

Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas

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Abstract Although most bird species avoid agricultural areas, nearly a third of all birds regularly to occasionally use such habitats, often providing important ecosystem services like pest control, pollination, and seed dispersal. Combining literature review with large-scale analyses of the ecological characteristics of the world's birds, I compared tropical bird species that prefer forests, agricultural areas or both, with respect to body mass, diet, range and population size, frequency, conservation status, habitat and resource specialization. Compared to primary forests, species richness of large frugivorous and insectivorous birds (especially terrestrial and understorey species) often declines in agroforests. In contrast, nectarivores, small-to-medium insectivores (especially migrants and canopy species), omnivores, and sometimes granivores and small frugivores do better, frequently by tracking seasonal resources. However, changes in guild species numbers do not necessarily translate to changes in relative abundance, biomass or function, and more studies are needed to quantify these important measures. These findings indicate that the replacement of forests and agroforests with simplified agricultural systems can result in shifts towards less specialized bird communities with altered proportions of functional groups. These shifts can reduce avian ecosystem

function and affect the ecosystem services provided by birds in agroforests and other agricultural landscapes.

Keywords Avian function · Biodiversity conservation · Ecosystem engineers · Land use · Predation · Trophic cascade

Introduction

Although less than 1 % of the world's bird species primarily prefer agricultural areas, nearly a third of all bird species occasionally use such habitats (Sekercioglu et al. 2007), often providing important ecosystem services, such as pest control, pollination, seed dispersal, and nutrient deposition (Sekercioglu 2006). Even though most bird species are found in the tropics, studies of functional changes in bird communities are disproportionately focused on the European and North American ecosystems (Sekercioglu 2006). There is growing interest in avian functional diversity in tropical forests and agroecosystems, especially in tree-dominated agroforestry systems such as shade coffee and cacao plantations that harbor higher bird diversity than open agricultural systems with few or no trees (Thiollay 1995; Greenberg et al. 1997, 2000b; Wang and Young 2003; Perfecto et al. 2004; Waltert et al. 2005; Marsden et al. 2006; Clough et al. 2009; Tschardt et al. 2008). However, recent research has focused disproportionately on Neotropical coffee plantations (Komar 2006), and we need more studies on other types of tropical agroforest systems (Marsden et al. 2006; Round et al. 2006), particularly in Africa (Naidoo 2004; Waltert et al. 2005; Holbech 2009) and Pacific Ocean islands (Marsden et al. 2006), where there has been less research on these issues than in Asia and the Neotropics. There is a need for a

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global synthesis of these studies in order to understand how bird communities and the proportions of bird functional groups, such as granivores, frugivores, insectivores, and nectarivores, change from forests to agroforests to open agricultural systems. Not only is this important for a better understanding of the ecology of tropical bird communities and for improving tropical bird conservation but it is also essential for estimating the changes in birds' ecosystem services (Wenny et al. 2011) and for calculating the economical contributions of these services to tropical farmers' incomes. The objectives of this study are:

1. to conduct a global assessment of the ecological traits of bird species primarily found in tropical forests, open agricultural areas or both,
2. to review the tropical avian ecology literature in order to quantify the changes in bird functional groups in these habitats, and
3. to improve our understanding of the changes in bird ecosystem services and ecological function in tropical agroforests and agricultural areas as a result of the declines or increases in predators, seed dispersers, pollinators, and other avian functional groups.

Methods

To compare the functional diversity and species richness patterns of birds in tropical forests, agroforests, and open agricultural areas, I conducted large-scale ecological analyses of a world bird ecology database with standardized entries on the ecology of all the bird species of the world (Sekercioglu et al. 2004; Tschamntke et al. 2008). I also reviewed studies that compared tropical agroforestry and open agricultural ecosystems to native forests nearby. I used the combination of keywords bird* AND tropic* AND forest* AND [agriculture OR agroforest] in the Web of Knowledge database and generated a list of peer-reviewed research articles published between 1970 and 2010. Of these, I chose relevant articles that compared tropical forest birds to agroforest birds, open agricultural birds, or both. Under forests, I included natural primary or secondary forests and woodlands, and excluded plantations. Most tropical woodland species also spend time in forests, so they were included in the analyses. Agroforests are defined as agricultural areas that have significant tree cover, such as cocoa, rubber, or shade coffee plantations.

For the global analyses, I compared the species richness patterns of 6,093 entirely tropical bird species that prefer tropical forests and woodlands (4,574 species), tropical agricultural areas (303 species), or both (1,216 species), with respect to habitat use, global range size, population size, frequency, clutch size, conservation status, dispersal

ability, body mass, diet (proxy for ecological function), habitat, and resource specialization. Threat status, range size (extent of occurrence), population, and frequency data came from BirdLife International (2010).

I excluded aquatic species (primary habitat sea, coastal areas, or wetlands), but included species that prefer coastal forests, swamp forests, or riparian forests (such as kingfishers, fishing-owls, and other riparian species that are not completely aquatic), since these habitats are important components of forested areas. I classified as “forest specialists” bird species that prefer forests and/or woodlands as one of their top three habitat choices, and are not found in agricultural areas. I did the reverse for agricultural species, whereas I defined agroforest species as birds that have both agricultural areas and forests/woodlands among their top three preferred habitats. I restricted my analyses to tropical species, which comprise 93, 91, and 79 % of the world's forest, agroforest, and agricultural species, respectively. As my goal was to compare forest and agricultural specialists to those that regularly use both habitats, I excluded from my analyses 78 agricultural species that are occasionally seen in forests and 944 forest bird species that are occasionally recorded in agricultural areas. Analyses of various categories indicated that these species had average values between agricultural specialists and agroforest birds, and agroforest birds and forest specialists, respectively.

Results

Global analyses

Forest specialists comprise 53 % of all the bird species found in the tropics, whereas 14 % of tropical species are agroforest species and 3 % are agricultural specialists (Fig. 1). Bird families and genera exhibit similar percentages. Forest is the first habitat choice of 897 agroforest species, whereas 150 agroforest species prefer woodlands most, 97 species favor shrub/scrublands, and 16 species favor open agricultural areas.

Analyses of the distributions of known global range sizes (Fig. 2a), of restricted range species (Fig. 2b), of island endemics (Fig. 2c), and of species limited to one bio-geographical region (Fig. 2d) show that agricultural species have bigger ranges and are more widespread than are forest (all $\chi^2 > 27.1$, all $p < 0.0001$) or agroforest species (all $\chi^2 > 15.2$, all $p < 0.0001$), which do not differ significantly from each other (all $\chi^2 < 3.66$, all $p > 0.16$). Forest birds have smaller populations ($\chi^2 = 21.0$, $p < 0.002$) and are less common than agroforest birds ($\chi^2 = 21.4$, $p < 0.001$), which in turn occur in lower numbers ($\chi^2 > 100$, $p < 0.0001$) than do agricultural birds

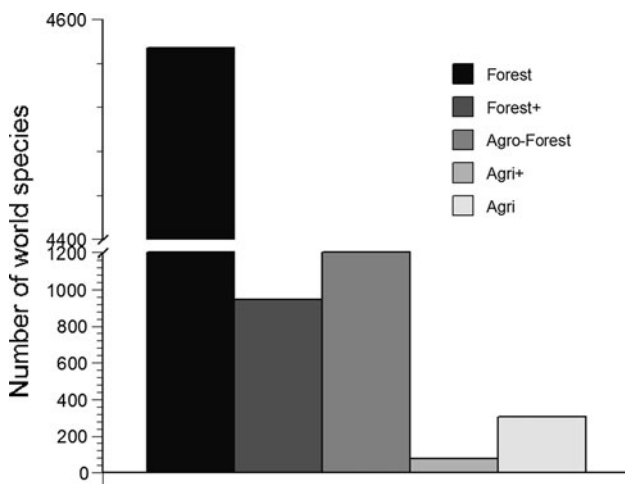


Fig. 1 Habitat choices of tropical forest and/or agricultural bird species. Species that prefer forests and/or woodlands as one of their top three habitat choices are either classified as *Forest* (no use of agricultural areas) or *Forest+* (agricultural areas used, but not among top three habitats). The opposite is the case for agricultural species, whereas agroforest species are those that have both agricultural areas and forests or woodlands among their top three preferred habitats

(Fig. 3a), but show a similar frequency distribution ($\chi^2 = 3.35, p = 0.5$; Fig. 3b). Lower population sizes of forest birds are not because of having lower clutch sizes than agroforest birds ($\chi^2 = 3.97, p = 0.554$), whereas both groups have lower clutch sizes than agricultural birds ($\chi^2 > 76.2, p < 0.0001$; Fig. 4). These global population size differences between forest, agroforest, and agricultural birds likely play an important role in determining the proportions of each group that are extinct, threatened, or near threatened with extinction (Fig. 5).

As expected, long-distance migrants comprise a higher proportion of agricultural birds than of agroforest birds ($\chi^2 = 36.7, p < 0.0001$), which, in turn, have a greater proportion of migrant species than do forest birds ($\chi^2 = 5.45, p < 0.02$; Fig. 6). Increasing specialization, reflected in reduced niche breadth, means higher extinction likelihood (Sekercioglu 2011). Agroforest species had significantly greater habitat ($\chi^2 = 114, p < 0.0001$) and diet breadth ($\chi^2 = 21.9, p < 0.0001$) than did forest species, but agroforest birds did not differ from agricultural species ($\chi^2 < 2.99, p > 0.39$), indicating that habitat and

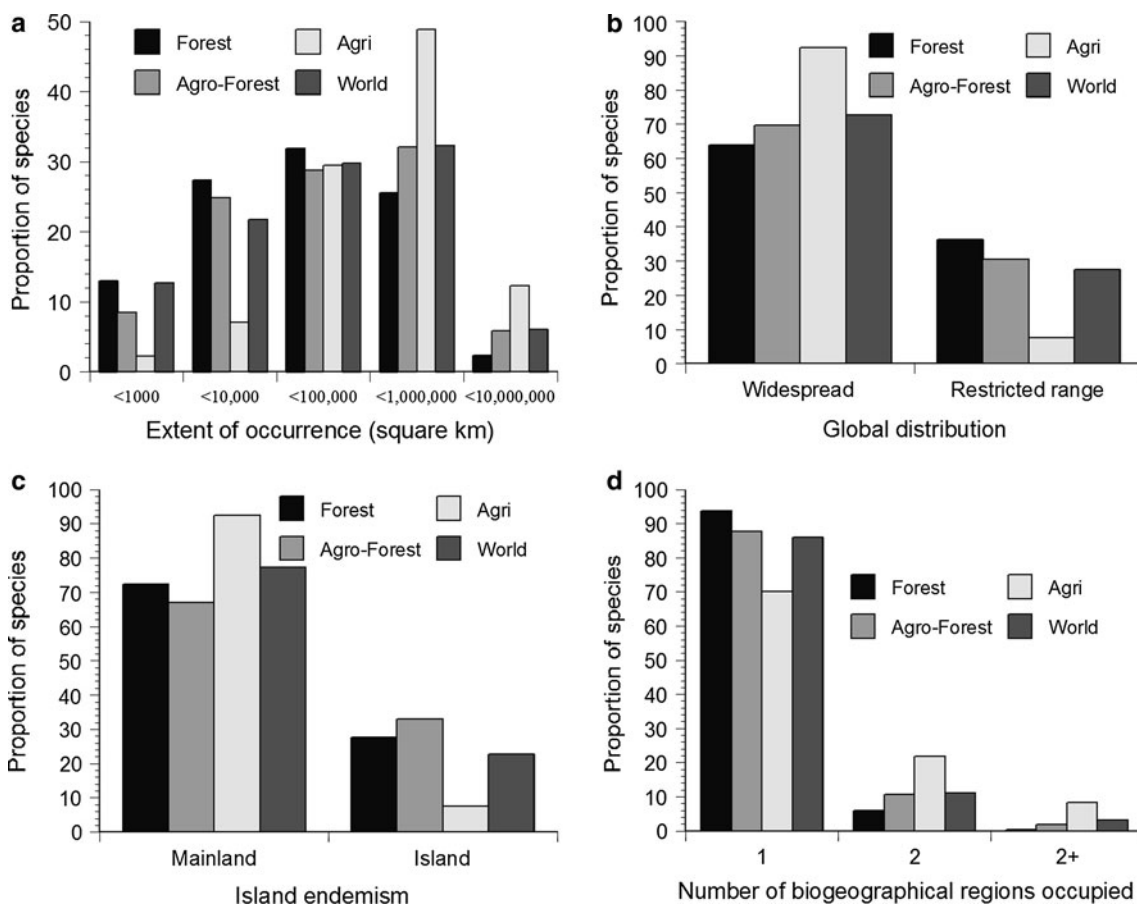


Fig. 2 a Global range sizes of bird species. Extents of occurrence are known for 88 % of bird species analyzed (BirdLife International 2010). b Restricted range species are those whose global range is less

than 50,000 km². c Mainland species and island endemics. d Number of biogeographical regions occupied by bird species

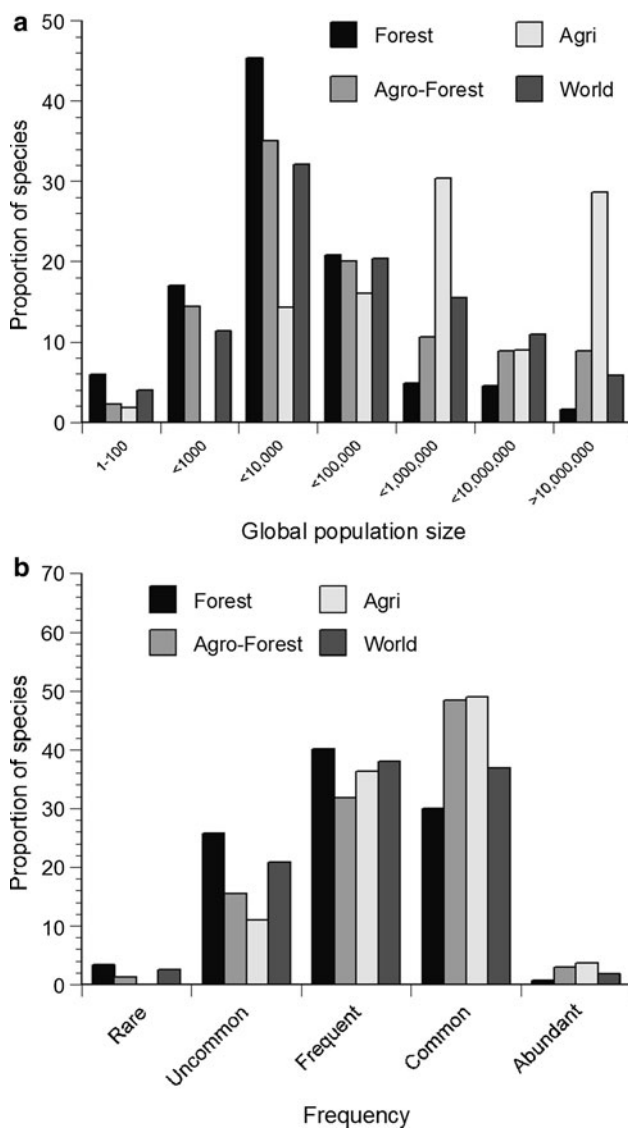


Fig. 3 **a** Population size distribution of bird species, based on population sizes of 825 forest, 180 agroforest, and 56 agricultural species (BirdLife International 2010). Population sizes of 78 % of world bird species are unknown. **b** Frequency distribution (BirdLife International 2010) of 2,593 forest, 764 agroforest, and 190 agricultural species whose populations are unknown

dietary specialists are often lost from both agroforest and agricultural habitats (Fig. 7a, b). There were no differences between the body mass distributions of forest, agroforest, and agricultural bird species ($\chi^2 < 4.03$, $p > 0.25$; Fig. 8), although field studies show that large birds are often eliminated from tropical agricultural habitats (Thiollay 2006).

Even though overall distributions of bird functional groups did not significantly differ between forest and agroforest species ($\chi^2 = 11.9$, $p = 0.16$), their functional distributions differed from that of agricultural species ($\chi^2 > 94.2$, $p < 0.0001$), with substantial differences in some categories (Fig. 9). Nearly a quarter of agroforest

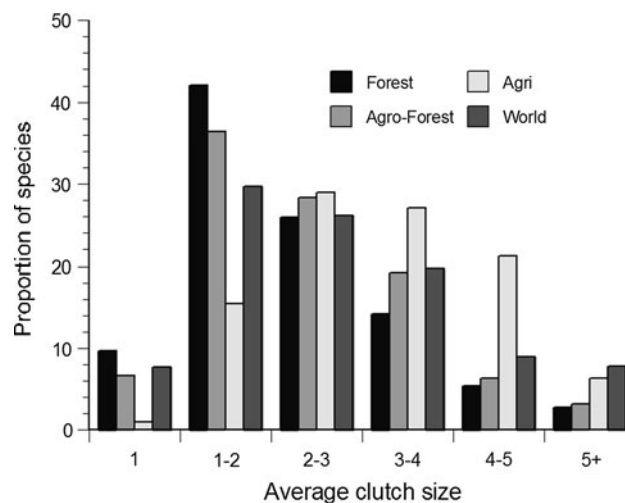


Fig. 4 Distributions of average clutch size among 6,139 bird species of different habitats

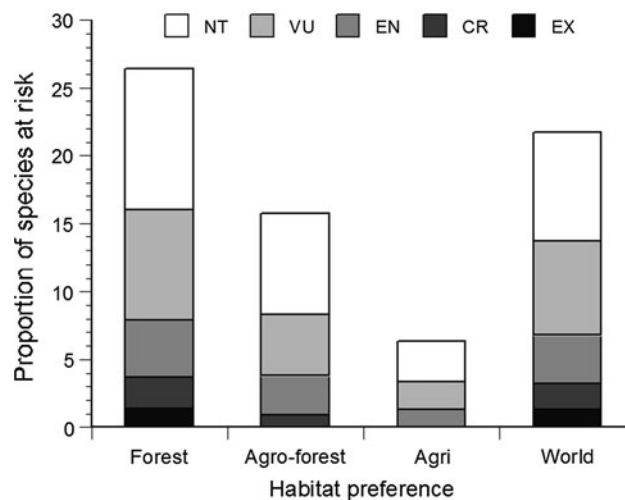


Fig. 5 Distribution of extinct (*EX*), threatened (critically endangered (*CR*), endangered (*EN*), and vulnerable (*VU*), and near threatened (*NT*) species (BirdLife International 2010). Four species that are extinct in the wild were included with the critically endangered species

species are primarily frugivorous, whereas frugivorous birds comprise only 4 % of agricultural bird species. Nectarivores showed a similar pattern, doubling in proportion among agroforest species when compared to forest species. However, the proportion of nectar-eating birds in agricultural areas was only a quarter of their proportion in agroforest bird communities, suggesting a decline in potential pollinators.

In contrast to frugivores, the proportion of tropical insectivorous birds, many of which are highly sensitive to fragmentation (Sekercioglu et al. 2002), is lower by about 25 % in both agroforest and agricultural communities. Seed predation may be higher in agricultural areas with low tree cover, since granivorous bird species comprise a third

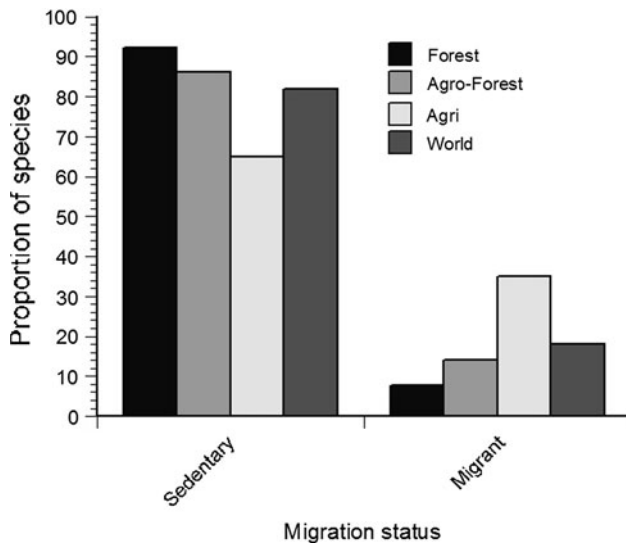


Fig. 6 Proportions of bird species in different habitats that are long-distance migrants

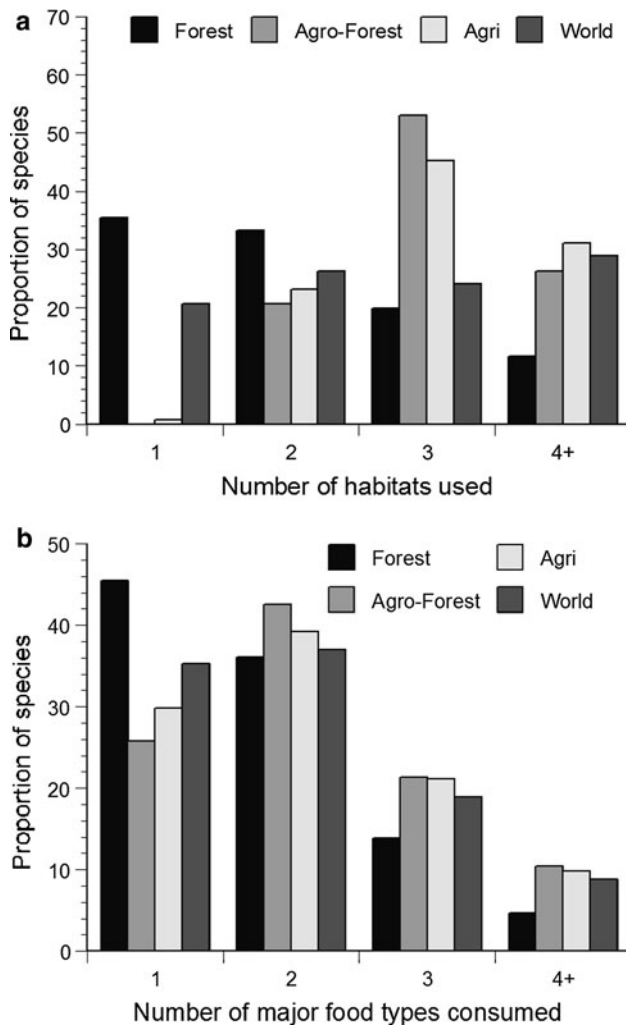


Fig. 7 **a** Habitat breadth of bird species. **b** Diet breadth of bird species. For food types, see Fig. 9

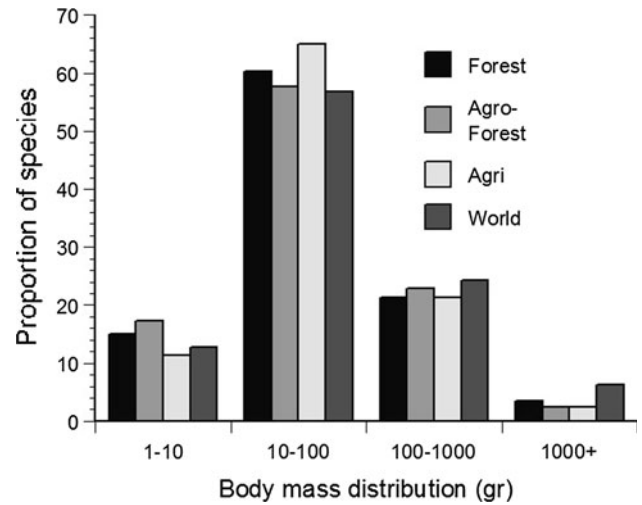


Fig. 8 Body mass distribution of 7,434 bird species

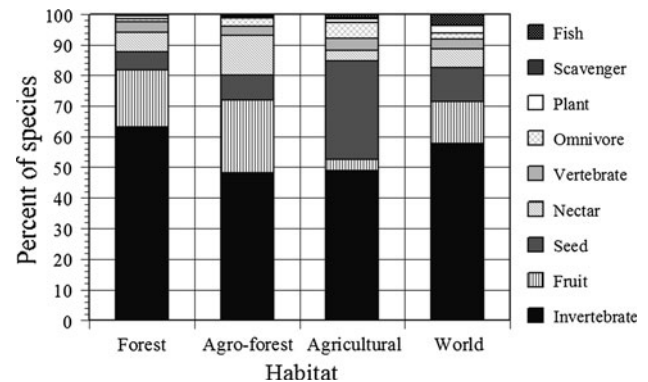


Fig. 9 Proportions of bird species in each habitat based on primary diet which is a proxy for ecological function. Reprinted with permission from Tschantke et al. (2008)

of all agricultural bird species, four or five times greater than their share of agroforest or forest bird species, respectively (Fig. 9).

Literature review

Although the variety of schemes used in the literature for guild classifications make generalizations difficult (Komar 2006), some important patterns emerge. When agroforest systems are compared to primary forests, species numbers of large frugivorous and insectivorous birds (especially terrestrial and understorey species) are often lower in agroforests. In contrast, nectarivores, small-to-medium insectivores (especially migrants and canopy species), omnivores, and sometimes granivores and small frugivores do better or even thrive in agroforests (Petit et al. 1999; Vereá and Solozano 2005), frequently by tracking seasonal resources (Greenberg et al. 1997; Johnson and Sherry

2001; Carlo et al. 2003). However, changes in guild species numbers do not necessarily translate to changes in relative abundance (Verea and Solozano 2005; Marsden et al. 2006), biomass or function (Greenberg et al. 2000b; Perfecto et al. 2004), and more research is needed to quantify these important measures (Beehler et al. 1987).

Tropical agroforestry systems often vary in their functional diversity patterns, but insectivores often have lower representation than in forests. In Paraguay *yerba mate* plantations shaded by forest trees and close to extensive forest, fruit-and-insect eaters, insectivores, and nectarivores were less abundant than in nearby forest, and two-thirds of carnivorous species were not found in plantations (Cockle et al. 2005). Over 60 % of the birds captured in the understorey of Venezuelan shaded cacao plantations were hummingbirds, whereas insectivores had reduced abundance and species richness (Verea and Solozano 2005). Shade cacao plantations in southeast Brazil had fewer species of frugivores and understorey insectivores, and more species of nectarivores and omnivores, than nearby forest fragments (Faria et al. 2006). Landscape effects were not pronounced, although proportional representation of frugivorous species was higher and that of gleaning insectivores was lower in the less forested landscape. In Mexican cacao plantations shaded by 60 species of planted native trees but distant from extensive forest, forest specialists were scarce and resident insectivorous species were mostly missing, whereas small foliage-gleaning insectivores comprised most of the migrant birds (Greenberg et al. 2000a). However, omnivorous or frugivorous bird species were also few, again suggesting the importance of landscape composition. In Mexican shade coffee plantations, disturbance-sensitive bark insectivores, understorey bark insectivores, and large canopy frugivores had fewer species in comparison to native forest, whereas facultative and obligatory insectivores, omnivores, and midstorey and understorey/undergrowth granivores increased in shade coffee (Leyequien et al. 2010). On the other hand, Mexican tropical dry forests and tree orchards did not differ in their guild composition (Macgregor-Fors and Schondube 2011).

Even in Cameroon agroforestry systems with relatively high tree cover and surrounded by primary forest, Waltert et al. (2005) observed reduced species richness, and in some cases abundance, of insectivorous species, especially those of the understorey. Frugivores and omnivores did not differ whereas nectarivores and granivores had higher richness in agroforests. Unusually, in Uganda, there were no differences in the detection rates of insectivores versus non-insectivores between forests and smallholder agricultural areas, whereas larger, mostly frugivorous birds were more likely to be detected in the latter (Naidoo 2004). In Ghana, Holbech (2009) found the trophic organization of the lower storey birds in luxuriant tree plantations versus

native forest to be similar, although there were fewer ant-following birds in plantations (69 % of the numbers found in forests). Cardamom and coffee plantations were better for forest birds than cacao plantations. In the plantations, the presence of a canopy per se was more important than the number of species making up the canopy, and the choice of native versus exotic tree species was less important than the presence of a well-developed and diverse secondary plant community, especially in the sub-canopy layers (Holbech 2009). A similar finding was reported by Najera and Simonetti (2010) in a review of 167 case studies from 32 countries comparing birds in forests and in plantations.

Interestingly, in traditional agroforests in tropical China, there were no consistent differences in bird guilds (Wang and Young 2003) between traditional economic forests, monsoon evergreen broadleaf forests, and montane rain forests, but this was not the case for other Asia–Pacific sites studied. Compared to nearby primary forest, the fruit orchards of Thailand were dominated by smaller frugivores, nectarivores, and widespread generalists, whereas understorey insectivores were poorly represented (Round et al. 2006). In Malaysian mixed agricultural habitats consisting of oil palms, rubber, and fruit trees, smaller primary forest frugivores and trunk-feeding insectivores tended to persist whereas ground and understorey birds were likely to disappear (Peh et al. 2005). Malaysian oil palm plantations, rubber tree plantations, and orchard gardens had only a third of the bird species found in the nearby primary forest, but proportions of insectivores and frugivores did not differ between habitats (Peh et al. 2006). In Sulawesi cacao plantations, frugivores and nectarivores had lower species richness at increasing distances from the forest, while in granivores the opposite trend was found (Clough et al. 2009). Increasing tree cover in these cacao plantations led to higher species richness in frugivores and insectivores. In Sumatra, larger frugivores and larger insectivores of both canopy and understorey, and terrestrial insectivores of the forest interior had mostly disappeared from agroforests, while small frugivores, smaller foliage-gleaning insectivores, nectarivores, and edge species persisted (Thiollay 1995). Similarly, large frugivores, some insectivores, and ground foragers declined in small-scale mixed agriculture/agroforestry systems of Papua New Guinea (Marsden et al. 2006). Worldwide, insectivorous birds are lower by 40 % in tree plantations whereas the proportion of granivores is higher by more than threefold (Najera and Simonetti 2010).

Discussion

The results of the global analyses of avian ecological data mostly agree with the findings of field studies in Afro-tropical (Waltert et al. 2005), Indomalayan (Peh et al.

2006), Australasian (Marsden et al. 2006), and Neotropical (Leyequien et al. 2010) regions. These findings suggest that the replacement of forests with agricultural areas results in a shift towards less specialized bird communities, comprised of more widespread and relatively common species, and with altered proportions of functional groups. Insectivores and other invertebrate predators often make up a smaller proportion of bird communities outside forests, whereas seed-dispersing frugivores and pollinating nectarivores are higher in agroforests, especially compared to open agricultural areas that can experience substantial increases in avian seed predators compared to forests and agroforests. Given that there are considerable differences in functional distribution, specialization, global range, population size, mobility, and conservation status between forest, agroforest, and agricultural bird communities, there is an urgent need for detailed field studies comparing bird community ecology and avian function in these habitats.

Because of the fivefold reduction in the proportion of frugivores in agricultural bird communities in comparison to forest bird communities, agroforest birds are likely to be the primary seed dispersers in agricultural areas, a pattern also observed in the field (Luck and Daily 2003; Pizo 2004). Integrating agroforests with open agricultural areas may result in a spillover of nectarivores and partially make up for the decline in avian pollinators among open agricultural species. The high primary productivity of agroforestry in the tropics is likely to attract more fruit and nectar eating birds than other groups. Since trophic cascades are more likely in more productive ecosystems (Van Bael et al. 2003), reductions in insectivorous bird species in simplified agricultural systems may lead to increases in insect outbreaks (Mellink 1991). The use of pesticides to control insect pests in agricultural areas may offer a poor prey base for insectivorous birds. This is counterproductive as insectivorous birds can be important for agriculture by removing and controlling insect pests (Greenberg et al. 2000b; Perfecto et al. 2004; Johnson et al. 2010). Low richness and abundance of insectivorous forest birds in agricultural areas may also be due to their poor dispersal abilities (Sekercioglu et al. 2002).

Higher mobility and better dispersal capacity often improve birds' ability to adapt to land use change and reduce their extinction likelihood, as indicated by the fact that long-distance migratory bird species are 2.6 times less likely to be threatened or near threatened with extinction than are sedentary species (Sekercioglu 2007). Field studies on the intensification of coffee management on local bird species also indicate that resident, sedentary birds are more sensitive than long-distance migrants to habitat alteration (Mas and Dietsch 2004). Even though resident birds decline in response to the conversion of native habitats to coffee plantations, Wunderle (1999) found no effect

of plantation size on migrant bird populations. Many migrants make extensive use of habitats with intermediate disturbance, such as shade coffee and other agroforests. Consequently, there may be some conservation trade-offs if migrants reach higher numbers at lower levels of shade (tree cover) and drop off in numbers as tree cover increases to levels that benefit the residents more. Such conservation trade-offs in different groups need more study.

A large portion of published studies on agroforest avian communities have focused on Neotropical coffee (Komar 2006), and to a lesser extent, cacao plantations. We need more research in other agro-ecosystems (particularly traditional mixed agroforests) and in different parts of the world. This is especially important since some studies in other regions and different agroforest types have found no differences among avian guilds or have observed patterns contrary to the general trends revealed in this review and global analyses. The research on shade-grown coffee and cacao provides a sound foundation, but this can be improved by incorporating distinctive aspects of regional ecology with more targeted research. There is also a need for studies focused on raptors and seed-eaters in agroforest systems since these groups can be important pest and seed predators, respectively, but remain understudied in agroforestry systems (Komar 2006).

Agro-ecosystems frequently comprise the matrix in which forest fragments, protected areas, and other native habitat remnants are embedded. Tropical agro-ecosystems often have substantial amounts of arboreal vegetation in the form of remnant trees (Fischer and Lindenmayer 2002), living fences (Harvey et al. 2005), riparian strips (Martin et al. 2006), and agroforestry plots (Schroth et al. 2004), all of which often have conservation values disproportionate to their land cover. These trees can provide connectivity (Graham 2001), dietary resources (Sekercioglu et al. 2007), nesting opportunities (Manning et al. 2004; Sekercioglu et al. 2007), and microclimatic refugia (Sekercioglu et al. 2007) to many forest species, and mediate the effects of forest fragmentation (Kupfer et al. 2006).

Despite the ecological importance of shifts in avian function in agroforests and agro-ecosystems, it is surprising that many studies comparing bird communities in forest, agroforest, and agricultural ecosystems do not report on the ecologically important changes in the proportions of avian functional groups, and such studies report on relative abundance or estimated biomass even less frequently. Furthermore, as Komar (2006) points out, most coffee studies have not sufficiently quantified observer bias or detectability differences between habitats, making abundance estimates problematic. He also notes that none of these studies have carefully quantified the effects on bird abundance of plantation distance from forest. These criticisms also apply to most studies in other agro-ecosystems.

Studies that rigorously compare and manipulate relative abundance and biomass of avian functional groups in tropical agro-ecosystems, while incorporating landscape effects, comprise a critical frontier in ecology and will help illuminate the ecological causes and consequences of bird community changes in these rapidly expanding, human-dominated landscapes.

This overview has shown that the replacement of forests and agroforests with simplified agricultural systems results in shifts towards less specialized bird communities with altered proportions of functional groups. These ecological shifts can affect the ecological functions of and ecosystem services provided by birds in agroforests and other agricultural landscapes. The proportions of insectivores are lower among agroforest and agricultural birds, while the proportions of frugivores and nectarivores, which act as important seed dispersers and pollinators respectively, increase among birds with agroforest habitat preferences, especially in comparison to the bird communities of open agricultural areas. The increased presence of grasses in open agricultural areas contributes to the higher number of granivorous birds which can become major seed predators and agricultural pests, especially when non-crop species are not producing seeds.

Nevertheless, reduced or increased species richness does not necessarily mean there will be parallel changes in abundance, biomass, or function (Greenberg et al. 2000b; Perfecto et al. 2004). For example, although insectivorous bird diversity in tropical agroforestry systems is positively related to the magnitude of predator effects, Van Bael et al. (2008) observed no differences in the magnitude of bird effects on plant pests between agroforestry systems and forests, even though agroforest communities have fewer insectivorous bird species (this study), as well as simplified habitat structure and plant diversity (Van Bael et al. 2008). Given these uncertainties, there is an urgent need for detailed field studies comparing avian function and functional diversity between forests, agroforests, and simplified agricultural systems, ideally in landscapes that vary in their forest cover and composition.

High biodiversity can be successfully combined with high yields in tropical agroforests (Clough et al. 2011), and Perfecto and Vandermeer (2008) concluded that “diverse, low-input agroecosystem systems using agroecological principles are probably the best option for a high-quality matrix”. Diverse, low-input agro-ecosystems include traditional shade coffee and cacao plantations and a number of other agroforestry types. The findings of these global analyses and review indicate that such agroforestry systems with some native cover also maintain a significantly larger proportion of important avian guilds such as frugivores and nectarivores, and their respective services. These agroforestry systems also harbor substantially lower numbers and

proportions of granivorous birds, some of which are major seed and crop predators. Agroforests and other agricultural habitats rich in tree cover are essential for connecting isolated protected areas and their meta-populations. Maintaining diverse, low-input, and preferably traditional agroforestry systems interspersed with tropical forest remnants will not only sustain more native biodiversity in tropical agricultural areas but these landscapes will also support higher proportions of avian seed dispersers, pollinators, insect predators, and their valuable ecosystem services.

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