



## Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico

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Received 7 January 2002; accepted in revised form 3 July 2002

**Key words:** Ants, Biodiversity, Birds, Butterflies, Coffee, Indicator taxa, Mexico, Species richness

**Abstract.** We compare species richness of birds, fruit-feeding butterflies and ground-foraging ants along a coffee intensification gradient represented by a reduction in the number of species of shade trees and percentage of shade cover in coffee plantations. We sampled the three taxa in the same plots within the same period of time. Two sites were selected in the Soconusco region of the state of Chiapas, Mexico. Within each site four habitat types were selected and within each habitat type four points were randomly selected. The habitat types were forest, rustic coffee, diverse shade coffee, and intensive coffee (low density of shade). We found different responses of the three taxa along the intensification gradient. While ants and butterflies generally decrease in species richness with the decrease of shade cover, birds declined in one site but increased in the other. Ant species richness appears to be more resistant to habitat modification, while butterfly species richness appears to be more sensitive. Bird species richness was correlated with distance from forest fragments but not with habitat type, suggesting that scale and landscape structure may be important for more mobile taxa. For each of these taxa, the rustic plantation was the one that maintained species richness most similar to the forest. We found no correlation between the three taxa, suggesting that none of these taxa are good candidates as surrogates for each other. We discuss the implications of these results for the conservation of biodiversity in coffee plantations, in particular, the importance of distinguishing between different levels of shade, and the possibility that different taxa might be responding to habitat changes at different spatial scales.

### Introduction

#### *Coffee and biodiversity*

Recent studies in traditional shaded coffee plantations have demonstrated this agroecosystem's potential as a refuge for biodiversity (Perfecto et al. 1996; Moguel and Toledo 1999). These studies have been carried out independently with a variety of taxa, but primarily with birds (Wunderle and Latta 1996; Estrada et al. 1997; Greenberg et al. 1997a, 1997b; Calvo and Blake 1998; Wunderle 1999; Johnson 2000) and arthropods (Nestel and Dickschen 1990; Ibarra-Núñez et al. 1993; Perfecto and Vandermeer 1994, 2002; Perfecto and Snelling 1995; Perfecto et al. 1997; Ibarra-Núñez and Garcia-Ballinas 1998; Johnson 2000).

The last 15 years have seen an intensification of production in many coffee

plantations in Northern Latin America (Perfecto et al. 1996). The intensification process involves the use of high-yielding coffee varieties and the reduction or complete elimination of shade trees (Rice 1996). The phenomenon has been most profound in Costa Rica and Colombia, where more than 40% of the coffee farms have experienced a high degree of shade reduction (Perfecto et al. 1996). However, in Mexico, the intensification process was not as ubiquitous and only certain areas were affected (Rice 1997). In a recent review, Moguel and Toledo (1999) estimated that between 60 and 70% of the coffee areas in Mexico are under traditional management with relatively high levels of shade created by the canopy of a variety of shade tree species. Furthermore, they reported that many of the coffee-growing areas in southern Mexico coincide with areas that the CONABIO (a government agency responsible for the conservation of biodiversity) has designated as priority areas for conservation due to their species richness and high levels of species endemism (Moguel and Toledo 1999).

There are still many gaps in our knowledge of biodiversity in coffee agroecosystems. Although it is clear that biodiversity declines along the intensification gradient, we do not know the shape of the biodiversity loss curve, nor can we say that the curve will be identical for different taxa.

#### *Taxa comparisons*

In this study we present data on species richness for three taxa – birds, butterflies, and ground-foraging ants – collected on coffee farms along a gradient of increasing management intensity and decreasing shade cover. Several studies have examined the diversity of birds (Wunderle and Latta 1996; Greenberg et al. 1997a, 1997b; Calvo and Blake 1998; Johnson 2000) and ants (Nestel and Dickschen 1990; Perfecto and Vandermeer 1994; Perfecto and Snelling 1995) on coffee plantations but no other study has examined these taxa in the same plots during the same period of time. Butterflies have been widely examined for their potential to serve as indicators of ecological disturbance, but most previous research has concentrated on disturbance associated with logging activities (Noss 1990; Kremen 1992, 1994; Brown 1996; Hamer et al. 1997; Lawton et al. 1998). Furthermore, very little research has been done with butterflies on coffee farms. Examining species richness data from these three taxonomic groups therefore allows us to compare how each group responds to changes in management, and sheds light on the question of whether any group is suitable to serve as a surrogate for the others. The recent interest in shade coffee certification programs requires a better understanding of how coffee technification affects different taxa in order to develop a realistic and effective strategy for biodiversity conservation in the coffee agroecosystem.

### **Study site and methodology**

#### *Coffee cultivation and study site*

The study was conducted during the summer of 1998 in coffee farms and forest

fragments at two locations in the Soconusco region of the State of Chiapas, in southern Mexico. The Soconusco region is located in the extreme southern part of Mexico along the border with Guatemala on the Pacific slope of the Sierra Madre de Chiapas (Figure 1). The coffee zone ranges from 300 to 1400 m a.s.l. (Richter 1992). However, our plots were located within a narrower altitudinal band, ranging from 900 to 1100 m a.s.l. Precipitation data taken from one of the study sites (*Finca Irlanda*) for a 70-year period indicate a steady decline in annual precipitation from 4500 to approximately 4200 mm (Richter 1992).

Traditional or rustic methods are used only to a limited extent in the Soconusco region, which is dominated by large-scale farms. However, because of the rugged topography the intensification of coffee farms has been also limited in this region. In the late 1980s and early 1990s, government programs as well as the high productivity achieved by highly technified farms in Guatemala and Costa Rica, stimulated the 'technification' of large farms in the Soconusco region. On many farms, shade trees were cut, traditional coffee varieties were replaced by new varieties, weeds were controlled by herbicides, and chemical fertilization replaced the use of nitrogen-fixing shade trees (Richter 1992; Rice 1997). However, this technification was short-lived as farms began experiencing high levels of soil erosion. During the period that this study was conducted, the region had examples of management systems that ranged from rustic farms in certain areas highly susceptible to soil erosion to farms with a low density of shade trees belonging to a few genera, but primarily *Inga*. Low-density monospecific shade coffee or shadeless sun coffee farms are rarities in this region.

The study was conducted in several coffee farms (herein referred to as *Fincas*) in the municipalities of Tapachula and Huixtla. In Tapachula, plots were established at *Finca Irlanda* and *Finca Hamburgo*, while in Huixtla plots were established at *Finca Belén* and *Finca Bélgica*. Both *Finca Irlanda* and *Finca Belén* are large (approximately 300 ha) organic farms. On each of these farms there are small fragments (10–30 ha) of forests that are maintained as reserves for wildlife or water conservation purposes or because they are located in areas of extreme slope. Several shade management systems can also be found within each of these organic farms. *Finca Hamburgo* and *Finca Bélgica* are two non-organic farms adjacent to *Finca Irlanda* and *Finca Belén*, respectively. Given this landscape, in each of the two sites (Tapachula and Huixtla) we established plots in four different management systems: (1) a forest fragment (Forest), (2) an area of rustic organic coffee (Rustic), (3) a diverse shade organic coffee farm [Diverse shade; similar to the 'traditional polyculture' in Moguel and Toledo's (1999) classification], and (4) a low diversity shaded non-organic coffee farm [Intensive; similar to the 'commercial polyculture' in Moguel and Toledo's (1999) classification] (Figure 2).

During the analysis of the vegetation it became evident that the rustic coffee farms in the two sites (Tapachula and Huixtla) were different in terms of vegetation characteristics (Table 1). While there were no significant differences in canopy cover between the Tapachula and Huixtla sites for the Forest, Diverse shade, and Intensive habitats (Wilcoxon signed rank tests,  $P > 0.1$ ), there were slight significant differences for the two Rustic habitats (Wilcoxon signed rank tests,  $P = 0.068$ ). The Rustic habitat in Huixtla, with 92.25% canopy cover and 54 tree

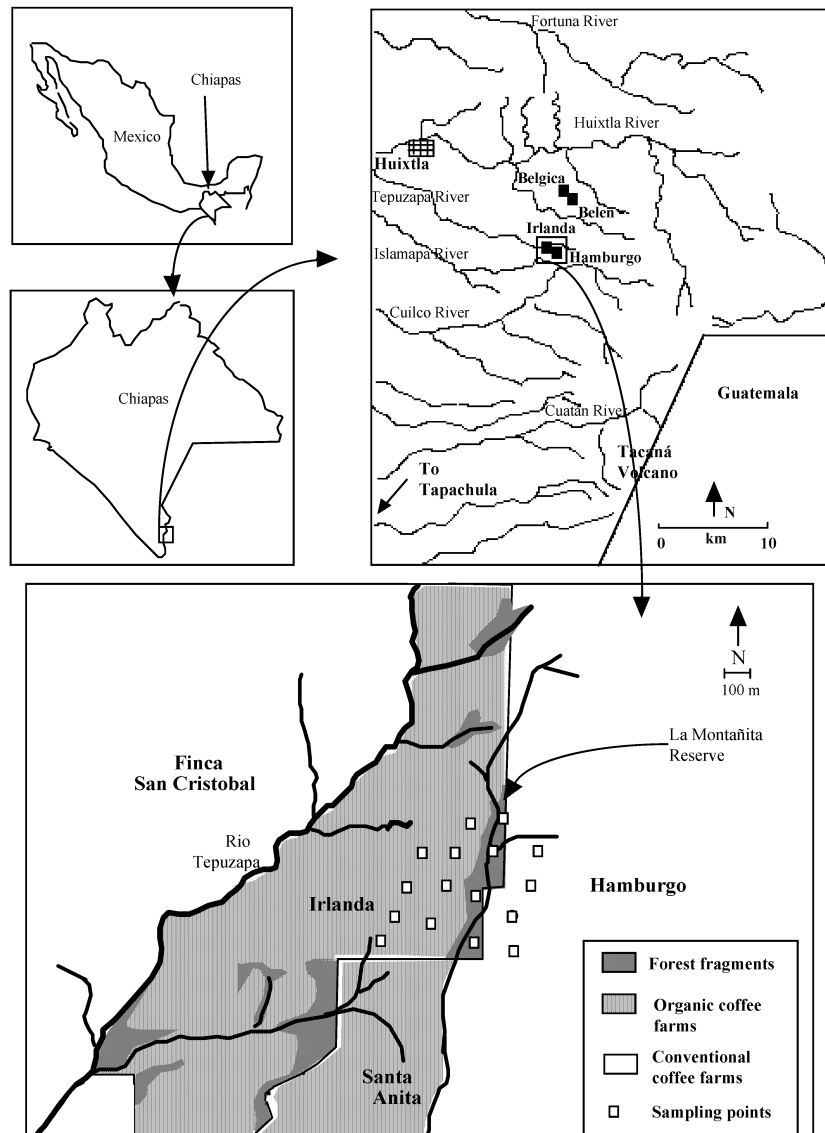
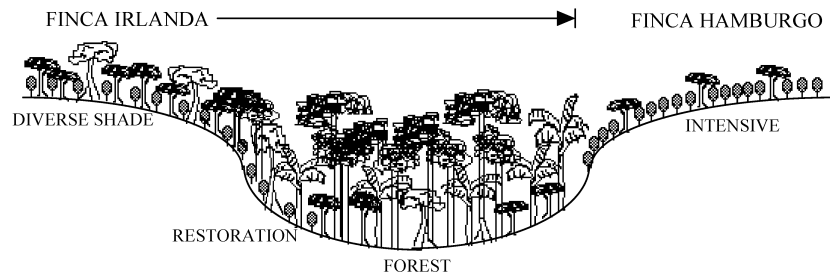


Figure 1. Map of the region where the study was conducted, indicating the two study sites and the four coffee farms.

species, was more floristically diverse and densely shaded than the Rustic habitat in Tapachula with 54% canopy cover and 16 tree species. Because in the Tapachula site we could not find a truly rustic farm, we located the sampling points in *Finca Irlanda* within an area that is being restored to rustic by planting trees from the forest fragments, therefore increasing the density and diversity of shade trees. For this

## A. TAPACHULA



## B. HUIXTLA

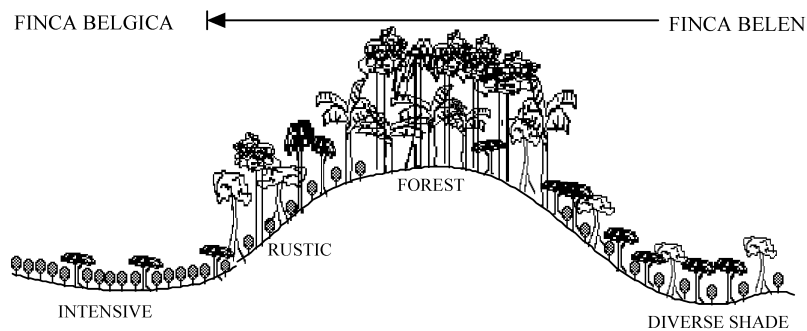


Figure 2. Diagram of the location of the three coffee habitat types with respect to the location of the forest reserve for each study site. Note that the forest reserve in Tapachula is a riparian forest while the reserve in Huixtla is a hill top.

Table 1. Average percent shade cover and total tree species richness for the four habitats at the Tapachula and Huixtla sites.

	% Canopy cover		Tree spp. richness	
	Tapachula	Huixtla	Tapachula	Huixtla
Forest	100	100	–	–
Rest/Rust	54	92.25	16	54
Diverse shade	59	48.22	9	10
Intensive	14	25	7	6

reason, we decided to separate these two habitats in our analysis of the tri-taxa comparison and called the habitat in *Finca* Irlanda, Restoration.

In each of these habitats we selected four random points separated by a minimum 100 m and located, where possible, 100 m from edges with other habitat types.

These same points were used to sample the three focal taxa: ground ants, fruit-feeding butterflies and birds. The linear shape of the *Finca* Irlanda forest fragment, a riparian zone, and the adjacent restoration area limited distance from edge to 50 m in some cases for both habitat types. Samples in all habitats in the Tapachula site were taken from June 11–23, 1998 and in all habitats of the Huixtla site from June 30 to July 11, 1998.

#### *Ant sampling*

Ground-foraging ants were sampled by establishing a  $14 \times 14 \text{ m}^2$  plot with the random point located at the center of the plot. Tuna fish baits (with a volume of approximately  $1 \text{ cm}^3$ ) were placed on the ground, forming a  $7 \times 7$  grid system with baits separated by 2 m from each other for a total of 49 baits per plot (Perfecto and Snelling 1995). Baits were examined 30 min after they were placed and, when necessary, samples were collected for further identification in the laboratory. Samples of ground-foraging ants were conducted only in three of the four random points per habitat.

#### *Butterfly sampling*

Two standard butterfly bait traps (Kremen 1994; DeVries et al. 1997) were set as closely as possible to the center of each sampling point, one in the understory (approximately 1 m above the ground) and one in the canopy (hung from a branch of an emergent tree). Traps were set for a period of 8 days within each treatment and were baited with a mash of fermented plantain or banana before each sampling day. Traps were checked on alternate days within the 8-day period for a total of four samples per trap. Each station was visited at approximately the same time of day during each sample to ensure an equal period of time between samples (48 h). Due to logistical problems butterfly data were not collected at *Finca* Bélgica (the Intensive habitat in Huixtla).

While Sparrow et al. (1994) noted that visual censuses were necessary as well to get a more complete assessment of the tropical forest butterfly community (primarily Pieridae and Papilionidae families), G.T. Austin (personal communication) commented that visual censuses are extremely hard to standardize, particularly if the researcher is not familiar with local butterfly fauna. Due to the importance of standardizing effort between treatments, sampling focused on the fruit-feeding guild of butterflies (primarily Nymphalidae) that are attracted to hanging traps. All captured individuals were collected as voucher specimens for later identification, or recorded, marked and released. Recaptures were recorded but not counted as new sightings. All field identifications were performed using *The Butterflies of Costa Rica* (DeVries 1987) and *Mariposas Mexicanas* (de la Maza Ramírez 1987). Voucher specimens were confirmed with Roberto de la Maza of the National Institute of Ecology in Mexico City.

### *Bird sampling*

Birds were sampled by means of point counts (Wunderle and Latta 1996; Greenberg et al. 1997a, 1997b) at each habitat type. Four point counts (10 min each) were conducted at each sample location (four per habitat type). Each morning, beginning at dawn, points were sampled, altering direction and starting point to minimize temporal bias (Bibby et al. 1992). All birds heard and seen within 25 m were noted during each 10-min point count, with the exception of soaring birds that were not included in this study. Unrecognized bird songs were recorded for later evaluation and comparison with reference tapes. Due to logistical problems bird data were not collected at *Finca* Bélgica.

### *Vegetation sampling*

At each point vegetation was sampled using a modification of the Breeding Biology Research and Monitoring Database protocol (Martin and Geupel 1993). Data were taken on shade tree species, tree height, number of coffee plants, height of coffee plants, presence or absence of epiphytes, vegetation structure, and percentage canopy cover. Percent canopy cover was obtained using a LAI 2000 Plant Canopy Analyzer (LICOR, Lincoln, Nebraska, USA). This instrument estimates canopy gap fraction by means of the diffuse non-interceptance, which indicates the probability of diffuse radiation from the upper hemisphere penetrating the canopy to a particular location (Welles 1990). Ten measurements were taken at random within a 5 m radius of the sampling point. For details of the other methods for the vegetation data see Mas (1999). Here we report data only for percentage canopy cover and tree species diversity (Table 1).

### *Species richness and statistical analysis*

One of the biggest challenges of studying and managing tropical diversity is the impossibility of completely surveying all of the species present. As a result, any attempt to compare biodiversity between different locations or among different taxonomic groups confronts the problem that an unknown number of species were left out of every sample, making comparisons of sampled diversity equivocal. Various diversity indices have been created to compensate for this limitation, but all come with their own sets of assumptions and drawbacks (Magurran 1988). For comparisons of species richness, Nichols et al. (1998) provide an elegant solution in the form of a software package, COMDYN, that uses a bootstrap approach to predict an estimate of total species richness. The details of this approach and citations where it has been used are available on-line (<http://www.mbr-pwrc.usgs.gov/software/comdyn.html>; Community Dynamics Computations 1999). Using this software package, we estimated total species richness for each taxonomic group and used these estimated values for pairwise comparisons. The relationships between the three taxa were examined with Pearson correlation analyses.

## Results

We found no consistent pattern of diversity reduction with habitat intensification for the three taxa (Figure 3). While, as in previous studies, species richness of ground ants and butterflies generally declined with habitat intensification or disturbance (Bowman et al. 1990; Perfecto and Vandermeer 1994; Hill et al. 1995; Perfecto and Snelling 1995; Lawton et al. 1998), bird species richness showed a different pattern in the two sites. Furthermore, no one taxa appeared to be a good indicator of species richness for the other taxa included in this study. There were no statistically significant correlations among birds, butterflies and ground ants (Table 2).

Generally, with the exception of birds in the Tapachula site (Figure 3A), species richness declines with agricultural intensification. However, this decline follows a

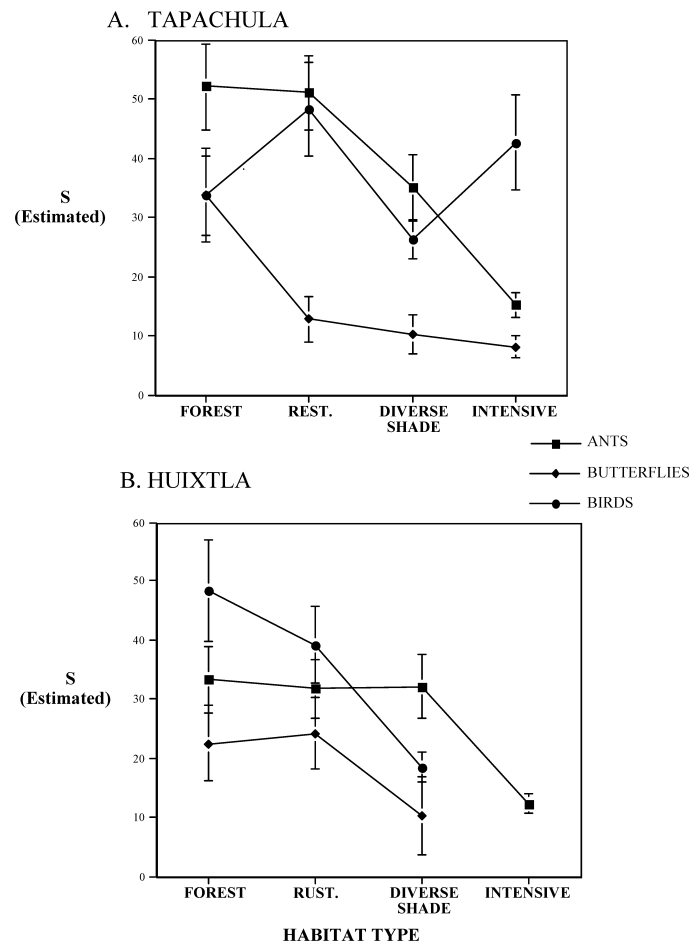


Figure 3. Estimated species richness for ants, butterflies and birds for four habitat types for the Tapachula (A) and the Huixtla (B) sites separately. Error bars were constructed with the standard error of the means.



Table 2. Pearson correlations between all three taxa for the Tapachula and Huixtla sites combined.

	Butterflies	Birds
<i>Ants</i>		
Pearson correlation	-0.260	0.265
Significance	0.256	0.246
<i>n</i>	21	21
<i>Butterflies</i>		
Pearson correlation		-0.094
Significance		0.634
<i>n</i>		28

different pattern for each group. At the Tapachula site, ants follow a convex pattern of richness reduction, while butterflies follow a concave pattern. On this site birds had the highest levels of species richness in the Restoration and Intensive habitats. At the Huixtla site all three taxa show a concave pattern of decline in species richness, but this pattern is exaggerated for the ants, which exhibit a decline only in the Intensive habitat (Figure 3B). However, we suspect that the high species diversity recorded for the Diverse shade habitat in Huixtla was the result of the short period of time (3 months) that had passed since the area was converted from a rustic plantation to a diverse-shade plantation. Of the coffee habitats, the Rustic habitat at the Huixtla site appears to be the most similar to the forest habitat in terms of species richness for all taxa.

## Discussion

This study suggests that the response of species richness to habitat modification, and in particular to the intensification of the coffee agroecosystems in southern Mexico, is different for different taxa. Other studies that have examined species richness for different organisms along a disturbance gradient have found similar results (Brown 1996, 1997; Lawton et al. 1998). Others have warned about the difficulties of using one or a few taxa to predict the species richness of other groups (Oliver and Beattie 1993; Prendergast et al. 1993; Dobson et al. 1997; Prendergast and Eversham 1997; Lawton et al. 1998). While the appeal to study surrogate taxa remains strong, the results thus far have been equivocal. Studies bringing together large assemblies of taxa from tropical regions have found some correlations between taxa, but have revealed no single species or groups of species suitable for use as predictors of overall biodiversity (Howard et al. 1998; Lawton et al. 1998). Ricketts et al. (1999) provide an expansive analysis for nine taxa in North America and found similar scatter of pairwise correlations once they had corrected for latitude, and no single taxon that was significantly correlated with the index they created to represent overall species richness. They were able to create a richness index composed of butterflies, plants and reptiles that they felt could serve as a predictor of overall richness, but they cautioned that geographic patterns of prediction error required careful selection of taxa appropriate for every region.

Although in this study both butterflies and ground ants showed a general pattern of species richness decline at both sites, the pattern was different for the two groups (Figure 3). The results presented here suggest that ground ants may be more resistant to habitat modification and/or disturbance than butterflies. The difference between ground ants and butterflies can best be illustrated by examining the response in species richness of these two groups in the Tapachula site, and in particular the change in species richness from Forest to Restoration (Figure 3A). While ant species richness was practically identical between Forest and Restoration, butterfly species richness declined dramatically. Other studies have shown that butterfly diversity and species composition change predictably in response to changes in vegetative structural diversity and microhabitat characteristics such as temperature and moisture (Estrada et al. 1997; Hamer et al. 1997). The Restoration habitat had a significantly lower canopy cover than the Forest, and, although we did not take any data on moisture and temperature, the Forest habitat was noticeable cooler and more humid than the Restoration habitat. Microclimatic factors might have been particularly important the year that this study was conducted because it was the summer after a drought caused by the 1997 El Niño event. The dramatic decline of butterfly species richness in every agricultural habitat except for the Rustic habitat (Huixtla) could have been a consequence of the very dry conditions of the less shaded farms. This study was conducted during a narrow period of the annual cycle and therefore results should be interpreted with caution. The results presented here apply only to the wet season, since shade and microclimatic conditions change during the dry season.

Ground ants, on the other hand, have been shown to be good indicators of coarser changes in habitat (Majer 1983; Andersen 1997) and the vegetation differences between Forest and Restoration do not appear to be enough to generate a change in ant species richness.

In this study, bird response was different in the two sites. At the Huixtla site species richness declined with habitat modification, similar to what has been reported in previous studies (Wunderle and Latta 1996; Greenberg et al. 1997a, 1997b; Calvo and Blake 1998). However, at the Tapachula site bird species richness might have been confounded by distance from the forest, since both Restoration and Intensive habitats were adjacent to the Forest habitat. We did find a significant correlation between birds and distance from the forest fragment at the Tapachula site (Table 3). No correlation was found for butterflies or ground ants. While this correlation is based only on three distances from the forest, it still suggests a possible explanation for the difference in patterns between the two sites. If this is the case, birds may be responsive to landscape level factors, such as the presence of forest fragments or riparian corridors. With generally higher mobility, bird diversity may respond to management at a different scale than other taxa. At the scale of the plantations included in this study (approximately 300 ha), the location of less intensively managed patches (such as forest fragments) may have affected bird species richness as much or more than actual management practices. Thus, landscape structure should be a consideration when evaluating how birds are distributed in coffee management systems (Wunderle 1999). The importance of forest frag-

Table 3. Pearson correlations between estimated species richness and distance from the forest for ants, butterflies and birds for the Tapachula site.

	Distance from the forest
<i>Ants</i>	
Pearson correlation	-0.195
Significance	0.875
<i>n</i>	3
<i>Butterflies</i>	
Pearson correlation	-0.312
Significance	0.798
<i>n</i>	3
<i>Birds</i>	
Pearson correlation	-1.000
Significance	0.007
<i>n</i>	3

ments has also been demonstrated for moths species richness in Costa Rica, where this variable was shown to be more important than habitat (Ricketts et al. 2001). Evaluating the relative importance of landscape and habitat related factors is further complicated because often shade increases closer to forest fragments in areas that can be more difficult to manage intensively. Steeper slopes and distance from the center of plantation activity (the processing plant) may mean that these areas receive less attention during the busy annual cycle. Thus distance from forest and management intensity (vegetation data) may co-vary. Further studies are needed to determine how the presence of forest fragments affects bird species richness in the coffee matrix.

These results should be taken with caution since the data we present here is only of overall species richness (number of species), not taking into account the identity of those species. This we consider to be only one aspect of biodiversity conservation in agroecosystems. The other, and crucial aspect is the identity of species. In particular it would be important to know how many forest species are maintained in shaded coffee agroecosystems, and what level of shade maintains the highest number of forest species. (For an analysis that includes the identity of species and changes in forest species along the intensification gradient see Mas and Dietsch 2003.)

Recently, conservation organizations have begun to pay attention to the coffee agroecosystem as a way to combine biodiversity conservation and economic development. One tool that has gained popularity in recent years is the certification of shade coffee. As conservation organizations develop programs for the conservation of biodiversity in coffee plantations, it is important to gather data that could inform these conservation programs. Initially the issue was framed in the context of shade versus sun coffee. This study highlights the importance of distinguishing between different levels of shade when developing criteria for shade coffee certification. Furthermore, it suggests that only the more rustic coffee plantations are able to maintain levels of biodiversity similar to those found in forests for a variety of taxa. Therefore, shade coffee certification (with a premium price attached to it)

may be an effective mechanism for maintaining very diverse shade coffee agroecosystems (see also Mas and Dietsch 2003). Finally, the results of this study suggest that different taxa might be responding to changes at different spatial scales and that landscape level processes might be more important for birds, which have a high degree of mobility, than for ants.

### Acknowledgements

We wish to thank Walter Peters of *Finca Irlanda*, Tomas Edelman from *Finca Hamburgo* and the ISMAM cooperative for allowing us to conduct this study on their farms and giving us support throughout the time that we were conducting the study. We also thank ECOSUR-Tapachula and Dr Guillermo Ibarra-Núñez and Gustavo López for providing logistical support and access to laboratory facilities. Alvaro García-Ballinas from ECOSUR helped with the identification of some of the ant species, Dr Javier de la Maza helped with the design of the butterfly traps and Dr Roberto de la Maza corroborated butterfly identification. Darci Andresen, Jay West and Daniel Griffith helped with data collection in the field. This study was partially funded by the Latin American and Caribbean Study Program, the School of Natural Resources and Environment of the University of Michigan, the Horace Rackham Graduate School of the University of Michigan, the Kalamazoo Audubon Society and an NSF grant DEB-9981526.

### References

- Andersen A.N. 1997. Using ants as bioindicators: multiscale issues in ant community ecology. *Conservation Ecology* (on-line) 1 (<http://www.consecol.org/Journal/vol1/iss1/art8/>).
- Bibby C.J., Burgess N.D. and Hill D.A. 1992. *Bird Census Techniques*. British Trust for Ornithology and the Royal Society for the Protection of Birds. Academic Press, London.
- Bowman D.J.M.S., Woinarski J.C.Z., Sands D.P.A., Wells A. and McShane V.J. 1990. Slash-and-burn agriculture in the west coastal lowlands of Papua New Guinea: responses of birds, butterflies and reptiles. *Journal of Biogeography* 17: 227–239.
- Brown K.S. 1996. The use of insects in the study, inventory, conservation and monitoring of biological diversity in Neotropical habitats, in relation to land use systems. *Decline and Conservation of Butterflies in Japan III*: 128–149.
- Brown K.S. 1997. Diversity, disturbance, and suitable use of Neotropical forests: insects as indicators for conservation monitoring. *Journal of Insect Conservation* 1: 1–18.
- Calvo L. and Blake J. 1998. Bird diversity and abundance on two different shade coffee plantations in Guatemala. *Birds Conservation International* 8: 297–308.
- de la Maza Ramírez R. 1987. *Mariposas Mexicanas: Guía para su Colecta y Determinación*. Fondo de Cultura Económica. S.A. DE C.V., México, D.F.
- DeVries P.J. 1987. *The Butterflies of Costa Rica and Their Natural History*. Princeton University Press, Princeton, New Jersey.
- DeVries P.J., Murray D. and Lande R. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* 62: 343–364.
- Dobson A.P., Rodríguez J.P., Roberts W.M. and Wilcove D.S. 1997. Geographic distribution of endangered species in the United States. *Science* 275: 550–553.

- Estrada A., Coates-Estrada S. and Merrit D. Jr 1997. Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. *Biodiversity and Conservation* 6: 19–43.
- Greenberg R., Bichier P., Cruz Angon A. and Reitsma R. 1997a. Bird populations in shade and sun coffee plantations in Central Guatemala. *Conservation Biology* 11: 448–459.
- Greenberg R., Bichier P. and Sterling J. 1997b. Bird populations in rustic and planted shade coffee plantations of Eastern Chiapas, México. *Biotropica* 29: 501–514.
- Hamer K.C., Hill J.K., Lace L.A. and Largon A.M. 1997. Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *Journal of Biogeography* 24: 67–75.
- Hill J.K., Hamer K.C., Lace L.A. and Banham W.M.T. 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology* 32: 754–760.
- Howard P.C., Viskanic P., Devenport T.R.B., Kigenyi F.W., Baltzer M., Dickinson C.J. et al. 1998. Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* 394: 472–475.
- Ibarra-Núñez G. and García-Ballinas J.A. 1998. Diversidad de tres familias de arañas tejedoras (Araneae: Araneidae, Tetragnathidae, Theridiidae) en cafetales del soconusco, Chiapas, Mexico. *Folia Entomologica Mexicana* 102: 11–20.
- Ibarra-Núñez G., García Ballinas J.A. and Moreno- Próspero M.A. 1993. La comunidad de artrópodos de dos cafetales con diferentes prácticas agrícolas: El caso de los Hymenópteros Resúmenes, XXVIII Congreso Nacional de Entomología, Sociedad Mexicana de Entomología, 23–26 May 1993. Universidad de las Américas, Cholula, Puebla, Mexico.
- Johnson M.D. 2000. Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation. *Biotropica* 32: 133–145.
- Kremen C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 4: 407–422.
- Kremen C. 1994. Biological inventory using target taxa: a case study of the butterflies of Madagascar 4: 407–422.
- Lawton J.H., Bignell D.E., Bolton B., Bloemers G.F., Eggleton P., Hammond P.M. et al. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391: 72–75.
- Magurran M. 1988. *Ecological Diversity and its Measurements*. Princeton University Press, Princeton, New Jersey.
- Majer J.D. 1983. Ants: bioindicators of mine site rehabilitation, land use and conservation. *Environmental Management* 7: 375–383.
- Martin T.E. and Geupel G.R. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64: 507–514.
- Mas A.H. 1999. Butterfly diversity and the certification of shade coffee in Chiapas, Mexico, M.S. Thesis, University of Michigan, Ann Arbor, Michigan.
- Mas A.H. and Dietsch T.V. 2003. An index of management intensity for coffee agroecosystems to evaluate butterfly species richness. *Ecological Applications* (in press).
- Moguel P. and Toledo V.M. 1999. Biodiversity conservation in traditional coffee systems in Mexico. *Conservation Biology* 12: 1–11.
- Nestel D. and Dickschen F. 1990. The foraging kinetics of ground ant communities in different coffee agroecosystems. *Oecologia* 84: 58–63.
- Nichols J.D., Boulinier T., Hines J.E., Pollock K.H. and Sauer J.R. 1998. Inference methods for spatial variation in species richness and community composition when not all species are detected. *Conservation Biology* 12: 1390–1398.
- Noss R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4: 355–364.
- Oliver I. and Beattie A.J. 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology* 7: 562–568.
- Perfecto I. and Snelling R. 1995. Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecological Applications* 5: 1084–1097.
- Perfecto I. and Vandermeer J.H. 1994. Understanding biodiversity loss in agroecosystems: reduction of

- ant diversity resulting from transformation of the coffee ecosystem in Costa Rica. *Entomology (Trends in Agricultural Sciences)* 2: 7–13.
- Perfecto I. and Vandermeer J.H. 2002. The quality of the agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conservation Biology* 16: 174–182.
- Perfecto I., Rice R.A., Greenberg R. and Van der Voort M.E. 1996. Shade coffee: a disappearing refuge for biodiversity. *BioScience* 46: 598–608.
- Perfecto I., Vandermeer J.H., Hanson P. and Cartín V. 1997. Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. *Biodiversity and Conservation* 6: 935–945.
- Prendergast J.R. and Eversham B.C. 1997. Species richness covariance in higher taxa: empirical test of the biodiversity indicator concept. *Ecogeography* 20: 210–216.
- Prendergast J.R., Quinn R.M., Lawton J.H., Eversham B.C. and Gibbons D.W. 1993. Rare species: the coincidence of diversity hotspots and conservation strategies. *Nature* 365: 335–337.
- Rice R.A. 1996. The coffee environment of Northern Latin America: tradition and change. In: Rice R.A., Harris A.M. and McLean J. (eds), *Proceedings from the First Sustainable Coffee Congress*. Smithsonian Migratory Bird Center, Smithsonian Institution, Washington, DC, pp. 105–114.
- Rice R.A. 1997. The land use patterns and the history of coffee in eastern Chiapas, Mexico. *Agriculture and Human Values* 14: 127–143.
- Richter M. 1992. Landwirtschaftliche Schäden in verschiedenen Höhenstufen der Sierra Madre de Chiapas/Südmexiko. *Patermann's Geographische Mitteilungen* 136: 295–308.
- Ricketts T.H., Daily G.C., Ehrlich P.R. and Fay J.P. 2001. Countryside biogeography of moths in fragmented landscapes: biodiversity in native and agricultural habitats. *Conservation Biology* 15: 378–388.
- Ricketts T.H., Dinerstein E., Olson D.M. and Loucks C. 1999. Who's where in North America? *BioScience* 49: 369–381.
- Sparrow H.P., Sisk T.D., Ehrlich P.R. and Murphy D.D. 1994. Techniques and guidelines for monitoring Neotropical butterflies. *Conservation Biology* 8: 800–809.
- Welles J.M. 1990. Some indirect methods of estimating canopy structure. In: Norman J. and Goel N. (eds), *Instrumentation for Studying Vegetation Canopies for Remote Sensing in Optical and Thermal Infraser Regions*. Harwood Academic, London.
- Wunderle J. 1999. Avian distribution in Dominican shade coffee plantations: area and habitat relationships. *Journal of Field Ornithology* 70: 58–70.
- Wunderle J. and Latta S. 1996. Avian abundance in sun and shade coffee plantations and remnant pine forest in the Cordillera Central, Dominican Republic. *Ornitologia Neotropical* 7: 19–34.