

# Shade Coffee: A Disappearing Refuge for Biodiversity

*Shade coffee plantations can contain as much biodiversity as forest habitats*

Ivette Perfecto, Robert A. Rice, Russell Greenberg, and Martha E. Van der Voort

**W**ithin the expanding agricultural frontier in the tropics, one can find a variety of small, managed forest patches and traditional agricultural systems, which provide a refuge for forest-dwelling organisms. These managed habitats are frequently overlooked as potential areas of biodiversity conservation (Pimentel et al. 1992). Furthermore, the conservation biology literature often refers to forest reserves as islands in a sea of devastation, in which the sea is formed by agriculture. Although chemically intensive monocultural systems may fit well with this perception of low

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**The importance of shade coffee as a refuge for biodiversity may not be in the total land it involves, but in its location in areas that have been particularly hard hit by deforestation**

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biodiversity, many other agroecosystems, especially in the tropics, are characterized by high vegetational diversity. One such agroecosystem is coffee, when managed with traditional cultural practices. This popular beverage, used worldwide for centuries, constitutes a major source of household income and foreign exchange for many tropical countries, especially in Latin America.

Coffee is traditionally grown under a canopy of shade trees. Because of the structural and floristic complexity of the shade trees, traditional coffee plantations have relatively high biodiversity. However, coffee plantations increasingly are being transformed into industrial plantations with little or no shade (Figure 1). The way that coffee production evolves in the coming decades is likely to have a tremendous impact on its ability to provide a refuge for tropi-

cal biodiversity. In this article we discuss the role of shade coffee plantations in protecting biodiversity. We focus on northern Latin America, an area encompassing the Caribbean islands, Mexico, Central America, and the Andean countries of South America. However, many of the issues and conclusions discussed here also apply to coffee-exporting countries throughout the tropics.

## **The economic importance of coffee**

Coffee was introduced into the New World by the Dutch in 1723 (Wrigley 1988). During the twentieth century it has reached considerable importance in the world market as an export crop. Production has tripled in northern Latin America since World War II, and area under cultivation has nearly doubled (UNFAO Production Yearbooks).

It is hard to overestimate the importance that coffee production and exportation has had for northern Latin America. More than 32% of the world's coffee comes from this region, where it is the leading source of foreign exchange. Although coffee is produced on only 7.4% of the total arable land, coffee lands at present take up approximately 44% of the area of permanent cropland (UNFAO Production Yearbook 1991). In northern Latin America, coffee plantations cover approximately 2.7 million ha. This total includes roughly 700,000 ha in Mexico, 300,000 ha in the Caribbean, 750,000 ha in Central

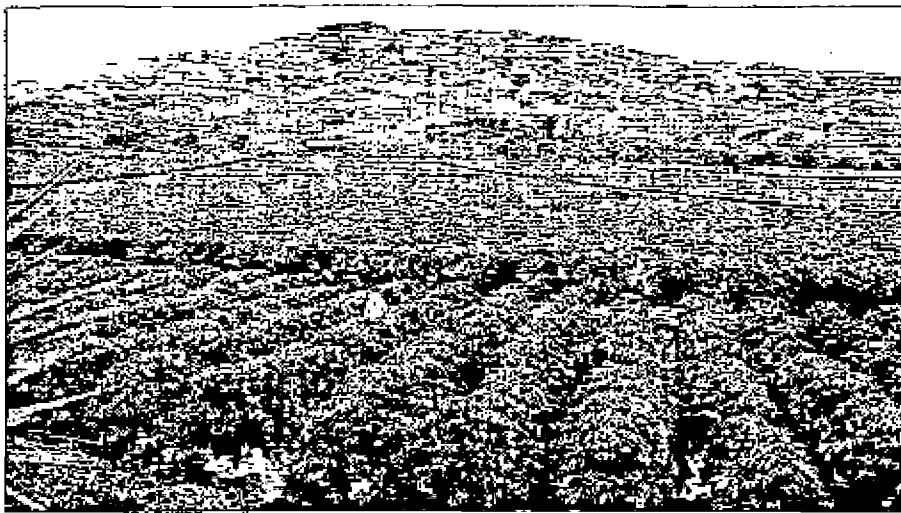


Figure 1. (Left) A sun plantation near San Jose, Costa Rica (photo by I. Perfecto). (Right) A traditional shade plantation near Tapachula, Chiapas (photo courtesy of M. Van der Voort).

America, and 1,000,000 ha in Colombia.

### Coffee cultivation techniques

Coffee cultivation systems fall along a continuum, ranging from the "traditional" to the "modern" (Table 1).<sup>1</sup> The modern system is characterized by a reduction in shade, increased reliance on new high-yielding varieties, and an increase in chemical inputs, pruning, and coffee plant density (Coyner 1960, De Graaf 1986). The removal of shade in coffee farms helps establish a suite of characteristics of a coffee cultivation system aimed at increasing yields, at least over the short run. However, with the loss of canopy cover, modern plantations, also known as sun plantations, become more prone to water and soil runoff, threatening the long-term sustainability of the system (Rice 1990).

One of the most striking features of the conversion from traditional to modern coffee cultivation is the rapidity with which it has occurred. After a largely unsuccessful attempt in the 1950s to modernize coffee growing using new strains and more

agrochemicals, modernization intensified in the 1970s. We estimate that almost half of the area in coffee production in northern Latin America had been converted by 1990. The speed and extent of conversion, however, have been uneven. The percentage of land converted in the region varies from as low as 15% in Mexico to more than 60% in Colombia (Figure 2).

Modernization was initially seen as a way of combating fungal diseases, particularly coffee leaf rust (*Hemileia vastatrix*). The role that coffee leaf rust played in plantation modernization is significant, because the disease ranks as the most feared obstacle to production in most coffee-producing areas (Agrios 1982). Early on, coffee leaf rust provided the hook on which the entire coffee modernization process hung its hat. Phytopathological reasoning maintained that less shade would allow moisture on coffee plants to dry more readily, therefore reducing fungal germination success. The arrival of rust in Brazil in 1970 and in Central America in 1976 brought to life the agronomic nightmares that had plagued coffee growers and governments in the Old World for generations. However, coffee leaf rust has not been as problematic as predicted, and the major motivation behind modernization has since become increased production.

Modernized coffee represents a major departure in economic strat-

egy for the coffee farmer. Simán found that modern farms out-produced semi-modern (a combination that includes some shade reduction, a change to new coffee varieties, and at least some use of agrochemicals) and traditional farms, with yields of 1397, 953, and 317 kg/ha, respectively.<sup>2</sup> However, the levels of production had considerably different costs as well; in absolute terms, the cost (in US dollars) of production for a hectare of modern, semi-modern, and traditional coffee was \$1738.94, \$1092.00, and \$269.47, respectively. The cost to produce 1 kg of coffee was thus \$1.24 for modern coffee, \$1.14 for semi-modern coffee, and \$0.85 for traditional coffee. Actual profits, of course, vary with world coffee price fluctuations. The traditional technology, with a much lower use of chemical inputs, represents a passive production system in which the coffee unit receives little attention in the way of labor and/or capital. Traditional production devotes 2% of its expenditures to chemical inputs, whereas semi-modern and modern production spend 19% and 25% on chemical inputs, respectively. In addition,

<sup>1</sup>We use the term *modern* here, a system also referred to as *intensified* and *technified*. This last term, although cumbersome, is used by development agencies and local institutions and describes quite well the technical and industrial approach to what has heretofore been a traditional production system.

<sup>2</sup>J. J. Simán 1991, unpublished manuscript. Tropical Agronomic Center for Research and Teaching, Managua, Nicaragua.

Table 1. Distinguishing characteristics of traditional and modern coffee production technologies.

Characteristic	Traditional	Modern
Coffee variety	Typica, bourbon, maragogipe	Caturra, catuai, Colombia, Guarnica catimor
Coffee height	3–5 m	2–3 m
Shade cover	Moderate to heavy, 60%–90% coverage	None to moderate, up to 50% coverage
Shade trees used	Tall (15–25 m), mixed forest trees, legumes, fruit trees, bananas	Short (5–8 m), legumes; often monocultures
Density of coffee plants	1000–2000/ha	3000–10,000/ha
Years to first harvest	4–6	3–4
Plantation life span	30+ years	12–15 years
Agrochemical use	None to low	High, particularly fertilizers, herbicides, fungicides, nematocides
Pruning of coffee	Individualized pruning or no pruning	Standardized stumping back after first or second year of full production
Labor requirements	Seasonal for harvest or pruning	Year-round maintenance with higher demands at harvest
Soil erosion	Low	High (particularly on slopes)

nonharvest labor accounts for the single largest cost in modernized systems because it entails an array of intense cultivation practices such as standardized pruning, fertilization, and insecticide, fungicide, and nematocide applications to individual plants.

Comparisons have also been made between modernized and organic coffee production by Akkerman and Van Baar (1992) and Boyce et al. (1994). They reported that despite

lower total income, organic coffee production resulted in a significantly higher net revenue (approximately \$350.00/ha), in part because of lower production costs. Furthermore, when externalities generated by environmental costs associated with coffee production (e.g., pesticides and/or soil erosion) were incorporated into the analysis, the differences in net revenue between organic and non-organic production increased (Boyce et al. 1994).

### Shade coffee and biodiversity conservation—an overview

On a geographical scale, the importance of shade coffee as a refuge for biodiversity may not be in the total land it involves, but in its location in areas that have been particularly hard hit by deforestation. In fact, the total land area planted in coffee is moderate compared with some other land uses (particularly pasture). However, plantations tend to be localized on relatively high-quality soils and in the mid-elevation (500–2000 m) ecological zone. Natural habitats in these zones, which include pine–oak woodland and premontane tropical forest, are often highly fragmented and degraded, and few reserves have been established to protect the many organisms endemic to these habitats. The Pacific slope of the central cordillera in Central America has been particularly devastated.

In areas where deforestation is high and coffee is still produced on traditional shade plantations, these plantations are likely to be a critical refuge for the forest biota. In fact, coffee plantations may already have served as a critical refuge during a human-caused habitat bottleneck. Brash (1987) suggested that the relatively low rate of avian extinction experienced on Puerto Rico during recent periods of deforestation may be due in part to the presence of shade coffee plantations. Similarly, Nir (1988) argued that many rare orchids survived deforestation in Puerto Rico on shaded coffee farms. By the turn of the nineteenth century, 99% of the original forest cover

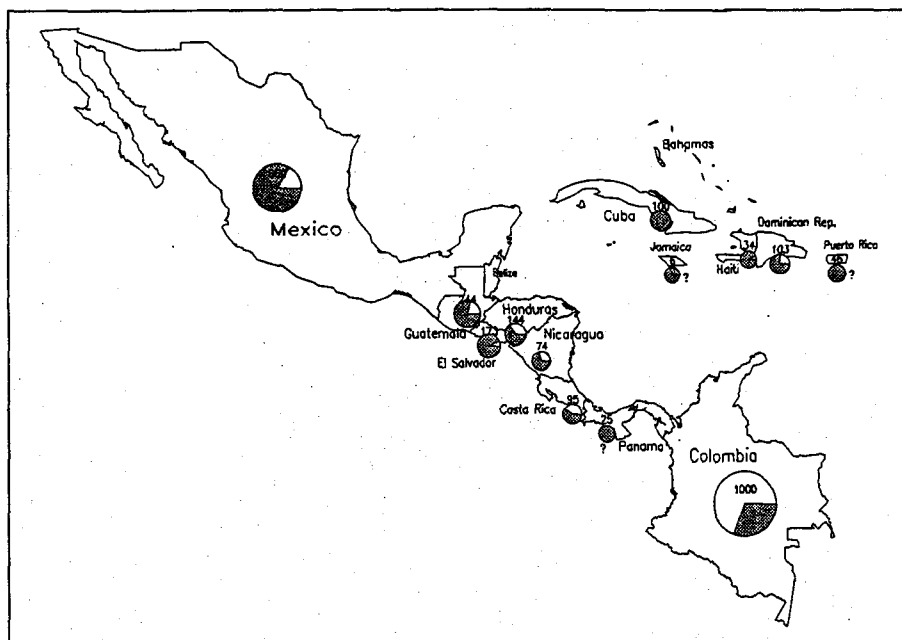


Figure 2. A map of northern Latin America with proportional circles depicting relative coffee area by country (figures in thousands of hectares; based on UNFAO Production Yearbook 1990) and approximate area modernized (white portion of circle) and nonmodernized (shaded portion of circle). The modernized area does not include lands designated as “semi-modernized.” Question marks indicate no data available for modernized coffee area. Data are from a variety of sources for the early 1990s, except area estimates from Mexico and Nicaragua, which are for the early 1980s (see Rice 1993 for details).

on Puerto Rico had been lost, with essentially no second-growth forest replacing it. However, shaded coffee plantations still covered 9% of the island. As the rural economy has been abandoned, forest is returning to much of the island, and the "seed" for its regrowth is often the abandoned coffee estates (Weaver and Birdsey 1986).

The plant diversity of coffee plantations results from two distinct processes. First, a small percentage of plantations ("rustic") are planted in forest cleared of its understory. Therefore, the diversity of the natural forest canopy is preserved in a modified form. In addition, rustic plantations are often unweeded during periods of low coffee prices, which adds to the maintenance of biodiversity as well. Purata and Meave (1993) found that rustic plantations provide the only habitat for several forest trees in the mid-elevation zone of Oaxaca, Mexico. The term *rustic* is also often conferred on highly diverse indigenous agroforestry systems that incorporate coffee production. One well-studied example is the *te'lom*, or managed forests, of the Huastec Maya of Tamaulipas, Mexico. *Te'lom* forests contain more than 300 plant species and cover a quarter of the Huastec's agricultural land (Alcorn 1984). The incorporation of coffee into such a traditional agroforestry system is not surprising because cacao (chocolate) was cultivated in this manner for 2000 years before the Conquest (Bergmann 1969).

In the second and more common process, the shade canopy is of substantially lower diversity than in rustic plantations and is maintained through deliberate planting. The overstory species found in traditional coffee plantations vary from country to country and regionally within each country (see Fuentes-Flores 1979 for a classification for Mexican systems), as does the intensity with which shade trees are pruned. Nitrogen-fixing legumes such as *Inga* spp., *Erythrina* spp., and *Gliricidia sepium* form an important component of many coffee farms. The latter two genera lose most or all of their leaves during the dry season, which renders plantations on which they are grown similar to sun plantations for this period.

Table 2. Number of species of beetles, ants, wasps, and spiders in the canopy of shade trees and coffee plants in different types of coffee farms, based on fogging with Pyrethrin-based insecticides.\*

Species	Type of farm	Beetles	Ants	Non-ant Hymenoptera	Spiders
<b>Shade trees</b>					
<i>Erythrina poeppigiana</i>	Traditional	126	30	103	NA†
<i>Erythrina fusca</i>	Traditional	110	27	61	NA
<i>Annona</i> sp.	Traditional	NA	10	63	NA
<i>E. poeppigiana</i>	Technified with shade	48	5	46	NA
<b>Coffee plants</b>					
<i>Coffea arabica</i> ‡	Traditional	39	14	34	44
	Technified with shade	29	9	31	NA
	Technified without shade	29	8	30	29

\*I. Perfecto, 1996, manuscript in preparation.

†Data not yet available.

‡Coffee based on ten plants per treatment.

Throughout northern Latin America, it is common to find banana (*Musa* spp.), citrus (e.g., tangerine, orange, grapefruit, and lemons), or other fruit trees (e.g., avocados, mamey, mangoes, and zapotes) mixed in with the coffee, filling out the multistrata systems in which coffee itself forms the shrub layer. Some fuel wood- and timber-producing trees, including *Cedrela mexicana*, *Cordia alliodora*, and *Swietenia macrophylla*, are also found in diverse coffee farms. Traditional planted coffee farms commonly have more than 40 tree species. Larger plantations tend to be less diverse, planted with one or a few species of native legumes, which are often heavily pruned. In many plantations, exotic trees are used, particularly *Grevillea robusta*, which grows well at higher elevations and survives low temperatures.

The high structural complexity of the traditional coffee plantation is a result of the various vegetative layers in the agroecosystem. This structural complexity offers living and nesting sites for a variety of organisms. In addition to increasing primary structural diversity of foliage layers, the canopy of plantations can support secondary structures comprised of epiphytes, parasites (e.g., mistletoes—Loranthaceae), mosses, and lichens, which in turn support a community of arthropods, amphibians, and other creatures. The canopy also affects the microclimate of the coffee understory. Sun coffee plantations lack the protection provided by

canopy trees from the impact of rain and wind, and they also lack the input of canopy leaf litter (Beer 1988). Therefore, even structurally equivalent layers of shade and sun plantations are dramatically different habitats. Finally, shade trees provide a high diversity of food items for herbivores, frugivores, and nectarivores. Where there is a diversity of canopy species, differences in the timing of fruit and flower production are likely to reduce phenological gaps (periods when no fruit or nectar resource for a particular taxa is available).

## Arthropod diversity

Studies that have compared arthropod diversity in coffee plantations with that in forests have reported either similar or higher diversity in plantations. In Sulawesi, Stork and Brendell (1990) found the number of arthropod species in coffee plantations to be almost double that of mid-elevation forests. In a comparative study in Puerto Rico, Torres (1984) reported a more diverse ant fauna in a coffee plantation than in an upland tropical forest in the same region. Similar high ant diversity has been reported for cacao (*Theobroma cacao*) plantations, which are structurally similar to coffee plantations but are typically found at lower elevations (Majer 1978, Room 1971, 1975).

Studies of arthropod assemblages in the canopy of shaded plantations

attest to the high diversity of arthropods in these systems (Stork and Brendell 1990). The most dramatic finding to date is that of Perfecto et al.<sup>3</sup> from a shaded plantation in Heredia, Costa Rica (Table 2). By fogging with pyrethrin-based insecticides, in a manner similar to some tropical forest studies (Erwin and Scott 1980, Stork and Brendell 1990), Perfecto and colleagues sampled the arthropods in the canopy of four shade trees and ten coffee bushes. Ants, other hymenopterans, beetles, and spiders were sorted into morphospecies. In the canopy of a single *Erythrina poeppigiana* they recorded 30 species of ants, 103 species of other hymenopterans, and 126 species of beetles. A second tree yielded 27 species of ants, 61 species of other hymenopterans, and 110 species of beetles. Although the two sampled trees were less than 200 m apart, the overlap of species was only 14% for beetles and 18% for ants. These preliminary results suggest that shaded plantations can have a local species diversity within the same order of magnitude as undisturbed forest. For example, Wilson (1987) reported 62 and 47 ant species from two trees each in upland rain forest in Peru, and Adis et al. (1984) reported 38 ant species in one *Dipterix alata* and two *Eschweilera cf. odora* in an upland rain forest in Brazil.

## Birds and other vertebrates

With the possibility of deforestation causing declines in several species of birds that migrate from North America to northern Latin America (Askins et al. 1990), many studies have focused on the status of overwintering populations in different agricultural and natural habitats. Coffee plantations have often been singled out for their ability to support numbers of forest migrants, those species most likely to be affected by conversion of forest to farmland. Wunderle and Waide (1993) conducted a regional survey of the Greater Antilles and concluded that shade coffee plantations support high densities of certain species that de-

pend on closed canopy forest. A more detailed study in the Dominican Republic supports this finding (Wunderle and Latta in press). In addition, Wunderle and Latta (1994) found that individuals of several migratory species in shade coffee plantations survived the winter at a rate comparable with those in natural forest habitats. Greenberg et al. (1995) classified the migratory avifauna of eastern Chiapas, Mexico, as forest specialists, forest generalists, and scrub/open species, and then determined that shade coffee plantations support a high number of species of forest migrants (both generalists and specialists) compared with other habitats in the region, and often at higher densities than natural forests.

Shade coffee plantations may also be an important dry season refuge, providing fruit and nectar for birds when insect populations are otherwise dwindling. Several of the commonly planted shade trees are native species that produce flower crops favored by omnivorous birds. It is likely that the movements of latitudinal and altitudinal migrants (Vannini 1994) are timed to take advantage of the asynchrony of flower crops available in shade plantations. Greenberg et al. (in press) examined the seasonality of bird use of coffee plantations and other habitats in eastern Chiapas through the repeated censusing of transects. Of the 23 habitats censused in eastern Chiapas, only the two plantation types (rustic and planted with *Inga*) showed an overall significant increase in bird numbers over the winter. Both the number of individual birds and the number of species nearly doubled, a pattern that held for resident tropical species as well as migrants. This increase was specific to omnivorous species; insectivores showed stable or slightly declining populations through the winter. In the *Inga*-dominated plantations, the increase consisted largely of flower-feeding species such as Baltimore orioles (*Icterus galbula*) and Tennessee warblers (*Vermivora peregrina*).

Shade coffee plantations are particularly well represented by canopy omnivores and nectarivores. During the dry season in Chiapas, more than 45% of the individual birds were in

these guilds (Greenberg et al. in press), a figure that is significantly higher than for other forest habitats in the region. Shade coffee also supports a high concentration of nectarivores or partial nectarivores in the Dominican Republic (Wunderle and Latta in press). The high concentration of euphonias (small tanagers that eat mistletoe berries) in taller, less-pruned plantations suggests that parasitic plants support additional diversity as well.

In general, migratory birds seem to fare better than resident birds in shade plantations, perhaps because migratory birds have less stringent habitat requirements than those species committed to breeding in the region. Resident birds may be affected by a variety of local ecological and landscape factors. The small size of the average coffee plantation makes it susceptible to fragmentation, whose effects are known to be severe in tropical areas (Lovejoy et al. 1986). Structural modifications that remove foraging and nest sites for some species probably account for the loss of many forest specialists. In addition, larger birds, such as cracids, parrots, and raptors, may be susceptible to hunting pressures.

Nevertheless, Aguillar-Ortiz (1982), Corredor (1989), and Greenberg et al. (in press) found that the species richness of birds in coffee plantations with a structurally and floristically diverse canopy compares well with other natural forest habitats with which many species are shared. Greenberg et al. (in press) also showed that diversity of birds in coffee plantations (and other forest types) is considerably higher than in other agricultural habitats. In part, the high diversity of shade plantations results from the number of edge and second-growth species that occur along with a smaller number of true forest birds (Corredor 1989, Greenberg et al. in press). Greenberg et al. (in press) showed that in Chiapas, the avifaunal similarity between pine-oak woodland and planted and rustic coffee is high (75%–80%). Similarity with mesophilous forest, however, was low, and several of the more specialized species found commonly in premontane forest, such as the spectacled foliage-gleaner (*Anabacerthia varie-*

<sup>3</sup>I. Perfecto et al., 1995, unpublished manuscript. University of Michigan, Ann Arbor, MI.

*gaticeps*), were never recorded in coffee plantations. The bird diversity of heavily pruned shade plantations dominated by a single canopy species, a common plantation type, was only two-thirds of that of the more forestlike coffee plantations.<sup>4</sup> In particular, forest frugivores, bark-gleaners, and understory species were poorly represented in the more monospecific and heavily trimmed shade plantations.

Shade coffee plantations support a high diversity of other vertebrate groups as well as birds. Estrada et al. (1993) found that, compared with other agricultural habitats, a high diversity and abundance of bats use various shade plantations with diverse canopies. However, diversity was considerably lower than in lowland tropical forest. As with birds, a large proportion of individuals and species were partially frugivorous and nectarivorous, feeding on the flowering and fruiting trees of the canopy. Estrada et al. (1993) argue that the mobility of bats (like some birds) allows them to forage over shade plantations and other forest patches scattered over a large area. A strong relationship between the presence of a structurally diverse canopy and a high diversity of small terrestrial and scansorial mammals was found by Gallina et al. (1992) in Veracruz, Mexico. In this study, species dependent on canopy trees made up more than half of the fauna of the plantations, and more than 40% of the species were omnivores that commonly fed on fruit.

A similar high abundance and diversity, as well as proportion of omnivores, was found for nonflying mammals in the Las Tuxtlas region of Mexico (Estrada et al. 1993, 1994). This observation is not surprising, considering that many of the trees managed in coffee plantations produce fruit that is eaten not only by humans but also by other mammals. Gallina et al. (1992) also reported that in addition to the many omnivorous species, some more specialized mammals, such as small cats and otters, can be found in shade

plantations in Veracruz. Estrada et al. (1994) did not find such mammals in plantations in Las Tuxtlas but did regularly observe howler monkeys (*Alouatta palliata*). And working in Guatemala, Seib (1986) reported that mixed-shade plantations can support up to 50% of the original forest snake fauna.

### Biodiversity and the impact of coffee conversion

The few direct comparisons between sun and shade plantations focus on the ground or coffee strata, and generally they show a decrease in diversity with the conversion from shade to sun types. Perfecto et al.<sup>5</sup> (Table 2) showed that arthropod diversity was lower in the ground strata of monospecific shade farm and shadeless coffee monoculture than in that of shaded canopy. Although Hanson (1991) reported a high hymenopteran diversity in coffee monoculture (80 species of parasitoids) in the same region of Costa Rica, species richness was still lower than on traditional plantations. Perfecto and Snelling (in press) surveyed ant species diversity using bait transects on 16 coffee farms and found a positive correlation between species diversity and vegetational complexity. Once again, the highest diversity was found in the traditional farm and the lowest in sun coffee plantations. Perfecto and Vandermeer (1994) and Perfecto (1994) suggested that both direct (e.g., loss of nesting sites) and indirect (e.g., changes in competitive interactions) mechanisms are responsible for reductions within the ant community in the coffee monoculture. Working in Mexico, Nestel and colleagues (Nestel and Dickschen 1990, Nestel et al. 1993) reported a reduction in the diversity of ant and macrocoleopteran assemblages in sun coffee plantations as compared with shaded coffee plantations.

Studies restricted to the coffee layers are likely to greatly underestimate the difference in overall diversity between plantation types. The elimination of trees, with their foliage, flower, fruit mesocarp, and extrafloral nectaries, results in a dra-

matic reduction in hymenopterans.<sup>6</sup> Aside from the loss of food provided by the trees, the habitat structure becomes simplified through loss of canopy foliage layers, tree trunks, and associated epiphytes. Canopy trees provide a host of poorly known microhabitats. The effect of canopy loss is likely to be severe for trees with a specialized canopy fauna. For example, the high diversity of arboreal beetles, with more than 100 species in a single tree, is undoubtedly lost in systems that lack canopy trees (Table 2). Preliminary studies<sup>7</sup> suggest that a large percentage of the ants found in the canopy of shade trees are also exclusively arboreal. For example, in a shaded plantation in Costa Rica, an average of 72% of the ants were found exclusively in trees.

The loss of the shade in coffee plantations also means the loss of resources for many species in the detritivore food chain, particularly saproxylic and leaf litter arthropods. Shaded plantations in Costa Rica produce between 5000 and 20,000 kg ha<sup>-1</sup> · yr<sup>-1</sup> of leaf litter and pruning residues (Beer 1988)—values that fall within the range for tropical forests (Vitousek 1984). Shaded plantations, particularly rustic ones, contain old and dead trees that provide habitats for a diverse saproxylic arthropod community. In Mexico, a single coffee and cacao plantation was reported to contain 78 families of saproxylic invertebrates, with 93% belonging to the orders Coleoptera, Diptera, Hymenoptera, or Collembolla (Moron and Lopez-Mendez 1985). Although studies directly comparing saproxylic communities between shade and nonshaded plantations are apparently lacking, the reduction in decaying wood and leaf litter suggests that these assemblages are greatly reduced along with shade elimination.

Changes in the coffee stratum itself due to loss of microclimate buffering are profound. The conversion of coffee plantations invariably results in an increase in the amount of solar radiation reaching the ground, with concomitant increases in temperature and wind speed, direct im-

<sup>4</sup>R. Greenberg, P. Bichier, A. Cruz, and R. Reitsma, 1996, manuscript in review. Smithsonian Migratory Bird Center, Washington, DC.

<sup>5</sup>See footnote 3.

<sup>6</sup>See footnote 3.

<sup>7</sup>See footnote 3.

part of precipitation, and a decrease in relative humidity (Beer 1987). In sun coffee plantations, fluctuations of both temperature and humidity become more extreme. Perfecto and Vandermeer<sup>8</sup> demonstrated that by experimentally increasing shade, the diversity of ground-foraging ants in coffee plantations increased, at least partly as a result of changes in microclimate.

The modernization of coffee plantations frequently includes a substantial increase in agrochemicals (De Graaf 1986). Insecticides are known to decrease biological diversity in agroecosystems (Jepson 1989). Fungicide applications are also more common in modern plantations than in traditional ones. Certain fungicides also are known to have insecticidal activity and can have a detrimental impact on insect diversity (Sotherton and Moreby 1988). Moreover, it is likely that fungicide applications adversely affect the decomposition of leaf litter in modern systems. The shade of traditional plantations reduces weed growth (Nestel and Altieri 1992), so intense herbicide applications are necessary to reduce the ground cover of forbs and grasses in sun plantations. The removal of shade has also been shown to disrupt the natural nitrogen cycle associated with litter decomposition and with the actions of nitrogen-fixing bacteria associated with commonly planted leguminous shade trees, therefore requiring the addition of chemical fertilizers (Babbar 1993). These compounds can pollute local water supplies.

Even the most cursory observation in sun plantations shows them to be almost devoid of birds. Borrero (1986) first noted the dramatic decrease in bird diversity in plantations in Colombia. In part, birds respond to the same loss of food resources, structural complexity, and microclimate buffering that is responsible for changes in arthropod assemblages. Most observers have noted that the high abundance and diversity of birds in coffee plantations is associated primarily with the canopy trees. Not surprisingly, then,

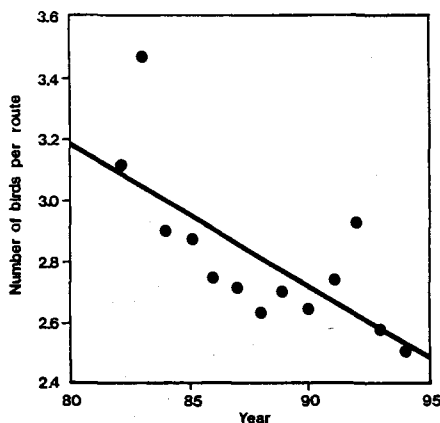


Figure 3. Annual population indices of the Baltimore oriole from 1978 to 1994 based on 1351 Breeding Bird Survey routes throughout North America (courtesy of US National Biological Service).

Wunderle and Latta (in press) found a reduction in overall diversity and a significant shift from forest to matorral (shrubby second growth) species when comparing monotypic *Inga* shade and sun plantations in the Dominican Republic.

Greenberg et al.,<sup>9</sup> working in Guatemala, determined that the density and diversity of birds in sun coffee plantations is approximately half that in traditional coffee plantations. Furthermore, sun coffee plantations support few individual birds and bird species than adjacent areas of matorral, and many common matorral species avoid sun plantations. This finding probably reflects the low density of arthropods associated with coffee plants and the high degree of weed control associated with sun plantations. Birds make relatively little use of coffee flowers or berries, and consequently the nectarivorous and frugivorous species so prevalent in shade coffee plantations largely disappear. Gallina et al. (1992) estimated that approximately half of the species diversity of nonflying mammals is lost due to coffee conversion. An even higher percentage of reptile and amphibian diversity appears to be lost (Seib 1986).

Migratory birds often occur in a range of habitats, so the impact on them of coffee modernization is difficult to assess. Three largely nectarivorous migratory songbird

species are probably the most specialized migratory species on shaded plantations (although smaller populations may occur in urban gardens): the Baltimore oriole and the Tennessee warbler in Mesoamerica, and the Cape May warbler (*Dendroica tigrina*) in the Antilles.<sup>10</sup> Data from the Breeding Bird Survey of the US National Biological Service indicates that all three species have experienced sharp and statistically significant population declines from 1980 to 1994, corresponding to the period of intense coffee modernization. The annual estimated declines are 2.2%, 5.7%, and 4.2% for the oriole, Tennessee warbler, and Cape May warbler, respectively (Figure 3). The three species experienced significantly expanding populations during the previous 16 years, which would also be predicted from the continuing increase of area under coffee cultivation. Other factors may be responsible for population declines, for example, habitat fragmentation, parasitism, and long-term cycles in prey abundance (Askins et al. 1990). The two warblers, for example, are boreal forest "spruce budworm" species and may be tracking long-term caterpillar cycles on the breeding grounds. However, the sharp decline in orioles is less likely to be caused by these breeding season factors because this species is not known to respond to insect cycles, it breeds successfully in edge situations, and it is rarely parasitized by cowbirds.

### Predator-prey interactions and coffee pests

Coffee, at least when grown in the Western Hemisphere, is well known for its lack of insect pests. Although many herbivores can potentially damage coffee plants, only a few are economically important (Le-Pelley 1973). Coffee's resistance to herbivores may lie in the fact that it is a chemically well-defended plant (Frischknecht et al. 1986), with young leaves containing high quantities of alkaloids. In addition, older leaves are tough. Furthermore, there may simply be no native species in

<sup>8</sup>I. Perfecto and J. Vandermeer, 1995, unpublished manuscript. University of Michigan, Ann Arbor, MI.

<sup>9</sup>See footnote 4.

<sup>10</sup>J. Wunderle, 1995, personal communication. Institute for Tropical Forestry, US Forest Service, Palmer, Puerto Rico.

Latin America that have evolved mechanisms to overcome coffee's defenses—a common phenomenon in plant introductions.

In addition, it has been argued that the structurally complex and floristically diverse traditional coffee plantation supports a high density and diversity of predators and parasitoids, which are ultimately responsible for the reduced number of insect pests in traditional plantations (Ibarra-Nunez 1990). The few comparative studies in coffee plantations support this assertion (Benitez and Perfecto 1990, Nestel and Dickschen 1990, Perfecto and Snelling in press, Perfecto and Vandermeer 1994). For example, of the arthropod taxa sampled by Perfecto et al.,<sup>11</sup> ants, other hymenopterans, and spiders were all more diverse in shaded plantations than in sun plantations. Robinson and Robinson (1974) estimated spider abundance in shade plantations in Papua New Guinea and suggested that the spiders have considerable insecticidal effects. Web-building spiders, for instance, consume 40 million insects per hectare per year (Robinson and Robinson 1974). Perfecto et al.<sup>12</sup> reported 34% more spiders in the coffee bushes in a traditional plantation than in a coffee monoculture. Ants, which show high diversity in traditional plantations, are effective predators as well (Carroll and Risch 1989). These observations suggest that the elimination of shade may ultimately result in increased pest problems as well.

### Diversity and economic risk reduction

Biological diversity can provide important economic returns to coffee growers. Because of the larger number of products derived, the diverse plant community within a traditional farm fits much better into the risk-averse mentality of many small farmers (Reeves and Lilieholm 1993). Although much coffee is grown on a relatively small number of large estates, in most coffee-producing countries the average coffee plantation is small. The size distribution of hold-

ings varies considerably from country to country. For example, Mexico is dominated by small holdings on private and *ejido* land—91% of the holdings are less than 5 ha. In Colombia this value is only 49%, and 5% of the holdings are greater than 100 ha.

For small farmers, committing oneself to total dependence on coffee puts one at great risk, not only with the vagaries of local weather and pest outbreaks, but with the often dramatic and unpredictable fluctuations of the global market. However, the traditional coffee farm sustains the grower beyond simply generating an income at harvest time because of the noncoffee products associated with the shade trees. For example, overstory species provide fruits, fuelwood, and construction materials for household consumption, as well as a potential source of income derived from the local market. Honey production is a common rural industry in northern Latin America. Cházaro (1982) found at least 90 species of bee-pollinated plants in the shade coffee plantations near Xalapa, Veracruz. Wood from natural and human prunings provides a steady supply of fuel and, in the case of larger shade species, construction materials for the home and household furnishings. Selling surplus wood also brings in added income. Where precious hardwoods are mixed within the shade trees, single trees can be sold to local sawmills or other buyers when times are tough economically. In situations in which a more managed coffee plantation system is possible, Somarriba (1990, 1992) has shown that timber production and harvesting based on *C. alliadora* as a shade species can occur. Production of various fruit provides a household with a continuous supply of nutritious products for consumption and for the local market. A single, well-tended avocado tree, for instance, can yield between 2000 and 3000 fruits per season. Aside from household use, such produce can fetch \$0.18 per fruit. For the two months of the avocado harvest, a producer can gain as much as \$360.<sup>13</sup> This single tree's

harvest represents an equivalent of 100 work days at minimum farm wage.

A shaded coffee farm displays two distinct types of biodiversity, managed and natural. The choices made by growers to use a variety of shade species yields an array of useful products and at the same time provides cover with varying degrees of structural diversity. This intentionally managed biodiversity by growers allows for higher levels of natural biodiversity as well in these shaded systems than is found in sun coffee. The issue now becomes how best to make use of the relationship between managed and natural biodiversity.

### Promoting biodiversity on coffee farms

**Defining an environmentally friendly coffee.** Research to address this issue is in its infancy; however, we believe that the broad aspects of a biologically diverse coffee farm can be outlined. Clearly the presence of a shade canopy is essential. Furthermore, the greater the structural and floristic diversity of this canopy, the greater the likelihood that resources will be provided for a greater array of organisms. A greater variety of animal-pollinated and -dispersed plants will support the diverse guild of omnivorous species that populate traditional shade plantations throughout the year. The canopy needs to provide sufficient coverage throughout the year to buffer the microclimate of the understory from rain and desiccating winds. Tree species selection and pruning practices should have minimal impact on the epiphytic plants, mosses, and lichens as well as on dead trunks and limbs that provide homes for so many canopy species.

On-farm presence of shrub vegetation along arroyos or on steep slopes will protect streams from erosion and provide an additional haven for understory species unable to cope with a coffee monoculture. Sun drying, or using more energy-efficient technology, will reduce the need for harvesting trees to provide fuel for coffee dryers used in bean processing. Finally, reduced or no use of pesticides, herbicides, and chemical fertilizers should be promoted. The

<sup>11</sup>See footnote 3.

<sup>12</sup>See footnote 3.

<sup>13</sup>R. Rice, field notes and personal observations.



use of natural or managed mulch will additionally foster a rich soil flora and fauna. Clearly, some of these recommendations, such as maintenance of a diverse shade structure and protection of epiphytes, are inconsistent with what are considered to be the most productive or expedient agronomic practices (Beer 1987, Boyce et al. 1994). The challenge will be to develop cultivation systems that are a workable compromise between what is good for the farmer and what will truly benefit biological diversity.

**Foreign assistance.** Because coffee plantations are managed primarily for export commodity production, the motivating force behind their existence is a powerful international market. Therefore, their continued ecologically sustainable management is likely to require the use of nontraditional policy tools. One possible approach is to influence the institutional programs providing assistance for rural development in the region. A principal institutional link for the projects involving modernization of the coffee sector of the region is the US Agency for International Development (USAID), although for some countries, such as Colombia and Mexico, USAID has played no role. (Influential national institutions in these two countries precluded any US involvement in their coffee sectors.) Working sometimes through its own (now-defunct) Regional Office on Central America and Panama and sometimes with regional institutions like the Inter-American Institute for Cooperation on Agriculture (IICA) of the Tropical Agronomic Center for Research and Teaching, both located in Costa Rica, USAID has played a major role in promoting modernized coffee. Since 1978, at least eight projects totaling US \$81 million have targeted small coffee producers for modernization through reduced shade, high-yielding varieties, and increased chemical application (Rice and Ward 1996). Coffee modernization continues in at least three USAID-sponsored projects in the region through 1997 (Haiti, El Salvador, and Guatemala; Rice and Ward 1996).

At a minimum, USAID should reduce or eliminate its role in the coffee

modernization process and augment projects that promote production of organic and other environmentally sustainable coffee. It should be noted that PROMECAFE (a Central American USAID-supported program aimed at coffee modernization) held a workshop in February 1995 that sought to explore a sustainable coffee sector. Subsequently, this IICA-sponsored endeavor has begun to question the strictly modern model. Moreover, recent developments and advances in organic coffee production in El Salvador point to USAID's burgeoning interest in alternatives to modernization.

**Marketing environmentally friendly coffee.** Perhaps market forces can be harnessed to provide economic incentives to farmers producing "environmentally friendly" coffee. Fortunately, because coffee functions as a segmented market, the possibility of providing market incentives for environmental coffee is better than for many export commodities. An increasing number of consumers are prepared to pay premium prices for so-called specialty coffees—the fastest growing segment of the coffee market. If shade-grown coffee can be marketed in this context, thereby providing higher prices to the producer, this could compensate for lower levels of production. Perhaps the closest that most US consumers can come to purchasing coffee with a high probability of coming from shaded plantations is to purchase "certified organic." The organic coffee sector, still a minuscule fraction of the total US coffee market (approximately 0.5%),<sup>14</sup> has grown considerably. Promotion of organic production has been embraced by grassroots institutions working with small cooperatives, particularly in Mexico, Costa Rica, and Nicaragua. Many producers have enthusiastically embraced organic production because it brings higher prices. However, the certification process can be time consuming, expensive, and bureaucratic.

**Farmer incentives.** Without additional long-term support, it may be

<sup>14</sup>M. Rozyne, 1994, personal communication. Equal Exchange Coffee Co., Stoughton, MA.

difficult for the majority of small, traditional coffee farmers to compete with more industrial production units. Probably the least explored set of policy tools with potential to influence coffee cultivation techniques is incentives that could be provided to traditional farms through tax easements, access to credit, and technical and marketing assistance. The rationale for such incentives would be that farmers employing traditional shade techniques are providing a long-term stewardship service of protecting topsoils, pure water supplies, and worker safety. This approach is at least partly addressed under programs participating in the International Coffee Register. The register certifies "fair trade" practices, in which roasters provide small farmers and producer cooperatives with, among other things, access to credit, prices above production cost indexed to world prices, and technical assistance to increase productivity using recently developed organic techniques and to diversify commodities produced. Currently, banks often tie access to credit, which is critical for farmers to bring coffee to market during periods of both low and high prices, to certain technological packages that include the use of agrochemicals, rather than to more ecologically sustainable technologies.

**Internalization of environmental costs.** Finally, growing coffee in modern plantations outcompetes more traditional systems in part because associated environmental costs are paid by the state or people in other sectors of the economy, rather than by the coffee producer. These costs include the cleanup of polluted water supplies or the development of alternative sources of water, production declines associated with long-term pesticide use or soil erosion, the treatment of workers exposed to pesticides, and the loss of fish production in streams suffering sedimentation. Establishing policies to ensure that some of the environmental costs are borne by the local producers would encourage more environmentally benign coffee production. One example could be an environmental or health fund supported by taxes on pesticides.

## Conclusions

Coffee lands within northern Latin American coffee-producing countries are undergoing fundamental changes. For the landscapes involved in this transformation, these changes translate into a reduced vegetative cover, lowered species diversity of the plant community and its associated fauna, and the application of agrochemicals onto lands that previously received little or no such inputs. Already, 1.1 million ha of coffee within the countries in northern Latin America qualify as modernized. The total potential area that could be modernized is just more than twice that, at 2.7 million ha. What little work has been done on the environmental impact of the landscape modifications suggests that, unless steps are taken, many of these coffee zones, characterized by high rainfall and broken terrain, are likely to suffer environmental degradation in the coming years. This degradation is likely to include a severe loss of biological diversity in areas where coffee plantations currently provide the last refuges. Actions that might reverse this loss include working with small farmers to market ecologically sustainable coffee and reduce the support for technification in favor of policies that reward land stewardship.

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## References cited

Adis J, Lubin YD, Montgomery GG. 1984. Arthropods from the canopy of inundated and Terra Firme forests near Manaus, Brazil with critical considerations on the pyre-

thrum-fogging techniques. Studies on Neotropical Fauna and Environment 19: 223-236.

Agrios GN. 1982. Plant pathology. Orlando (FL): Academic Press.

Aguilar-Ortiz F. 1982. Estudio ecologico de las aves del cafetal. Pages 103-128 in Avila-Jimenez E, ed. Estudios ecologia en el agroecosistema cafetal. Xalapa (Mexico): Instituto Nacional de Investigaciones Sobre Recursos Bióticos.

Akkerman A, Van Baar X. 1992. El cafe organico: la sostenible de ungramo de oro. San Jose (Costa Rica): Centro de Estudio para el Desarrollo Rural, Universidad Libre de Amsterdam.

Alcorn J. 1984. Development policy, forests, and peasant farms: reflections on Huastec-managed forests' contribution to commercial production and resource conservation. Economic Botany 38: 389-406.

Askins RA, Lynch JR, Greenberg R. 1990. Population declines in migratory birds in eastern North America. Current Ornithology 7: 1-57.

Babbar LL. 1993. Nitrogen cycling in shade and unshaded coffee plantations in the Central Valley of Costa Rica. [Ph.D. thesis.] University of Michigan, Ann Arbor, MI.

Beer J. 1987. Advantages, disadvantages and desirable characteristics of shade trees for coffee, cacao and tea. Agroforestry Systems 5: 3-13.

\_\_\_\_\_. 1988. Litter production and nutrient cycling in coffee (*Coffea arabica*) or cacao (*Theobroma cacao*) plantations with shade trees. Agroforestry Systems 7: 103-114.

Benitez J, Perfecto I. 1990. Efecto de diferentes tipos de manejo de cafe sobre las comunidades de hormigas. Agroecologia Neotropical 1: 11-15.

Bergmann JF. 1969. The distribution of pre-Columbian America. Annals of the Association of American Geographers 59: 85-96.

Borrero H. 1986. La substitucion de cafetales de sombrio por caturrales y su efecto negativo sobre la fauna de vertebrados. Caldasia 15: 725-732.

Boyce JK, Fernandez Gonzales A, Furst E, Segura Bonilla O. 1994. Cafe y desarrollo sostenible: del cultivo agroquimico a la produccion organica en Costa Rica. Heredia (Costa Rica): Editorial Fundacion UNA.

Brash AR. 1987. The history of avian extinctions and forest conversion on Puerto Rico. Biological Conservation 39: 97-111.

Carroll CR, Risch SJ. 1989. An evaluation of ants as possible candidates for biological control in tropical annual systems. Pages 30-46 in Gleisman SR, ed. Agroecology. New York: Springer-Verlag.

Cházaro M. 1982. Flora epicola de la zona cafetales de Coatepec, Veracruz. Pages 95-102 in Jimenez E, ed. Estudios ecologicas en el agrosistema cafetalero. Xalapa (Mexico): Instituto Nacional de Investigaciones Sobre Recursos Bióticos.

Corredor G. 1989. Estudio comparativo entre la avifauna de un bosque natural y un cafetal tradicional en el Quindío. [Professional thesis.] University del Valle, Cali, Colombia.

Coyner MS. 1960. Agriculture and trade in Nicaragua. Washington (DC): Foreign Agriculture Service.

De Graaf R. 1986. The economics of coffee. Wageningen (the Netherlands): Publika-

tien Documentatie Dienst Landbouw Onderzoek.

Estrada A, Coates-Estrada R, Merritt D Jr. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. Ecography 16: 309-318.

\_\_\_\_\_. 1994. Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas. Ecography 17: 229-241.

Erwin TL, Scott JC. 1980. Seasonal and size patterns, trophic structure, and richness of Coleoptera in the tropical arboreal ecosystem: The fauna of the tree *Leuhea seemannii* Triana and Planch in the Canal Zone of Panama. Coleopterist Bulletin 34: 305-322.

Frischknecht PM, Dufek JV, Baumann TW. 1986. Purine alkaloid formation in buds and developing leaflets of *Coffea arabica*. Phytochemistry 5: 613-617.

Fuentes-Flores R. 1979. Coffee production systems in Mexico. Pages 60-72 in de Salas G, ed. Agroforestry systems in Latin America. Turrialba (Costa Rica): The Tropical Agro-nomic Center for Research and Teaching.

Gallina SE, Mandujaro S, Gonzales-Romero A. 1992. Importancia de los cafetales mixtos para la conservacion de la biodiversidad de Mamíferos. Boletín Soc. Ver. Zool. 2: 11-17.

Greenberg R, Salgado-Ortiz J, Warkentin I, Bichier P. 1995. Managed forest patches and the conservation of migratory birds in Chiapas, Mexico. Pages 178-190 in Wilson M, Sader S, Santana E, eds. The conservation of migratory birds in Mexico. Technical Publication. Orono (ME): University of Maine, School of Natural Resources.

Greenberg R, Bichier P, Sterling J. In press. Bird populations and planted shade coffee plantations of eastern chiapas. Biotropica.

Hanson P. 1991. Los parasitoides asociados al cafeto en Costa Rica. Manejo Integrados de Plagas (Costa Rica) 20-21: 8-10.

Ibarra-Nunez G. 1990. Los artopodos asociados a cafetos en un cafetal mixto del Soconusco, Chiapas, Mexico. Variedad y abundancia. Folia Entomologica Mexicana 79: 207-231.

Jepson PC, ed. 1989. Pesticides and non-target invertebrates. Andover: Intercept.

Le-Pelley RH. 1973. Coffee insects. Annual Review of Entomology 18: 121-142.

Lovejoy TE, et al. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 275-285 in Soule ME, ed. Conservation biology: the science of scarcity and diversity. Sunderland (MA): Sinauer.

Majer JD. 1978. The maintenance of the ant mosaic in Ghana cocoa farms. Journal of Applied Ecology 13: 123-144.

Moron MA, Lopez-Mendez JA. 1985. Analisis de la entomofauna necrofila de un cafetal en el Soconusco, Chiapas, Mexico. Folia Entomologica Mexicana 63: 47-59.

Nestel D, Altieri MA. 1992. The weed community of Mexican coffee agroecosystems: effect of management upon plant biomass and species composition. Acta Oecologia 13: 715-726.

Nestel D, Dickschen F. 1990. The foraging kinetics of ground ant communities in different Mexican coffee agroecosystems. Oecologia 84: 58-63.

Nestel D, Dickschen F, Altieri MA. 1993. Diversity patterns of soil macro-coleoptera in

- Mexican shaded and unshaded coffee agroecosystems: an indication of habitat perturbation. *Biodiversity and Conservation* 2: 70-78.
- Nir MA. 1988. The survivors: orchids on a Puerto Rican coffee finca. *American Orchid Society Bulletin* 57: 989-995.
- Perfecto I. 1994. Foraging behavior as a determinant of asymmetric competitive interactions between two ant species in a tropical agroecosystem. *Oecologia* 98: 184-192.
- Perfecto I, Snelling R. In press. Biodiversity and tropical ecosystem transformation: ant diversity in the coffee agroecosystem in Costa Rica. *Ecological Applications*.
- Perfecto I, Vandermeer JH. 1994. Understanding biodiversity loss in agroecosystems: reduction of ant diversity resulting from transformation of the coffee ecosystem in Costa Rica. *Entomology (Trends in Agriculture)* 2: 7-13.
- Pimentel D, Stachow U, Takacs DA, Brubaker HW, Dumas AR, Meaney JJ, O'Neil JAS, Onsi DE, Corzilius DB. 1992. Conserving biological diversity in agricultural/forestry systems. *BioScience* 42: 354-362.
- Purata S, Meave J. 1993. Agroecosystems as an alternative for biodiversity conservation of forest remnants in fragmented landscapes. Page 9 in *Forest remnants in the tropical landscapes: benefits and policy implications*. Symposium abstracts. Washington (DC): Smithsonian Migratory Bird Center.
- Reeves LH, Lillieholm RJ. 1993. Reducing financial risk in agroforestry planning: a case study in Costa Rica. *Agroforestry Systems* 21: 169-175.
- Rice RA. 1990. Transforming agriculture: The case of coffee leaf rust and coffee renovation in southern Nicaragua. [Ph.D. dissertation.] University of California, Berkeley, CA.
- \_\_\_\_\_. 1993. New technology in coffee production: examining landscape transformation and international aid in northern Latin America. Report to the Smithsonian Migratory Bird Center, Washington, DC.
- Rice R, Ward J. 1996. Coffee, conservation, and commerce in the Western Hemisphere. Washington (DC): Smithsonian Migratory Bird Center.
- Robinson M, Robinson B. 1974. A census of web-building spiders in coffee plantations at Wau, New Guinea, and an assessment of their insecticidal effects. *Tropical Ecology* 15: 95-107.
- Room PM. 1971. The relative distribution of ant species in Guana's cocoa farms. *Journal of Animal Ecology* 40: 735-751.
- \_\_\_\_\_. 1975. Relative distribution of ant species in cocoa plantations in Papua New Guinea. *Journal of Applied Ecology* 12: 47-61.
- Seib R. 1986. Feeding ecology and organization of neotropical snake faunas. [Ph.D. dissertation.] University of California, Berkeley, CA.
- Somarriva E. 1990. Sustainable timber production from uneven-aged shade stands for *Cordia alliodora* in small coffee farms. *Agroforestry Systems* 10: 253-263.
- \_\_\_\_\_. 1992. Timber harvest, damage to crop plants and yield reduction in two Costa Rican coffee plantations with *Cordia alliodora* shade trees. *Agroforestry Systems* 18: 69-82.
- Sotherton NW, Moreby SJ. 1988. The effect of foliar fungicides on beneficial arthropods in wheatfields. *Entomophaga* 33: 87-99.
- Stork NE, Brendell MJD. 1990. Variation in the insect fauna of Salawesi trees with season, altitude, and forest type. Pages 173-194 in Knight WJ, Holloway JD, eds. *Insects and the rain forests of South East Asia (Wallacea)*. London (UK): The Royal Entomological Society of London.
- Torres JA. 1984. Diversity and distribution of ant communities in Puerto Rico. *Biotropica* 16: 296-303.
- [UNFAO Production Yearbook] United Nations Food and Agriculture Production Yearbooks. Rome (Italy): United Nations.
- Vannini JP. 1994. Nearctic migrants in coffee plantations and forest fragments of southwestern Guatemala. *Bird Conservation International* 4: 209-232.
- Vitousek PM. 1984. Litterfall, nutrient cycling and nutrient limitation in tropical forests. *Ecology* 65: 285-298.
- Weaver PL, Birdsey A. 1986. Tree succession and management opportunities in coffee shade stands. *Turrialba* 36: 47-58.
- Wilson EO. 1987. The arboreal ant fauna of Peruvian Amazon forests: a first assessment. *Biotropica* 19: 245-251.
- Wrigley G. 1988. *Coffee*. New York: John Wiley & Sons.
- Wunderle JM, Latta S. 1994. Overwinter turnover of Nearctic migrants wintering in small coffee plantations in Dominican Republic. *Journal fuer Ornithologie* 135: 477.
- \_\_\_\_\_. In press. Avian abundance in sun and shade coffee plantations and remnant pine forest in the Cordillera Central, Dominican Republic. *Ornitologia Neotropical*.
- Wunderle JM, Waide RB. 1993. Distribution of overwintering nearctic migrants in the Bahamas and Greater Antilles. *Condor* 95: 904-933.