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Priority Contribution

Ecology and conservation of birds in coffee plantations: a critical review

OLIVER KOMAR

Summary

Interest in the ecology and conservation of birds in coffee plantations around the world has greatly increased since the early 1990s, especially in the Neotropical region. Much of the interest was inspired by untested hypotheses proposing that extensive conversion of traditional coffee plantations, grown under a diverse canopy of shade trees, into modern, technified plantations with severely reduced shade canopy, contributed to concurrent declines of long-distance migratory birds. This possible relationship sparked major publicity campaigns during the late 1990s and continuing today, promoting shaded coffee plantations as quality habitat for migratory birds. Based on a review of the published scientific literature concerning avian use of coffee plantations, I summarize avian ecology in coffee agroecosystems, and evaluate the hypothesis that coffee plantations are important for the conservation of migratory or resident birds. While no literature has presented strong evidence that coffee plantations in general negatively affect bird populations of conservation importance, nonetheless published studies have not tested hypotheses that birds have greater survivability, fitness or productivity in coffee plantations compared with other available habitats (natural or artificial), or that any species selects coffee plantations over other available habitats for foraging or for breeding. While coffee plantations may have higher avian richness and abundance than other highly disturbed agricultural habitats and some natural habitats, more research is needed to evaluate whether and how certain coffee agroecosystems contribute to the conservation or decline of avian diversity.

Introduction

In the 1990s, awareness of possible conservation benefits to birds, especially migratory birds, from shaded plantations of coffee (*Coffea arabica* and, to a lesser extent, *C. canephora*) suddenly blossomed. This awareness resulted largely from a campaign in North America to promote coffee as habitat for migratory birds, and to reverse the trend of modernization ("technification") that had already converted millions of hectares of shaded coffee "forests" to open-sun coffee fields (Borrero 1986, Vannini 1994, Perfecto *et al.* 1996, Rice and Ward 1996). Until 1996, there were just a handful of papers about birds in coffee plantations[1] (e.g. Terborgh and Weske 1969, Aguilar-Ortiz 1982, Robbins *et al.* 1992, Wunderle and Waide 1993). Interest in the research community originated from reports of declining populations of migratory birds

[1] Throughout this paper, "coffee plantation" refers to any area of any size where coffee has been planted for cultivation.

(Robbins *et al.* 1989, Terborgh 1989, Askins *et al.* 1990, Tangley 1996) and was probably galvanized, in part, by Perfecto and co-workers' (1996) alert, proclaiming that an important refuge for wildlife and migratory birds — shade coffee plantations — was disappearing. While some of these reports implied that the loss of shade cover in coffee plantations may have been a cause of migratory bird declines, that hypothesis has not been critically tested. By 1994 and 1995, several conservation organizations, and in particular the Smithsonian Migratory Bird Center and the Rainforest Alliance, had begun campaigns to increase consumer interest in buying "bird-friendly" or "biodiversity-friendly" shade-grown coffee. In parallel, they developed criteria for certification and helped to build organisations or train auditors to carry out certification. These efforts have made substantial inroads into the mainstream coffee industry: the world's largest coffee importers, roasters and distributors now market certified shade-grown coffees (Wille 2004).

The consumer and industry interest in shade-grown coffee is largely related to the supposition that shaded plantations, especially rustic or traditional farms with many species of shade trees (sometimes remnants of the original forest cover), are beneficial to birds and therefore attractive to millions of coffee-drinking environmentalists and bird-lovers in North America, Europe and Japan. The issue attracted the attention of conservation biologists, some of whom began studies to test hypotheses that coffee plantations were valuable to birds. Perhaps as a byproduct of the conservation interest, a number of ecological studies about birds in coffee plantations have been published in the last few years. The growing interest in studying birds on coffee farms is demonstrated by the increasing frequency of published studies (Figure 1), and their wide geographic scope. The more than 45 studies reviewed herein have been undertaken in 15 coffee-producing countries (Table 1).

In this paper I critically review virtually all published literature pertaining to birds in coffee plantations, and summarize avian ecology in this tropical agroecosystem. I conclude by evaluating whether the conservation value of coffee for birds, widely proclaimed (Perfecto *et al.* 1996, Moguel and Toledo 1999, Philpott and Dietsch 2003, Donald 2004, and many other authors cited within these papers) but sometimes questioned (Rappole *et al.* 2003a, b), is adequately supported by scientific studies.

Study area and methods

Coffee is produced on 10.2 million ha of land (FAO 2005) in 60 countries, and is one of the world's most important commodities and economically valuable crops (O'Brien and Kinnaird 2003). Management styles for coffee production vary greatly in ways that could affect use by birds, ranging from open-sun monocultures with high agrochemical inputs, resembling vineyards, to rustic polyculture gardens grown under a variety of native shade trees with no chemical inputs, resembling original native forest. For this review, I have considered avian ecology in all of the various kinds of coffee agroecosystems, which are adequately described elsewhere (e.g. Fuentes-Flores 1982, Rice and Ward 1996, Moguel and Toledo 1999, Donald 2004, Somarriba *et al.* 2004).

I found published studies by scanning literature cited in journal articles and by searching three citations databases via the internet. I used the search terms "coffee" and "birds" with the BIOSIS and Zoological Record databases, accessed through the University of Kansas library, to produce lists of citations that contain both of these

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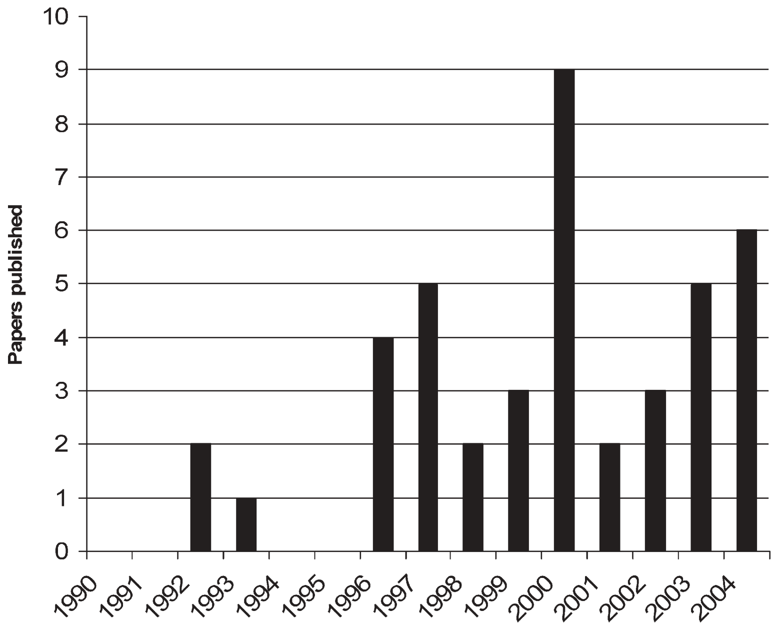

Figure 1. Chronology and publication trend for primary studies of birds in coffee plantations, published in peer-reviewed journals 1990–2004. No year prior to 1990 presented >1 publication.

terms somewhere in the title, abstract or key words. The BIOSIS database (Biological Abstracts, Inc.) contains citations from nearly 6,000 international journals published worldwide, dating from 1969 to the present. Zoological Record (also Biological Abstracts, Inc.) contains citations from 6,500 journals and other publications dating from 1978 to the present. Both databases were searched last on 15 March 2005. I also used the Searchable Ornithological Research Archive (http://elibrary.unm.edu/sora), searched 16 March 2005 with the search term "coffee", and examined citations that contained the search term at least four times in the entire article. This database covers just seven ornithological journals published in the United States over their entire publication history (which began in 1884).

Ecology of birds in coffee plantations

Avian diversity and abundance

Highly diverse and abundant bird communities in coffee plantations, despite high levels of anthropogenic disturbance, have attracted many ornithologists. For example, shaded coffee plantations in Chiapas, Mexico, had 180 bird species and a mean density of 51 birds/ha during winter bird surveys (Greenberg *et al.* 1997b). Structurally, shaded coffee plantations are intermediate between original natural forest cover and intensive agriculture, having many trees dispersed among the plantation but not as many as a natural forest. As expected, bird species-richness and diversity in shaded coffee plantations tend to be lower than in nearby forest patches (Terborgh and Weske 1969, Beehler *et al.* 1987, Thiollay 1995, Wunderle and Latta 1996, Estrada *et al.* 1997, Greenberg *et al.* 1997a, Petit *et al.* 1999), although studies in some landscapes

Table 1. Primary, published, peer-reviewed studies of birds in coffee plantations, by country (theses, dissertations and observational studies with no hypothesis testing are not included; full citations are given in the References).

Country	Authors	Year published
Brazil	Cintra	1988
Colombia	Botero and Verhelst	2001
Colombia	Verhelst *et al.*	2002
Costa Rica	Cohen and Lindell	2004
Costa Rica	González	1999
Costa Rica	Lindell and Smith	2003
Cuba	Wunderle and Waide	1993
Dominican Republic	Latta and Wunderle	1996
Dominican Republic	Wunderle	1999
Dominican Republic	Wunderle and Latta	1996
Dominican Republic	Wunderle and Latta	1998
Dominican Republic	Wunderle and Latta	2000
Dominican Republic	Wunderle and Waide	1993
Ecuador	Canaday	1996
Guatemala	Calvo and Blake	1998
Guatemala	Greenberg *et al.*	1996
Guatemala	Greenberg *et al.*	1997
Guatemala	Greenberg *et al.*	2000
India	Beehler *et al.*	1987
India	Shahabuddin	1997
Indonesia	Siebert	2002
Jamaica	Johnson	2000
Jamaica	Johnson and Sherry	2001
Jamaica	Robbins *et al.*	1992
Jamaica	Strong	2000
Jamaica	Strong and Sherry	2000
Jamaica	Wunderle and Waide	1993
Jamaica	Wunderle *et al.*	1992
Mexico	Aguila-Ortiz	1982
Mexico	Cruz-Angón and Greenberg	2005
Mexico	Estrada *et al.*	1997
Mexico	Greenberg *et al.*	1997
Mexico	Mas and Dietsch	2004
Mexico	Perfecto *et al.*	2003
Mexico	Perfecto *et al.*	2004
Mexico	Philpott *et al.*	2004
Mexico	Tejeda-Cruz and Sutherland	2004
Panama	Parrish and Petit	1996
Panama	Petit and Petit	2003
Panama	Petit *et al.*	1999
Panama	Pomara *et al.*	2003
Panama	Roberts *et al.*	2000
Peru	Terborgh and Weske	1969
Puerto Rico	Carlo *et al.*	2003
Puerto Rico	Carlo *et al.*	2004
Puerto Rico	Robbins *et al.*	1992
Puerto Rico	Wunderle and Waide	1993
Venezuela	Jones *et al.*	2000
Venezuela	Jones *et al.*	2002

have documented the same or even higher species richness as natural forest (Aguilar-Ortiz 1982, Greenberg *et al.* 1997b, Shahabuddin 1997, Tejeda-Cruz and Sutherland 2004). Species diversity in shaded plantations is nearly always reported to be considerably higher than in open-sun plantations or other types of monoculture (Beehler *et al.* 1987, Wunderle and Latta 1996, Estrada *et al.* 1997, González 1999, Petit *et al.* 1999, Tejeda-Cruz and Sutherland 2004).

The loss of forest-specific avian diversity in the plantations is countered by the presence of bird species typical of matorral, disturbed or open habitat (Terborgh and Weske 1969, Petit *et al.* 1999, Roberts *et al.* 2000, Petit and Petit 2003), and appears to follow patterns similar to degradation of natural forests by logging and agricultural expansion in general (Thiollay 1999). Many forest undergrowth-specialist birds are rare or absent in plantations, even when the shade canopy is largely composed of original forest trees, because of the nearly complete transformation of the undergrowth to coffee cultivation (Terborgh and Weske 1969, Roberts *et al.* 2000, Strong 2000). Middle-strata foragers are also negatively affected by conversion of forest to shaded coffee plantations (Tejeda-Cruz and Sutherland 2004).

Avian abundance is sometimes noted to be higher in shaded coffee plantations than in natural forest (Beehler *et al.* 1987, Estrada *et al.* 1997, Greenberg *et al.* 1997b, Petit *et al.* 1999), although none of these studies have corrected for differences in detectability, and the more open and shorter stature coffee habitat (compared with natural forest) suggests that bird detectability, rather than actual abundance, should be higher in coffee (Emlen 1971, Verner and Ritter 1988). The question of the higher abundance of migratory birds (rather than all birds) in coffee plantations is addressed below, in the section on seasonal use by birds.

Shaded coffee plantations tend to have higher avian abundance than open-sun coffee plantations (Wunderle and Latta 1996, Greenberg *et al.* 1997a) or other agricultural habitats (Beehler *et al.* 1987, Greenberg *et al.* 1997b, Petit *et al.* 1999). This is probably because the diverse floristic structure of the shaded plantation offers more feeding resources for birds (e.g. Greenberg *et al.* 2000, Johnson and Sherry 2001). The higher bird abundance in shaded than in sun coffee is due mostly to the greater abundance of resident, rather than migratory, birds. For example, Wunderle and Latta (1996) found significantly more resident birds in shaded coffee (23 birds/ha) than in sun coffee (11 birds/ha), but migrant birds had equal densities.

While diversity and abundance measurements have been a frequent focus of studies, their ecological and conservation significance are debatable. The overall species-richness situation in any given landscape is probably influenced by the sizes of the local habitat patches, following the predictions of island biogeography (MacArthur and Wilson 1967). In general, large patches of habitat will have greater avian diversity and small patches, less. Also following the predictions of island biogeography, patches of plantations relatively close to natural forests, or other sources of colonist birds, have greater abundance and richness than patches farther away, since some forest birds tend to wander into nearby plantations (Terborgh and Weske 1969, Parrish and Petit 1996, Roberts *et al.* 2000).

Effects of canopy structure on bird populations

Most studies of the effect of canopy structure on the richness or abundance of birds have considered entire avian communities, which can hide effects on individual species. Because bird communities are diverse and complex, changing conditions frequently lead to changing community membership or dynamics but do not necessarily cause change in diversity and abundance, which is why some studies may have failed to detect quantitative effects (e.g. Terborgh and Weske 1969). While a few authors have reported effects of canopy structure on overall bird abundance or diversity (Parrish and Petit 1996, Greenberg *et al.* 1997a), the effects have been small. Unfortunately, the authors did not standardize abundance counts of the community members in order to consider all species on equivalent scales; one or a few abundant species may have biased results and hidden stronger effects on rarer species. Some common generalist species are probably not affected by variation in canopy structure. Johnson and Sherry (2001) showed that canopy structure failed to explain variation in abundance of a group of canopy-feeding migratory warblers. At best, canopy structure is probably only an indirectly important variable, correlated with other parameters of greater importance such as food availability.

Effects of canopy tree species on bird populations

The community structure of shade trees in coffee plantations can vary greatly depending on geography and the management style of the coffee farmer. The dominant shade tree species and the diversity of shade tree species potentially influence bird populations. Plantations shaded mostly by either remnant natural forest trees or a planted *Inga* overstorey tend to have more bird species and higher abundance than plantations with overstorey dominated by *Pseudalbizzia* spp. or *Gliricidia* spp. (Greenberg *et al.* 1997a, Johnson 2000, Johnson and Sherry 2001). Another common shade tree in plantations, *Erythrina* spp., may provide abundant food resources (nectar and insects) for canopy-feeding birds (González 1999, Jones *et al.* 2002), although little quantitative data is available. The specific value for frugivorous birds of just a few fruit-producing shade trees has been documented (Carlo *et al.* 2004).

Microhabitat use and foraging guilds

Birds in shaded coffee plantations apparently forage mostly in the tree canopies (Aguilar-Ortiz 1982, Greenberg *et al.* 1997a, Wunderle and Latta 1998, Jones *et al.* 2002), where the majority of arthropod (Greenberg *et al.* 2000, Johnson 2000), fruit and nectar resources are located. Greenberg *et al.* (1997a) reported 74% of nearly 2,300 bird observations in Guatemala from the canopy, and Jones *et al.* (2002) found 66% of nearly 2,000 observations in Venezuela from canopy. Unfortunately, these studies did not attempt to quantify observer bias or differences in detectability among canopy and understorey foraging birds; birds may be more detectable in the relatively open canopy than in the dense coffee shrubs. Relatively few birds forage among epiphytes in some plantations (Wunderle and Latta 1998, Jones *et al.* 2002), but some frugivorous *Euphonia* spp. may forage exclusively in epiphytes (Carlo *et al.* 2003, 2004), and experimental evidence demonstrated that epiphyte removal significantly reduces bird abundance, especially for some breeding species that use epiphytes for nesting and foraging (Cruz-Angón and Greenberg 2005). Large canopy frugivores and insectivores, as well as understorey insectivores in general, were much reduced in Sumatran plantations compared with nearby natural forest (Thiollay 1995).

While ground or understorey foragers are a minority in shaded coffee plantation ecosystems, they nonetheless can be quite common (Cintra 1988, Roberts *et al.* 2000, Johnson and Sherry 2001, Perfecto *et al.* 2004, Tejeda-Cruz and Sutherland 2004). Ground-feeding granivores and some aerial insectivores may be most common in open-sun plantations. Forest understorey insectivores (e.g. antbirds, Formicariidae and Thamnophilidae), understorey bark insectivores (e.g. woodcreepers, Dendrocolaptidae) and mid-storey insectivores (e.g. members of Tyrannidae) are rare or absent in many Neotropical plantations (Canaday 1996, Roberts *et al.* 2000, Lindell and Smith 2003, Tejeda-Cruz and Sutherland 2004), especially at greater distances from forest source populations. (The distance from forest at which forest birds may still be noted probably varies with species and habitat structure; no studies have carefully quantified the effects of distance from source habitats on relative abundance of such species.) In one Veracruz plantation, only 33 of 136 species foraged on the ground or among coffee shrubs (Aguilar-Ortiz 1982). In Chiapas plantations, 57 of 147 species recorded on point counts were ground, understorey or open scrub foragers, the rest being trunk or canopy feeders (Greenberg *et al.* 1997b). In Venezuela, 93 of 191 species foraged on the ground or in the understorey, the rest being restricted to mid or upper canopy levels (Jones *et al.* 2002).

Dietary guilds

Generally, more omnivores, frugivores and nectarivores, but fewer insectivores, occupy coffee plantations than natural forest (Canaday 1996, Shahabuddin 1997, Petit *et al.* 1999). The dietary guild structures for several shaded coffee plantations are given in Table 2. A generalized trophic guild structure for coffee bird communities is difficult to produce, however, because of varying methodologies for classifying birds among guilds, and varying seasonality of studies. Precise quantification of food preferences for birds foraging in coffee plantations has been documented for just a few species, on Caribbean islands, including two insectivores (Strong 2000) and five frugivores (Carlo *et al.* 2004).

Despite being the avian group most negatively affected by disturbance of natural forests, insectivorous birds are nonetheless among the most abundant birds in coffee plantations. Using avian exclosures around branches in *Inga* canopies, Philpott *et al.* (2004) demonstrated experimentally that canopy-feeding birds reduce arthropod abundance by 37% in the dry season and 59% in the wet season. In that experiment, birds affected abundance of both small (<3 mm) and large (>5 mm) arthropods, with the greatest impact on large arthropods, which were reduced by 79% in the dry season and by 66% in the wet season. The arthropod taxa most reduced by avian predation were roaches (reduced 93%), beetles (62%), orthopterans (62%), spiders (56%) and mites (53%). While most insectivores in coffee farms feed in tree canopies and not in the coffee shrub understorey, experimental studies have shown that insectivorous birds significantly reduce (by up to 80%) arthropod presence and leaf damage of the coffee shrubs themselves (Greenberg *et al.* 2000). In another experiment involving coffee plants, birds significantly reduced abundances of experimentally placed lepidopteran larvae in a coffee plantation with high avian abundance, but not in a coffee plantation with low avian abundance (Perfecto *et al.* 2004). At least in some Indian (Le Pelley 1968, Yahya 2000) and Caribbean (Wolcott 1933, Sherry 2000) plantations, insectivorous birds have been noted to consume known coffee pests. In Java, *Collocalia* swiftlets were observed consuming swarming coffee berry borer beetles (*Hypothenemus hampei*) on the wing (Leefmans 1923).

Table 2. Avian community composition by dietary guild for selected shaded coffee plantations (left-hand columns show proportions of guilds formed by species, right-hand columns show proportions of guilds formed by individuals).

Trophic guild	Mexico (Veracruz): species, year-round (Aguilar-Ortiz 1982)[a]	Ecuador: species, breeding (Canaday 1996)	Mexico (Chiapas): species, non-breeding (Greenberg *et al.* 1997b)	Panama: species, non-breeding (Petit *et al.* 1999)[b]	Jamaica: species, non-breeding (Johnson 2000)	Venezuela: species, non-breeding (Jones *et al.* 2002)[a]	India: individuals, breeding (Shahabuddin 1997)[c]	Jamaica: individuals, non-breeding (Johnson 2000)[d]
Insectivore	56%	20%	32%	48%	55%	80%	26%	58%
Frugivore	52%	22%	12%	31%	7%	42%	19%	3%
Omnivore	NA	50%	45%	NA	20%	54%	41%	6%
Nectarivore	11%	5%	8%	10%	13%	21%	8%	24%
Granivore	11%	NA	3%	8%	5%	11%	6%	8%
Carnivore or other	4%	3%	NA	3%	0%	3%	0%	0%

[a]Omnivorous species were included in more than one category.
[b]Omnivorous species were categorized only with their chief feeding preference.
[c]Data compiled from a graphic.
[d]Proportions were calculated from raw data given in Johnson's Table 1. In his text, however, he gives different figures: insectivores 56%, omnivores 13% and nectarivores 20%.

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Just as insectivores forage primarily in the plantations' "forest" overstorey, so do the numerous frugivores and frugivorous omnivores (mostly frugivore/insectivores). Frugivores and omnivores are sometimes more common in plantations than in nearby natural forests. Carlo *et al.* (2003) demonstrated that in one region of Puerto Rico, relative abundance of fruit preferred by the principal avian frugivores (compared with the abundance of non-preferred fruits) was much higher (50%) in one coffee plantation than in three natural forest sites and another plantation (maximum 15%). Frugivores tracked fruit abundance, moving into coffee plantations when fruit was abundant; nonetheless several species studied in detail appeared to select natural forest habitat over coffee habitat in most months of the year (Carlo *et al.* 2004).

Only two studies have found any evidence that birds consume the fruits of coffee plants themselves: Wellman (1961) reported "small" birds in Costa Rica pecking at ripe coffee cherries. Three species in Puerto Rico were observed on seven occasions to eat coffee cherries (Carlo *et al.* 2004), but given the extensive foraging observations of the study and the abundance of the fruit, this result is consistent with the general belief in the Neotropics that birds virtually never consume coffee beans. The situation may be different in Africa, where coffee is native and birds are thought to be consumers of wild coffee fruits (of both *C. arabica* (Wellman 1961) and *C. canephora* (Kasenene 1998)).

Nectarivorous birds in the New World, such as hummingbirds (Wagner 1946), honeycreepers, icterid orioles and some parulid warblers (e.g. Tennessee Warbler, *Vermivora peregrina*), frequent the inflorescences of common canopy trees such as *Inga* spp. and *Erythrina* spp. One study documented the use of *Inga* flowers by seven nectarivorous birds; 72% of all visits were by just two species of *Amazilia* hummingbird (Greenberg *et al.* 1997a). No detailed studies on avian nectarivory or folivory are available from coffee plantations.

No information on foraging habits of granivores in coffee plantations was available, although ground-doves (*Columbina* spp.), buntings (*Passerina* spp.), seedeaters (*Sporophila* spp.), grassquits (*Tiaris* spp.) and other granivores can be quite common in some plantations. Equally scarce was foraging information or relative abundance information for carnivorous birds (Strigiformes, Falconiformes, cathartid Ciconiiformes) in plantations. Nonetheless, observations of bird-eating hawks (*Accipiter*, *Asturina*, *Buteo* spp.) and pygmy-owls (*Glaucidium* spp.) are common in many plantations, and mist-netting operations occasionally trap these predators attacking birds caught in mist nets (author's unpublished data).

Seasonal use of ephemeral or dynamic resources by birds

Many studies have noted that coffee plantations offer seasonal foraging resources, especially nectaries and associated insects on leguminous shade trees such as *Inga* spp. (e.g. Aguilar-Ortiz 1982, Greenberg *et al.* 1997b, Johnson 2000, Johnson and Sherry 2001) but also fruits of specific trees preferred by frugivores (Carlo *et al.* 2003, 2004). During parts of the dry season when many trees are flowering, certain nectarivorous and insectivorous birds are notably abundant in shaded coffee plantations. Some of these species are local resident birds that may occupy native forest patches at other times of year (Aguilar-Ortiz 1982); others are long-distance migrants that may also move among the plantations and local forest patches. Greenberg *et al.* (1997b) suggested that shaded coffee plantations may provide especially important dry season

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resources at a time when natural forest resources are minimal, although the data they presented to support this hypothesis were inconclusive, because the late season increases in plantation bird abundance they reported may have reflected immigration of north-bound migrants rather than local movements. Calvo and Blake (1998) noted temporal variation in bird abundance among plantation types even within the wet (breeding) season, which could possibly reflect ephemeral or dynamic resource availability during the rainy season, although other explanations (such as production of juveniles, variation in singing frequency or cryptic behaviour during incubation) are also possible.

Some studies have concluded that certain migratory bird species seem to have an affinity for shaded coffee plantations (e.g. Robbins *et al.* 1992, Wunderle and Latta 1996, Greenberg *et al.* 1997b, Tejeda-Cruz and Sutherland 2004). Johnson and Sherry (2001) found significantly higher abundance of a group of canopy-feeding insectivorous migratory warblers in coffee shaded with *Inga* trees when compared with other types of shade coffee and natural limestone forest in Jamaica, although thorn scrub and old-growth mangroves had comparable migrant abundances. Unlike other studies that have based their conclusions only on observations or captures (subject to detectability errors), this study also showed that migrants tracked arthropod food resources, and that these resources were highest in the *Inga*-shaded coffee plantations, thorn scrub and old-growth mangroves.

Nearctic-Neotropical migrants comprise a large portion of the bird communities in Neotropical shaded coffee plantations during the northern winter, which usually corresponds to the tropical dry season. At least 90 North American migratory bird species use Neotropical coffee plantations during the non-breeding season (Table 3). In Caribbean and northern Central American plantations, migratory birds (mostly parulid warblers) typically form 30–50% of individual birds and 25–40% of species observed during the dry season (Table 4). The proportion of Nearctic migrants in South America should be lower, in part because fewer species winter that far south, and in part because of greater diversity of resident species; as predicted, only 9% of species in Venezuelan plantations were migrants (Table 4; Jones *et al.* 2002). No published data are available from the Paleotropical region for long-distance migrants occupying coffee plantations. The high abundance of migratory birds reported in shaded coffee plantations has been represented erroneously to be evidence that sun coffee is used less by migrants (e.g. Rice and Ward 1996, Boot *et al.* 2003). In fact, migratory birds, most of which are generalists, can be equally abundant in sun coffee plantations (Table 5).

Philopatry and territoriality

Little has been reported on philopatry or territoriality of birds in coffee plantations. Greenberg *et al.* (1996) found male Yellow Warblers (*Dendroica petechia*) wintering in Guatemalan plantations to be territorial. Wunderle and Latta (2000) studied territorial Black-and-white Warblers (*Mniotilta varia*), Black-throated Blue Warblers (*D. caerulescens*) and American Redstarts (*Setophaga ruticilla*) wintering in Dominican Republic plantations, and found that individuals of all three species returned to the same wintering areas in successive years. Johnson and Sherry (2001) reported high site persistence for apparently territorial American Redstarts in Jamaican coffee plantations, comparable to persistence rates in local forest. Strong and Sherry (2000)

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Table 3. North American migratory birds[a] recorded in Latin American coffee plantations.

Species	Countries[b]	References[c]
Accipiter striatus	ES, MX	A, N
Accipiter cooperii	ES	N
Buteo platypterus	CO, ES	I, N
Falco sparverius	ES	N
Coccyzus americanus[d]	CO, ES	I, N
Chordeiles acutipennis	ES	N
Caprimulgus vociferus	ES	N
Cynanthus latirostris	MX	A
Archilochus colubris	ES, GT, MX	A, F, G, M, N
Sphyrapicus varius	MX	G
Contopus cooperi[e,g]	CO, ES, VE	I, L, N
Contopus sordidulus[d]	ES	N
Contopus virens[d]	MX	A
Contopus cinereus	MX	M
Empidonax flaviventris	ES, GT, MX, PA	F, G, K, N
Empidonax virescens[e]	CO, MX	A, I
Empidonax traillii[d,g]	ES	N
Empidonax alnorum[d,f]	CO, ES, VE	I, L, N
Empidonax minimus	ES, GT, MX	A, F, G, M, N
Empidonax hammondii	MX	G
Myiarchus crinitus	CO, GT, MX	A, F, G, I
Myiodynastes luteiventris[d]	MX	G
Tyrannus verticalis	ES	N
Tyrannus tyrannus[d]	CO	I
Vireo griseus	MX	A, G
Vireo flavifrons	ES, MX	G, M, N
Vireo solitarius	ES, GT, MX	A, F, G, M, N
Vireo gilvus	ES, GT, MX	G, H, M, N
Vireo philadelphicus	MX	G, M
Vireo olivaceus[d]	DR, ES	E, N
Vireo flavoviridis[d]	ES	N
Tachycineta thalassina	ES	N
Petrochelidon pyrrhonota[d]	ES	N
Petrochelidon fulva[d]	ES	N
Hirundo rustica	ES	N
Troglodytes aedon	MX	A
Polioptila caerulea	CU, ES, GT, MX	D, F, G, N
Catharus bicknelli[g]	DR	E
Catharus ustulatus	CO, ES, GT, MX, PA, VE	F, G, L, I, K, M, N
Catharus guttatus	MX	M
Hylocichla mustelina[g]	GT, MX	A, F, G
Dumetella carolinensis	DR, GT, MX	E, F, G, M
Bombycilla cedrorum	ES, GT, MX	A, F, G, M, N
Vermivora pinus[g]	ES, MX	A, G, N
Vermivora chrysoptera[g]	CO, ES, VE	I, L, N
Vermivora chrysoptera x *pinus*	DR	E
Vermivora peregrina	CO, CU, DR, ES, GT, JA, MX, PA, VE	A, B, D, E, F, G, H, I, K, L, M, N
Vermivora ruficapilla	ES, MX	A, G, M, N
Parula americana	CU, DR, ES, JA, MX, PR	B, C, D, E, G, J, N
Dendroica petechia	CO, ES, GT, MX, VE	F, G, I, L, M, N
Dendroica pennsylvanica	GT, JA, MX, PA	A, C, D, F, G, K
Dendroica magnolia	DR, ES, GT, JA, MX	B, C, E, F, G, J, M, N
Dendroica tigrina	DR, JA, PR	D, E, J

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Table 3. Continued

Species	Countries[b]	References[c]
Dendroica caerulescens	CU, DR, GT, JA, MX, PR	B, C, D, E, G, H, J
Dendroica coronata coronata	DR, MX	A, E
Dendroica coronata audubonii	MX	A
Dendroica chrysoparia[d,g]	MX	O
Dendroica virens	CU, DR, ES, GT, JA, MX	A, C, D, E, F, G, J, M, N
Dendroica townsendi	ES, MX	A, G, M, N
Dendroica occidentalis[g]	MX	G, M
Dendroica fusca[e]	CO, ES, MX, VE	A, I, L, N
Dendroica dominica	DR, MX, JA	A, E, J
Dendroica discolor[g]	DR, JA	B, C, D, E, J
Dendroica palmarum	DR, JA	C, D, E, J
Dendroica castanea[g]	CO, VE	I, L
Dendroica striata	VE	L
Dendroica cerulea[g]	CO, VE	I, L
Mniotilta varia	CO, CU, DR, ES, GT, JA, MX, PA, PR, VE	A, B, C, D, E, F, G, I, J, K, L, M, N
Setophaga ruticilla	CO, CU, DR, ES, GT, JA, MX, PR, VE	A, B, C, D, E, F, G, I, J, L, M, N
Helmitheros vermivorum[g]	DR, JA, MX	E, G, J
Limnothlypis swainsonii[g]	JA	J
Seiurus aurocapilla	CU, DR, ES, GT, JA, MX, PR	A, B, C, D, E, F, G, J, N
Seiurus noveboracensis	CO, JA, MX, PR, VE	B, G, I, J, L
Seiurus motacilla	DR, ES, MX	A, E, N
Oporornis formosus[g]	GT, MX, PA, PR	A, B, F, G, K
Oporornis philadelphia[e]	CO, MX, PA, VE	A, I, K, L
Oporornis tolmiei	ES, GT, MX	A, F, G, M, N
Geothlypis trichas	CU, DR, GT, JA, MX	A, B, C, D, E, F, G, J
Wilsonia citrina	GT, MX	F, G
Wilsonia pusilla	ES, GT, MX, PA	A, F, G, K, M, N
Wilsonia canadensis[e,g]	CO, ES, MX, VE	A, I, L, N
Icteria virens	ES, GT, MX	A, F, G, N
Piranga rubra	CO, DR, ES, GT, MX, VE	A, E, F, G, I, L, M, N
Piranga olivacea	CO	I
Piranga ludoviciana	ES, GT, MX	F, G, M, N
Pheucticus ludovicianus	CO, DR, ES, GT, MX, VE	A, E, F, G, I, L, M, N
Passerina caerulea	GT	F
Passerina cyanea	CU, DR, ES, GT, JA, MX, PR	A, B, D, E, F, G, N
Passerina ciris[g]	ES, MX	M, N
Icterus spurius	CO, ES, GT, MX	A, F, G, I, N
Icterus bullockii	MX	G
Icterus galbula	CO, ES, GT, MX	A, F, G, H, I, M, N

[a]Species locally resident, whether or not reported as migrants, were generally excluded, even if they visit plantations only seasonally. Examples: *Falco sparverius* and *Accipiter striatus* in Dominican Republic (Wunderle and Latta 1996), *Vireo leucophrys* in Mexico (Tejeda-Cruz and Sutherland 2004).

[b]CO, Colombia; CU, Cuba; DR, Dominican Republic; ES, El Salvador; GT, Guatemala; JA, Jamaica; MX, Mexico; PA, Panama; PR, Puerto Rico; VE, Venezuela.

[c]A, Aguilar-Ortiz 1982; B, Robbins *et al.* 1992; C, Wunderle *et al.* 1992; D, Wunderle and Waide 1993; E, Wunderle and Latta 1996; F, Greenberg *et al.* 1997a; G, Greenberg *et al.* 1997b; H, Calvo and Blake 1998; I, Botero *et al.* 1999; J, Johnson 2000; K, Roberts *et al.* 2000; L, Jones *et al.* 2002; M, Tejeda-Cruz and Sutherland 2004; N, O. Komar, unpublished data; O, Dietsch 2000.

[d]Possibly only transient in coffee plantations.

[e]Transient in Mexico and Central America, wintering in South America.

[f]Identified as "Traill's" Flycatcher (*E. traillii* or *alnorum*) in Colombia and Venezuela; *E. alnorum* is more likely for habitat reasons.

[g]Continental Watch List species (Rich *et al.* 2004).

Table 4. Proportion of birds in Neotropical coffee plantations during the non-breeding season that are long-distance (Nearctic) migrants.

Region/Country	Type of plantation	Migratory individuals	Migratory species	Reference
Mexico and Central America				
Guatemala	Shade	45%	40%	Greenberg *et al.* 1997a
Guatemala	Sun	45%	40%	Greenberg *et al.* 1997a
Mexico (Chiapas)	Diverse native shade	43%	34%	Greenberg *et al.* 1997b
Mexico (Chiapas)	*Inga* spp. shade	53%	33%	Greenberg *et al.* 1997b
Mexico (Veracruz)	Shade	17%	26%	Estrada *et al.* 1997
Panama	Shade	8%	11%	Petit *et al.* 1999
Caribbean				
Dominican Republic	Shade	31%, 41%	25%	Wunderle and Latta 1996
Dominican Republic	Sun	32%, 48%	35%	Wunderle and Latta 1996
Jamaica	Shade	50%	38%	Johnson 2000
Jamaica	Shade, damaged by hurricane	24%	42%	Robbins *et al.* 1992
Puerto Rico	Shade (understorey only)	10%	35%	Robbins *et al.* 1992
Puerto Rico	Sun	6%	26%	Robbins *et al.* 1992
South America				
Colombia	Sun and shade	NA	9–15%	Botero *et al.* 1999
Venezuela	Shade	NA	9%	Jones *et al.* 2002

Table 5. Migratory bird abundance in shaded versus open-sun coffee plantations[a].

Plantation location	Migrant bird density (birds/ha)		Source
	Shade	Sun	
Dominican Republic	10.2	10.3	Wunderle and Latta 1996
Guatemala	14.5	10.2	Greenberg *et al.* 1997a
Mexico (Chiapas)	24.8	N/D	Greenberg *et al.* 1997b
Mexico (Chiapas)	18.0	N/D	Tejeda-Cruz and Sutherland 2004
	Understorey migrant bird abundance (captures/100 net hours)		
Costa Rica	1.2	3.6	González 1999
Dominican Republic	8.4	11.9	Wunderle and Latta 1996
Puerto Rico	3.8	1.8	Robbins *et al.* 1992

[a]Studies may not be directly comparable, as they differ in seasonality and distance to natural habitats, which can influence bird abundance.

found ground-feeding migratory Ovenbirds (*Seiurus aurocapilla*) defending feeding spaces, and occupying home ranges persistently through the winter. All these species are migratory visitors to coffee plantations. Data on philopatry or territoriality in resident tropical birds using coffee plantations are not available.

During the non-breeding season, insectivores in tropical forest habitats tend to form mixed-species foraging flocks, even when they maintain fixed home ranges or territories (Hutto 1994, Latta and Wunderle 1996a). Such flocks, while common in Hispaniolan forests, were never found during extensive observations in Hispaniolan shaded coffee plantations (Latta and Wunderle 1996b). In Panama, such flocks are common in coffee plantations but less so than in natural forest (Roberts *et al.* 2000, Pomara *et al.* 2003). The reasons for these differences in habitat use are unknown, but could be related to differences in food availability, degree of territoriality (and defensibility of resources), feeding specializations or predation rates.

Breeding

While several researchers have studied birds in coffee plantations during the breeding season (e.g. Skinner 1901, Hardy 1976, Cintra 1988, Marcondes Machado 1988, Shahabuddin 1997, Calvo and Blake 1998, González 1999, Lindell and Smith 2003, Cohen and Lindell 2004, Cruz-Angón and Greenberg 2005), very little research has been published on breeding success in coffee plantations. The only such data come from two studies in recently abandoned coffee plantations with 30–60% canopy-cover in Costa Rica. Lindell and Smith (2003) documented that overall nesting success of 39 species was comparable to overall nesting success in natural forest understorey and in pasture habitats. None of the common nesting species of nearby forest understorey, however, nested in the plantations. Nesting density was at least 7.5 nests per hectare, and about 60% of the above-ground nests were placed in coffee bushes; these coffee nests were significantly more successful than nests placed on other plant species, suggesting that coffee plants provide quality nesting sites. Unfortunately, the study plantation, having been abandoned 5 years earlier, is not representative of an active, productive coffee plantation with higher human disturbance.

Cohen and Lindell (2004) studied the post-fledging period for White-throated Robins (*Turdus assimilis*) that nested in the same plantations and in neighbouring pastures. Survivorship of radio-tagged fledglings was significantly lower in the plantations than in the pastures, although higher than survivorship reported for turdids in temperate breeding areas in North America. All the robin fledglings considered to have survived the pre-dispersal period moved from their natal site (coffee or pasture) into neighbouring forest; fledglings born in the coffee plantation tended to spend more time near their natal site before moving into forest, but no fledglings that stayed in the coffee plantation until signals were lost were thought to have survived. The authors considered that fledglings in coffee were more susceptible to predation than in forest, but stayed longer in the plantation than in pasture because of the structural similarity of the plantation to forest, leading to lower survivorship (i.e. the plantation served as a death trap). Birds may breed in coffee plantations to take advantage of abundant nesting opportunities even when they forage in other habitats (Cintra 1988, Lindell and Smith 2003, Cohen and Lindell 2004). If this is true, then nesting densities should be highest near edges with non-coffee habitats, and the species of nesting birds would be largely influenced by the adjoining habitats.

Habitat quality and survivorship for non-breeding birds

High site persistence and fidelity rates (and, therefore, survival) on a par with some natural forest habitats have been reported for four migratory warbler species in coffee plantations (Wunderle and Latta 2000, Strong and Sherry 2000, Johnson and Sherry 2001). For these four species, at least, shaded coffee plantations in the Caribbean appear to be a quality winter habitat; their territorial behaviour implies that they have access to predictable food resources, although such resources may not necessarily be abundant; in fact, the need to form territories suggests that competition for food is great and that demand exceeds supply (Brown 1969). In one winter (but not another), Ovenbird site persistence was significantly higher than in undisturbed natural forest and second-growth scrub habitat. A study of foraging rates in Panama found that Wilson's Warblers (*Wilsonia pusilla*) appeared to forage as successfully in a rustic coffee site as in a natural forest site (Pomara *et al.* 2003), also suggesting that the coffee site was of reasonably high quality for yet another migratory warbler. However, these studies did not evaluate relative selection of available habitats by these species, so their preference for shaded coffee plantations has not been established (Johnson and Sherry 2001). Nonetheless, body condition of Ovenbirds was as high in coffee plantations as in natural forest, and feather growth rates were significantly higher in the coffee plantations (Strong and Sherry 2000). Shaded coffee plantations may offer relatively high quality habitat in another sense: a study in Jamaica provided evidence that an avian community in a shaded plantation was less affected by a hurricane than the community in a sun plantation (Wunderle *et al.* 1992); the topic requires further study because of small sample sizes.

Sex and age segregation of non-breeding migratory birds

In the Dominican Republic, Wunderle and Latta (1996, 2000) found male-biased sex ratios of Black-throated Blue Warbler and American Redstart in shaded coffee, and female-biased sex ratios of the same species in sun coffee. They interpreted this result to mean that shaded coffee offers stable resources and higher quality habitat used by dominant males. Greenberg *et al.* (1996) found only male Yellow Warblers defending scattered trees in Guatemalan sun coffee fields. Not all migratory birds sexually segregate in coffee plantations: Jones *et al.* (2000) found equal numbers of male and female Cerulean Warblers (*Dendroica cerulea*) in Venezuela. Almost no information is available on age segregation. Strong and Sherry (2000) found significantly different age ratios for Ovenbirds between two coffee sites in one year (but not another); age ratios among coffee and other habitats studied did not differ significantly.

Shaded plantations as dispersal corridors for locally breeding birds

Several authors have proposed that disturbed wooded habitats in general (Forman 1992, Harrison 1992, Franklin 1993), and shaded coffee plantations in particular (Ramírez and Komar 1996, Shahabuddin 1997, Komar 1998, Tejeda-Cruz and Sutherland 2004) could facilitate dispersal of forest birds across a landscape. Unfortunately, virtually no data have demonstrated that dispersers (1) choose to move through coffee plantations rather than other habitats available, or (2) have greater success finding new territories after dispersing through coffee plantations compared with other habitats. One recent study has shed some light on the possible role of coffee as a dispersal corridor. Cohen and Lindell (2004) used radio-transmitters to study pasture-breeding White-throated Robins (*Turdus assimilis*) in southern Costa Rica, where they nested in high densities near the edge of a large forest patch, and dispersed into the forest shortly after fledging. Also bordering the pastures were shaded coffee plantations. Some of the fledglings moved into the coffee plantations before moving into forest; thus the plantations served as a dispersal corridor for pasture-breeding individuals of this species. No study has reported evidence of avian dispersal of forest-breeding individuals in coffee plantations.

Conservation importance of birds in coffee plantations

Many authors have suggested that shaded coffee plantations, especially with abundant *Inga* trees in the canopy, may be important to the conservation of wintering migrant birds because of the seasonal resources provided when natural habitat food resources are low (e.g. Greenberg *et al.* 1997b, Johnson and Sherry 2001). Others have suggested that some shaded coffee plantations may be important to resident forest-specialist birds (Petit *et al.* 1999, Petit and Petit 2003, Mas and Dietsch 2004) because such species are often found feeding in the plantations. These studies have rarely evaluated whether the species found in coffee plantations are considered threatened or otherwise of high conservation importance. I found literature references for eight Globally Threatened bird species (IUCN 2004) that occupy shaded (but not sun) coffee plantations (Table 6). Furthermore, 16 of the migratory species known from plantations (Table 3) are on the Continental Watch List (Rich *et al.* 2004). Based on abundance of disturbance-sensitive forest birds, Petit and Petit (2003) ranked shaded coffee plantations higher for conservation importance than wooded riparian corridors, suburban areas, monoculture tree plantations and a variety of open agricultural habitats, and nearly as important as premontane forest, but the study may have been biased by the close proximity of natural forest patches to some of their coffee sites. Using the same classification as Petit and Petit (2003) for disturbance-sensitive species, Tejeda-Cruz and Sutherland (2004) found that shaded coffee plantations had a similar abundance of such species as nearby lower montane forest fragments, but significantly fewer than montane pine-oak forest.

What role does coffee play in bird conservation?

The arguments that shaded coffee plantations are important for bird conservation are based largely on three well-documented observations: (1) shaded coffee plantations tend to have more bird species than sun coffee plantations or other agricultural

Table 6. Globally Threatened bird species recorded in shaded coffee plantations.

Species	IUCN threat status	Countries where reported in coffee farms	References
Hispaniolan Parakeet (*Aratinga chloroptera*)	Vulnerable	Dominican Republic	Wunderle and Latta (1996)
Hispaniolan Parrot (*Amazona ventralis*)	Vulnerable	Dominican Republic	Wunderle and Latta (1996)
Three-wattled Bellbird (*Procnias tricarunculatus*)	Vulnerable	Honduras	Bonta (2003)
Bicknell's Thrush (*Catharus bicknelli*)	Vulnerable	Dominican Republic	Wunderle and Latta (1996)
Golden-cheeked Warbler (*Dendroica chrysoparia*)	Endangered	Mexico	Dietsch (2000)
Cerulean Warbler (*Dendroica cerulea*)	Vulnerable	Colombia, Venezuela	Botero *et al.* (1999), Jones *et al.* (2000)
Azure-rumped Tanager (*Tangara cabanisi*)	Endangered	Mexico	Dietsch (2000)
Turquoise Dacnis (*Dacnis hartlaubi*)	Vulnerable	Colombia	Botero and Verhelst (2001)

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habitats (Wunderle and Latta 1996, Estrada et al. 1997, Petit et al. 1999, Tejeda-Cruz and Sutherland 2004); (2) in some landscapes, shaded coffee plantations have as many or more bird species as local forest patches (Greenberg et al. 1997b, Tejeda-Cruz and Sutherland 2004); and (3) Nearctic-Neotropical migratory birds are frequently as abundant in shaded coffee plantations as in natural forest habitats (Wunderle and Latta 1996, Greenberg et al. 1997b, Tejeda-Cruz and Sutherland 2004). The above observations are widely assumed to indicate a positive conservation role. Furthermore, one can add the assumption, based on conservation theory, that shaded coffee plantations improve the quality of agricultural landscapes for forest birds, by buffering natural forest patches and providing dispersal routes among them. However, none of these assumptions have been tested by rigorous studies that assess conservation value specifically.

Most authors proposing an avian conservation role for shaded coffee have focused on the higher bird species richness and abundance in plantations with extensive shade canopies compared with open-sun plantations. High species richness, however, may actually be a result of factors unrelated to the conservation importance of the habitat (Remsen 1994, Komar 2003). In some areas where shaded coffee plantations dominate the landscape, relatively high species richness, compared with other habitats, is predicted by island biogeography theory alone (MacArthur and Wilson 1967). Given that shaded coffee plantations are intermediate on a disturbance gradient between natural forest and other agricultural habitats, high species richness is also predicted by the intermediate disturbance hypothesis (Connell 1978, Abugov 1982), because disturbance events may be frequent enough to prevent competitive exclusion of some species. Finally, coffee plantations may function as an ecotone or transition zone between natural forest patches and other land-use types, and species richness may thus be inflated by the presence of elements from both forest and open areas within the coffee plantations. These situations, however, do not imply that birds using the plantations are surviving or reproducing successfully, which are conditions necessary for bird conservation. Presence of species alone or even high abundance do not indicate high conservation value or high quality of the substrate habitat for those species, especially if the habitat represents a population sink or a death trap, unless correlated with high survivorship, productivity or fitness (van Horne 1983, Pulliam 1988, Soulé 1991, Remsen 1994, Latta and Baltz 1997, Gordon and Ornelas 2000, Komar 2003).

While long-distance migratory birds generally appear to be more abundant in shaded coffee plantations than in natural forest, most species are also abundant in a variety of disturbed habitats, including sun plantations. Also, most migrants are not threatened, and thus are of low conservation importance. The relative importance of coffee plantations for migratory birds, and especially selection of the habitat by them, has not been evaluated. Overwinter survival or persistence in coffee has been studied in just four migratory species, out of nearly 80 that spend winters in the Neotropical coffee plantations. Surprisingly, published studies on use of Paleotropical coffee plantations by long-distance migratory birds do not exist. Only one threatened migratory bird, Cerulean Warbler, is documented to use plantations frequently (Jones *et al.* 2000).

Several authors have suggested that coffee plantations may be important for biodiversity simply because they are located within biodiversity hotspots (e.g. Moguel and Toledo 1999, Dietsch 2000, Botero and Baker 2001, Somarriba *et al.* 2004) or near forests with important diversity (e.g. Petit *et al.* 1999, 2003), but the potential fallacy of this reasoning becomes evident if one substitutes a species-poor habitat for coffee;

i.e. no-one would argue that sugar-cane plantations may be important for biodiversity in countries recognized as biodiversity hotspots or because they are adjacent to natural forests. Some authors (e.g. Nestel 1995, Moguel and Toledo 1999) have assumed that the greater structural habitat diversity and floral diversity of rustic or polyculture shaded plantations must be beneficial to biodiversity when compared with agricultural monocultures such as sugar-cane. Other authors (e.g. Rappole *et al.* 2003a) are concerned that shaded plantations do not offer quality habitat for threatened forest species and that their promotion could be contributing to deforestation. The position that one may take about conservation value of shaded coffee plantations resembles the old argument about whether one perceives a glass to be half empty or half full, and depends therefore on one's point of view, but not generally on scientific principles (i.e. hard data).

Lack of evidence for a conservation role may be due to lack of research, as no studies have discredited the idea that coffee plantations could possibly contribute to conservation of avian diversity. Future research, however, should consider the hypothesis that coffee plantations, as a disturbed habitat, may in fact be undesirable or dangerous for some birds (Rappole *et al.* 2003a, Cohen and Lindell 2004), potentially being a sink habitat for forest bird species or a death trap for dispersers and some migratory visitors.

Despite growing interest in avian use of coffee plantations, scientific knowledge about avian ecology in this habitat is still quite limited. Many of the published studies have focused on entire avian communities, without paying close attention to the species that make up the community. More research on target bird species is needed to understand the dynamics of coffee–bird ecology and to evaluate whether avian conservation is possible in coffee plantations. The literature on birds in coffee plantations has left several gaping holes. Nothing has yet been reported about effects on birds of agrochemicals or organic farming practices in coffee plantations. Plantations have much greater human presence than do natural habitats, yet there are no studies of effects of direct human disturbance on nesting success, fitness or condition of birds. No studies have evaluated the role of coffee plantations as a dispersal corridor for forest birds, nor have ecologists studied habitat selection of coffee plantations by most bird species. Research is needed on nesting success or survivorship of resident birds, compared across habitats occupied by these species. Without such studies, it is difficult to evaluate the potential of coffee plantations to contribute to bird conservation.

If future research were indeed to demonstrate that there are few conservation benefits for birds living in shaded coffee plantations, there nonetheless may be numerous environmental benefits of shaded coffee compared with other agricultural land uses such as sun coffee or other monocultures. Such benefits may include reduced pollution, soil conservation, water conservation, pest control and climate regulation (Greenberg 1996, Moguel and Toledo 1999, Sherry 2000, Siebert 2002). Unfortunately, almost no work has quantified such benefits (Somarriba *et al.* 2004). Other forms of biodiversity less vagile than birds may garner greater conservation benefits from shaded coffee plantations than birds (Perfecto *et al.* 2003).

Almost all of the avian–coffee research to date has taken place in Mexico, Central America and the Caribbean region, with minor amounts from Colombia, Peru, India and Indonesia. Virtually no research on birds in coffee has been reported from some important coffee-producing areas such as Brazil, Africa and South-East Asia. These areas have large numbers of threatened or range-restricted birds that may be affected by coffee production (Dietsch 2000). Clearly much more research is needed to demonstrate the potential positive or negative impacts that different kinds of coffee management practices may have on birds of conservation interest.

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OLIVER KOMAR
SalvaNATURA, Conservation Science Program, Colonia Flor Blanca, 33 Ave. Sur #640, San Salvador, El Salvador; and University of Kansas Natural History Museum and Biodiversity Research Center, Lawrence, KS 66045, USA. E-mail: okomar@salvanatura.org

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