgo (low-shade), are located in the municipality of Tapachula, are described as commercial polyculture and shade monoculture (Moguel & Toledo, 1999), respectively, by Philpott et al. (in press), and are hereafter referred to as Tapachula high-shade and Tapachula low-shade. All farms are located between 950 and 1150 m elevation above sea level and receive ca. 4500 mm of rain per year (data provided by B. Peters of Irlanda farm). Although these four farms can generally be classified as high-shade and low-shade, they are all managed in different ways, and represent a gradient of management intensification based on diversity, density and height of shade trees and percent shade cover with Huixtla high-shade > Tapachula high-shade > Huixtla low-shade > Tapachula low-shade (Mas & Dietsch 2003; Philpott et al., 2006).

Flying vertebrate exclusion

Large (ca. 10 m × 5 m × 3 m) bird/bat exclosures were established in each of the four farms: 6 in Huixtla high-shade, 6 in Huixtla low-shade, 10 in Tapachula high-shade and 10 in Tapachula low-shade, for a total of 32 exclosures. Exclosures were constructed of transparent monofilamentous nylon (5 cm mesh) fishing net and established in November of 2000. Each exclosure enclosed at least ten coffee plants, with the exception of three exclosures that enclosed seven plants, one that enclosed eight plants, and one that enclosed nine plants. The same numbers of control plants were selected from a parallel row of coffee approximately 2–3 m from the paired exclosure, resulting in a total of 616 coffee plants sampled, half inside the enclosures and half outside.

Beetle sampling and classification

Arthropods were sampled using a D-vac, a reversed leaf blower modified with a fine mesh that allowed for

the collection of very small arthropods. Two coffee branches were randomly selected for arthropod sampling from each of the coffee bushes in each plot. Samples were taken a few days after the installment of the exclosures (November 2000), and at 3 months (February 2001), 6 months (May 2001), and 9 months (August 2001) after the establishment of the exclosures (see Appendix A: Graph 2). Arthropod collection was always performed during the first three hours of daylight, and not during rain or excessive wind. All arthropods were sorted to order. Beetles (Order: Coleoptera) were placed into separate vials containing 70% alcohol for each plot × date sample.

Beetle morphospecies analysis was conducted by Gordon, who examined all beetle specimens and first identified them to family using Arnett and Thomas (2001), Arnett et al. (2002), Borror, Triplehorn, and Johnson (1989), following the taxonomy of Arnett and Thomas (2001) and Arnett et al. (2002). Morphological features were then used to classify all specimens in each family into morphospecies. To provide limited ground-truthing of the morphospecies classification, specimens from five families representing 38 of the 293 total morphospecies (13%) were examined and identified by taxonomic specialists in their respective groups.

Statistical methods

One primary goal was to analyze species richness (α-diversity) according to the various treatment factors. To perform comparative analysis between different factors, we pooled all data within a factor and then used rarefaction analysis, in which the richness is estimated for some $N < \max (N_1, N_2)$, and then compared across treatment factors (Heck, Van Belle, & Simberloff, 1975; Hurlbert, 1971; Sanders, 1968; Simberloff, 1972).

The second main goal was to explore β-diversity, the variation in species composition across space or time (Legendre & Legendre, 1998). To do this, we used the Morisita–Horn Index, and the Jaccard Index (see Appendix A: Table 1 for analyses using additional diversity indices). The Morisita–Horn Index takes abundance information into account, whereas the Jaccard Index uses only presence/absence information (Magurran, 2004). These measures of community similarity were all converted to dissimilarity measures (i.e. distance) = (1–similarity). These distances were then used to create a dendrogram using nearest neighbor-joining on group averages (UPGMA) as implemented in MATLAB's LINKAGE function. All statistical analyses were performed in MATLAB v 2006b (Mathworks Incorporated, 2006).
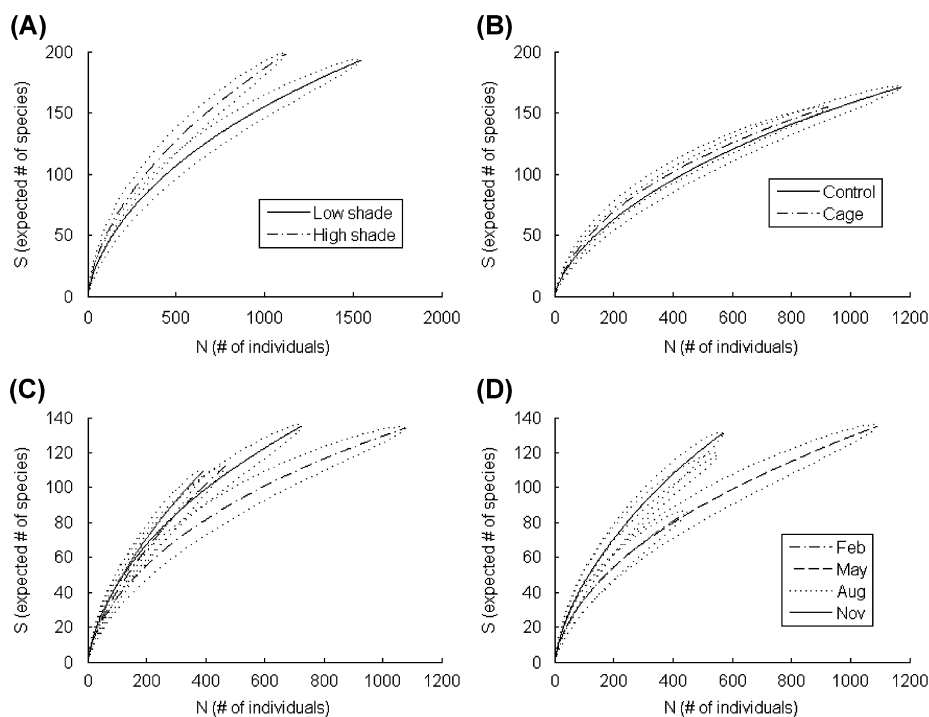
Fig. 1. Rarefaction comparisons. Each graph plots expected species richness (S) on the *y*-axis vs. sample size (*N*) on the *x*-axis. The dotted enclosing shapes represent 95% confidence intervals. (A) High-shade vs. low-shade management. (B) Flying vertebrate exclosure cage vs. uncaged control. (C) Site effects: the curves with fewer than 500 individuals are for the two Huixtla sites, while the curves with much greater than 500 individuals represent the Tapachula sites. The dashed lines are for low-shade and the solid lines are for high-shade. (D) Seasonal effects.

Results

Accuracy of morphospecies classification

Our ability to ground-truth the morphospecies classification was severely limited both by the limited availability of expertise for many beetle taxa, and also by the presence of undescribed species in all taxa examined by taxonomic specialists. Among the 38 morphospecies from five arbitrarily selected beetle families sent out for review by taxonomic experts, the morphospecies analysis contained two instances of inaccurate splitting, one instance of inaccurate lumping, and one instance of probable inaccurate splitting. This suggests that the correspondence between morphospecies and actual species was generally high.

α-Diversity (species richness)

In a sample with 2662 individual beetles, we identified 293 morphospecies from 42 families. The rarefaction curves depicted in Fig. 1 are still rising rapidly even at the largest sample sizes, indicating that the assemblage of beetles dwelling on coffee plants is extraordinarily rich.

Effects of treatments on α-diversity

The rarefaction curves indicate that:

1. High-shade sites have significantly greater richness than low-shade sites (Fig. 1A).
2. One area (Huixtla) has significantly greater richness than the other area (Tapachula) (Fig. 1C).
3. There is significant variation in richness between months, with February and May (dry season and beginning of wet season, respectively) significantly less species rich than August and November (wet season and end of wet season, respectively) (Fig. 1D).
4. There is virtually no difference in richness between plots with flying vertebrate exclusion cages and control plots (Fig. 1B).

β-Diversity (species composition)

Species composition patterns reveal a homogenizing effect of low-shade management. The high value of the Morisita–Horn index obtained for the comparison between the two low-shade sites stands out from all of the other pairwise comparisons between sites (Fig. 2A, and see Appendix A: Table 1). The patterns depicted in Fig. 2 suggest that moving to a low-shade management
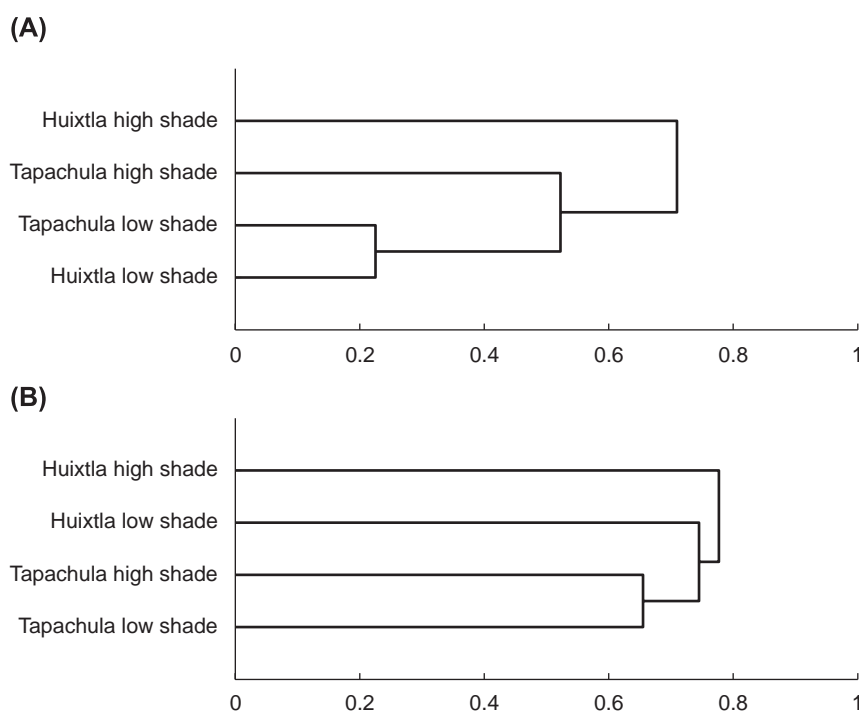
Fig. 2. Homogenization effect of production. The dendrograms illustrate the relationships between the two geographic areas and the two management types, using the abundance-based Morisita–Horn index (A) and the incidence-based Jaccard index (B). The x-axis indicates branch length.
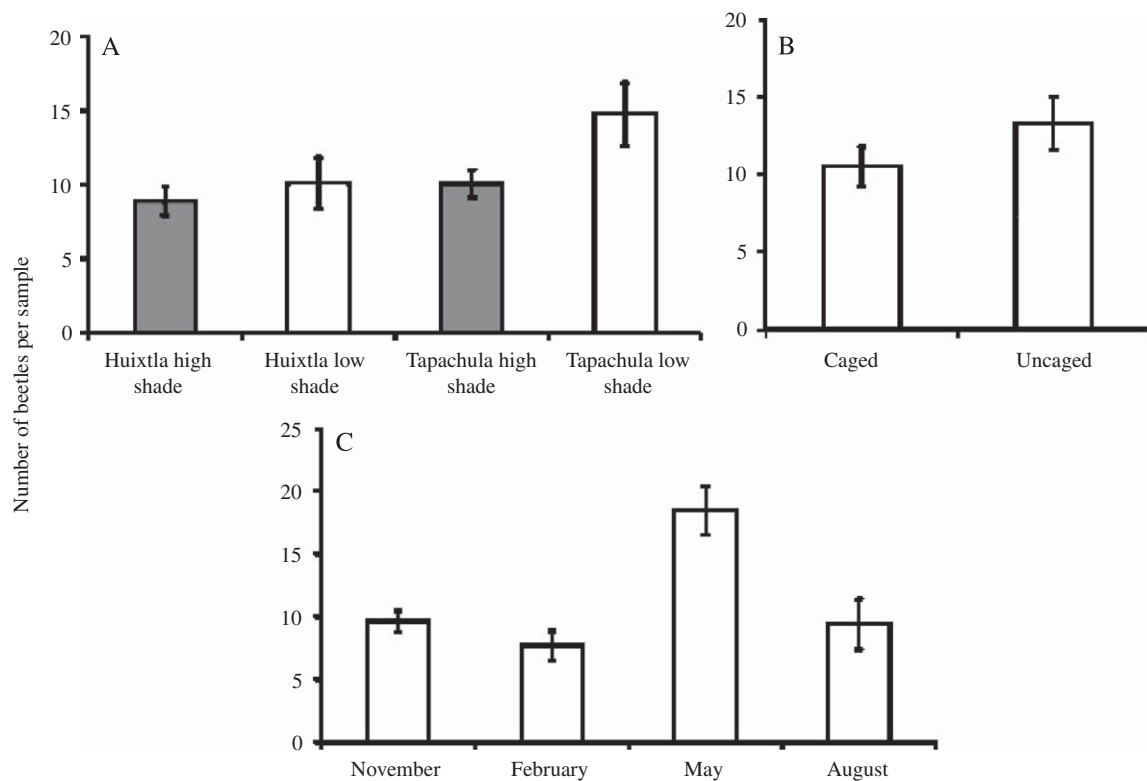
Fig. 3. Beetle abundance patterns. Mean (±standard error) number of beetles per sample is shown for (A) the four study sites (shading represents high-shade management). The abundance of beetles recorded at the Huixtla high-shade site may not be directly comparable to that of the other three sites because of a slight variation in the amount of foliage sampled for arthropods at this site; (B) plots in which flying vertebrates had been experimentally excluded (caged) vs. control plots (uncaged); and (C) the four different months in which beetles were sampled.

style moves the two sites away from the strong differences in composition found in the high-shade management to a highly homogenized community structure (i.e. both low-shade sites are similar). This pattern holds true for all indices of similarity that use abundance information but is less distinct for indices that use only presence/absence information (see Appendix A: Table 1).

Species composition patterns also reveal high β-diversity over both space and time in this system. The abundance-based Morisita–Horn Index reflects significant changes in species composition between months and between the two geographically separated areas (see Appendix A: Table 1). The between-month and between-area values for this index stand in contrast to the higher values of compositional similarity between flying vertebrate exclusion and control plots, indicating relatively weak effects of predator removal on beetle community composition.

Abundance

Comparisons of the numbers of individual beetles collected per sample reveal high beetle abundance

in May relative to the other 3 months of sampling (Fig. 3C), and at the Tapachula low-shade site relative to the other three sites (Fig. 3A). Pairwise comparisons between May and each of the other months, and between Tapachula low-shade and each of the other sites were statistically significant (two-tailed t-test not assuming equal variance across samples, $p < 0.05$), and were the only statistically significant differences between months or between sites in this system. Fig. 3B contains a suggestion of slightly higher beetle abundance in the uncaged control plots relative to the flying vertebrate exclusion plots, but this difference was not statistically significant (two-tailed t-test not assuming equal variance across samples, $p = 0.19$).

Discussion

Our data suggest that low-shade cultivation simplifies the understory foliage-dwelling beetle community of coffee agroecosystems. This simplifying effect can be seen in two distinct ways. First, low-shade sites demonstrate lower α-diversity (reduced species richness) relative to high-shade sites (Fig. 1). Fig. 1C reveals that while each high-shade site is significantly richer than its

low-shade neighbor, the two geographically separate areas differ in species richness such that the low-shade site in the Huixtla area appears roughly equivalent in species richness to the high-shade site in the Tapachula area. The most likely explanation for this result is that both cultivation type and geographic variation exert significant influences on species richness in this system.

Second, low-shade cultivation homogenizes the species composition of beetle communities (Fig. 2, see Appendix A: Table 1). In effect, low-shade coffee cultivation reduces geographic β-diversity in this system. It is important to note that this homogenizing effect is most strongly seen in the Morisita–Horn index, which takes species' abundances into account. This pattern appears to be driven more by similar relative abundance profiles of particular species in these communities than by shared sets of species that are exclusive to one cultivation type or another. The species that best illustrates this is a species of major agricultural significance, the coffee berry borer, Hypothenemus hampei (Ferr.). We sampled 72 and 129 individuals of this species in the two low-shade sites, and 16 and 7 individuals in the two high-shade sites, respectively, suggesting that high-shade cultivation may confer some degree of control of this pest species, consistent with the "insurance hypothesis" (Perfecto et al., 2004; Yachi & Loreau, 1999).

The strong effects of cultivation type evident in our data set are particularly notable given that differences in cultivation technique mostly impact the shade, or canopy stratum, while our samples were collected in the coffee understory. We expect that our sample contained mostly species that feed or forage directly on coffee, or on the herbaceous vegetation that grows in between coffee bushes. However, it is possible that an influx of beetles from a highly diverse pool of canopy-restricted species into the understory may account for the higher levels of α- and β-diversity we observed in high-shade coffee farms. This pattern could also have been produced by a high degree of interconnectedness and faunal exchange between the canopy and the understory, or by a microclimatic effect of increased shade on the beetle fauna of the understory, itself. A final possibility is a landscape $\times$ cultivation interaction effect, wherein high-shade cultivation permits an influx of beetles from a species-rich pool in the surrounding landscape.

Our analysis suggests that flying vertebrates exert a negligible effect upon beetles in the coffee stratum in this system. This is suggested by the lack of a significant effect of flying vertebrate exclusion on the abundance (Fig. 3B), species richness (Fig. 1B), or species composition (see Appendix A: Table 1) of beetles. This result contrasts strongly with the results of Greenberg et al. (2000), who demonstrated significant depression of large (>5 mm in length) arthropod abundance on coffee plants by flying vertebrates in low-shade coffee plantations in the Polochic Valley in Guatemala. Beetles smaller than 5 mm in length were not analyzed by Greenberg et al. (2000) but dominate our samples, representing 78% of the species and 90% of the individuals in our data set. However, large beetles ($\geqslant 5$ mm in length) show the same lack of flying vertebrate exclusion effects in our study (total abundances of 102 and 110 large beetles in post-cage samples from caged and control plots, respectively, two-tailed t-test not assuming equal variance $p = 0.69$). Of the 293 beetle morphospecies in our data set, only six occurred in significantly higher abundance in either experimental treatment at the $p < 0.05$ level (two-tailed t-tests not assuming equal variance), fewer than would be expected at random if there were no flying vertebrate exclusion effects. This rules out the possibility of any significant effect of flying vertebrates on any particular taxon or guild of beetles. We also found no evidence of significant seasonal variation in the effects of flying vertebrates on beetles. We therefore conclude that the direct or indirect trophic links between flying vertebrates and foliage-dwelling beetles in the coffee understory in this system are weak.

Our results, combined with those of several other studies in our system, suggest that the effects of flying vertebrates on arthropods are much stronger in the canopy stratum of coffee plantations than in the coffee-dominated understory. At one of our study sites, Philpott et al. (2004) demonstrated that flying vertebrates depress the abundance of arthropods, including beetles, on branches of Inga shade trees. Jedlicka et al. (2006) combined flying vertebrate exclosures in Inga shade trees with a subset of our exclosures in coffee at one of our study sites to show that flying vertebrates significantly depress the abundance of both large (>5 mm) and small (<5 mm) arthropods in Inga foliage of the canopy, but not in the coffee foliage of the understory. However, Perfecto et al. (2004) demonstrated increased removal rates of lepidopteran larvae, presumably by flying vertebrates, from coffee foliage outside of flying vertebrate exclosures in one of our high-shade sites.

The variation in species richness and composition across months reveals significant but complex seasonal variation in this system. The climate in this region is characterized by distinct wet-dry seasonality (Cardoso, 1979). Arthropod communities in seasonal tropical forests are known to undergo abrupt and dramatic increases in abundance and activity in response to the onset of the wet season (Janzen, 1983). Our May samples were collected at the end of April and beginning of May, roughly 1 week after the onset of significant wet season rains in 2001 (see Appendix A: Graph 2). These samples show a distinct abundance spike relative to the other months of sampling (Fig. 3C), yet the species

richness and species composition comparisons do not reveal a simple wet–dry season grouping of the monthly samples. The species accumulation curve of the February sample, taken during the heart of the dry season, is very similar to that of the May sample taken in the early wet season (Fig. 1D). Both of these months appear less species rich than do August and November in the middle, and toward the end of the wet season, respectively (Fig. 1D). The pairwise comparisons of species compositional similarity reveal roughly equivalent levels of species turnover across all 3-month intervals, hence, there is no clear separation of dry and wet season beetle faunas reflected in our data. The seasonality of rainfall in the year of our study was typical of the long-term average pattern in the region (see Appendix A: Graph 1).

Acknowledgments

Appendix A. Supporting Information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae. 2008.04.004.

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