

LANDSCAPE CONSTRAINTS ON FUNCTIONAL DIVERSITY OF BIRDS AND INSECTS IN TROPICAL AGROECOSYSTEMS

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Abstract. In this paper, we analyze databases on birds and insects to assess patterns of functional diversity in human-dominated landscapes in the tropics. A perspective from developed landscapes is essential for understanding remnant natural ecosystems, because most species experience their surroundings at spatial scales beyond the plot level, and spillover between natural and managed ecosystems is common. Agricultural bird species have greater habitat and diet breadth than forest species. Based on a global data base, bird assemblages in tropical agroforest ecosystems were composed of disproportionately more frugivorous and nectarivorous, but fewer insectivorous bird species compared with forest. Similarly, insect predators of plant-feeding arthropods were more diverse in Ecuadorian agroforest and forest compared with rice and pasture, while, in Indonesia, bee diversity was also higher in forested habitats. Hence, diversity of insectivorous birds and insect predators as well as bee pollinators declined with agricultural transformation. In contrast, with increasing agricultural intensification, avian pollinators and seed dispersers initially increase then decrease in proportion. It is well established that the proximity of agricultural habitats to forests has a strong influence on the functional diversity of agroecosystems. Community similarity is higher among agricultural systems than in natural habitats and higher in simple than in complex landscapes for both birds and insects, so natural communities, low-intensity agriculture, and heterogeneous landscapes appear to be critical in the preservation of beta diversity. We require a better understanding of the relative role of landscape composition and the spatial configuration of landscape elements in affecting spillover of functionally important species across managed and natural habitats. This is important for data-based management of tropical human-dominated landscapes sustaining the capacity of communities to reorganize after disturbance and to ensure ecological functioning.

Key words: agroforestry; beta diversity; biodiversity; biological control; global change; parasitoids; pollination; predators; seed dispersal; spatial ecology; spillover; sustainability.

INTRODUCTION

Ecological research in human-dominated regions of the tropics contributes to new concepts in community and landscape ecology (Bengtsson et al. 2003, Gaston 2004, Schroth et al. 2004). Landscape effects, including immigration, emigration, and extinction rates, as well as dispersal limitation, can be best tested in human-dominated and species-rich tropical landscapes, because of sharp contrasts between mosaics of well-defined habitat types (Tscharnkte et al. 2005). Further, transformation of natural habitat to managed systems may be regarded as a large-scale ecological experiment to explore functional biodiversity in simplified systems.

Population and community responses to ecological changes may be more easily detected in managed systems, allowing the identification of species traits associated with landscape changes. In this article, we identify two key landscape effects on functional biodiversity where research in tropical agricultural landscapes contributes to broader ecological theory: (1) the role of landscape composition (relative contribution of each habitat type to the landscape mosaic) and (2) landscape configuration (the geometry of landscape elements, including corridor and matrix effects influencing dispersal and community similarity), which affect spillover between managed and natural habitats.

The concept of functional diversity links species diversity to ecosystem processes through resource-use patterns (see Petchy and Gaston 2006). Here, we analyze landscape constraints on local patterns in the functional diversity of birds and insects. We provide a novel overview of patterns in avian functional diversity by

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analysing a recently created global bird database that includes birds' most preferred habitats and diets. Because such a database is not available for insects, we used new data from Indonesia and Ecuador showing similar links between diet and habitat type along gradients of land-use intensification. These original results and a conceptual overview based on recent publications provide new insights into how human-dominated mosaic landscapes shape functional biodiversity. The connection between functional diversity and ecosystem functioning in the tropics is discussed in more detail in Klein et al. (2008) and van Bael et al. (2008) and several previous papers (e.g., Klein et al. 2003, Perfecto et al. 2004, Bianchi et al. 2006, Tylianakis et al. 2006).

LANDSCAPE COMPOSITION AND LOCAL FUNCTIONAL DIVERSITY IN TROPICAL AGROECOSYSTEMS

Community composition differs in natural and managed habitats, but impacts on functional diversity, food web interactions, and ecosystem functioning are little known. First, we review studies of avian functional diversity in tropical forests vs. agroforests. Then we compare the ecological characteristics of tropical bird species that live in natural forests, agricultural environments, or both. Finally, changes in functional composition of insect communities are compared among pollinators, predators, and parasitoids in Ecuador and Indonesia, including a test of landscape effects on local species composition.

Bird functional diversity in tropical agroecosystems

Although <1% of the world's bird species primarily prefer agricultural areas, nearly one-third of all birds occasionally use such habitats (Sekercioglu et al. 2007), often providing important ecosystem services, such as pest control, pollination, and seed dispersal (Greenberg et al. 2000, Perfecto et al. 2004, Sekercioglu 2006, Van Bael et al. 2008). However, many studies have focused on Neotropical coffee plantations (Komar 2006), leaving gaps in knowledge about birds and the services they may provide in other crop types and tropical agroforest systems in Africa (but see Naidoo 2004, Waltert et al. 2005), Asia (Peh et al. 2006), and Pacific ocean islands (Marsden et al. 2006).

There is an urgent need for an understanding of the changes in avian functional diversity in tropical agroforest ecosystems worldwide. Therefore, we reviewed recent studies (listed in Appendix A), representing the world's major tropical regions, that compared tropical agroforestry systems to native forests nearby. All studies took place in landscapes formerly covered with tropical primary forest, but now consist of a mosaic of primary forest remnants, agroecosystems, and secondary growth. Although the variety of foraging guild classifications used makes generalizations difficult (Komar 2006), some patterns emerge. Compared to forests, species richness of large frugivorous and insectivorous birds (especially terrestrial and understory 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 or even thrive, frequently by tracking seasonal resources (e.g., Greenberg et al. 2000). However, changes in guild species numbers do not necessarily correlate with changes in relative abundance (Marsden et al. 2006), biomass or function (Greenberg et al. 2000, Perfecto et al. 2004), and more studies are needed to quantify their relationships (e.g., Van Bael et al. 2008). Numerous Neotropical studies of biodiversity in coffee and cacao agroforests provide a sound foundation (Komar 2006), but research in other agroecosystems (particularly traditional mixed agroforests) is especially important because some of these studies (e.g., Naidoo 2004) have found patterns contrary to those observed in coffee and cacao plantations. We also need a better understanding of raptors and granivores in agroforests since these birds can be important pest and seed predators, respectively, but remain understudied in tropical agroforests (Komar 2006).

Since the papers we reviewed varied greatly in the ways they classified bird guilds, we conducted a novel, global analysis based on a database with standardized entries on the ecology of all the world's bird species (Sekercioglu et al. 2004, see Appendix A). We classified 6093 tropical bird species based on their most preferred three habitats listed in published species accounts. The habitat preferences considered for this analysis were (1) only natural forest or woodland habitats ("forest birds," 4574 species), (2) agricultural areas including agroforests but not natural forest or woodland habitats ("agricultural birds," 303 species), and (3) both agricultural areas and forests/woodlands ("agriculture-forest birds," 1216 species). A high preference for forest cover limits most "agriculture-forest" species to high cover agricultural areas such as agroforests, whereas avoidance of forest/woodland cover means most "agriculture" species are limited to low cover agricultural areas outside agroforests. It is unlikely that an agriculture-forest bird species would spend most of its time in forests and open agricultural areas while avoiding agroforests. Therefore, "agriculture-forest birds" comprise a good proxy group for true agroforest birds.

We compared species richness patterns with respect to body mass (available for 76% of bird species), ecological function (diet), habitat, and resource specialization. Interestingly, there were no differences between the body mass distributions of forest, agriculture-forest, and agricultural bird species ($\chi^2 < 4.03$, $P > 0.25$), although field studies show that large birds are often eliminated from tropical agricultural habitats (Marsden et al. 2006, Thiollay 2006). Agriculture-forest birds 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 they did not differ from agricultural species ($\chi^2 < 2.99$, $P > 0.39$), suggesting that some specialists are lost from agroforest and agricultural habitats. The

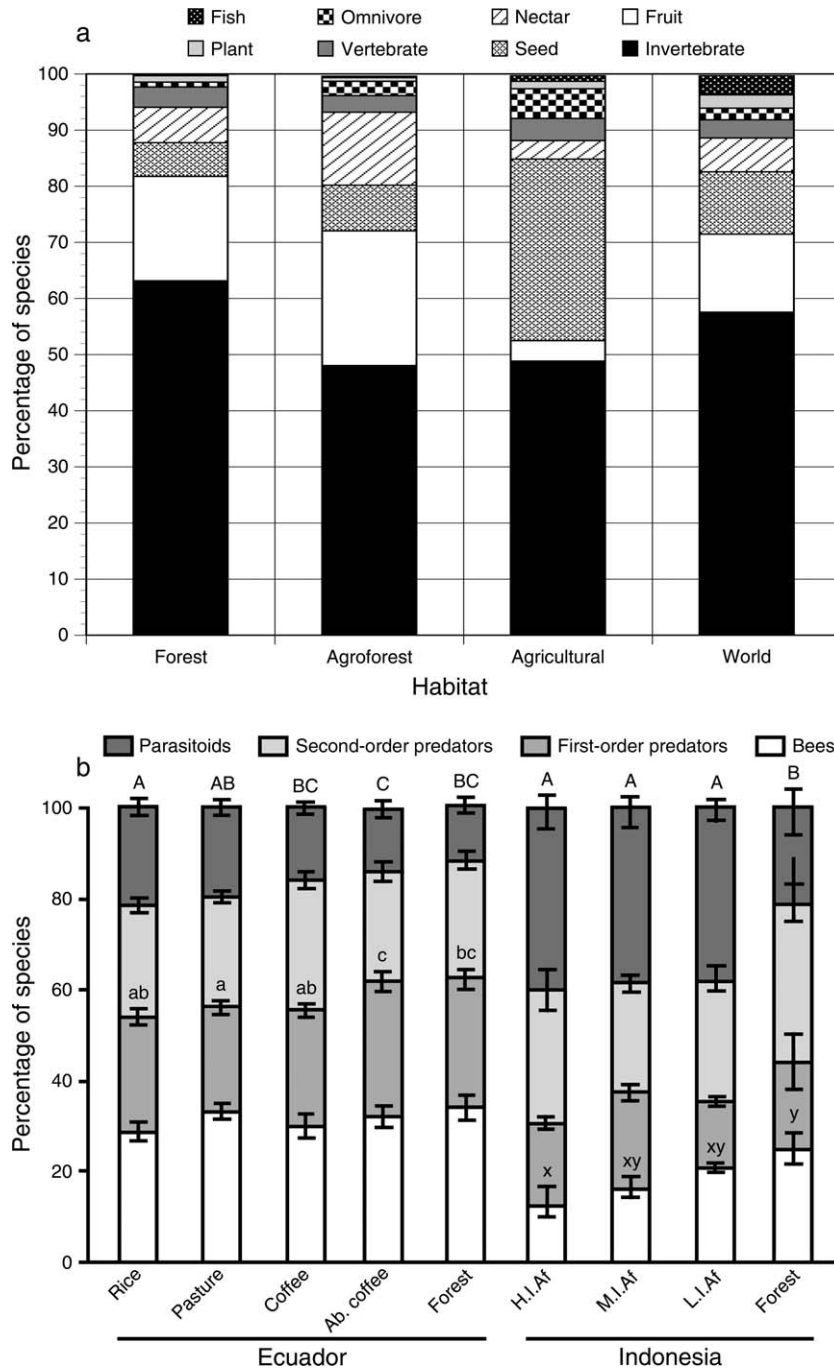


FIG. 1. (a) Relative bird species richness (percentage of all bird species) per habitat type based on primary diet, which is a proxy for ecological function (see *Bird functional diversity in tropical agroecosystems* for details). (b) Percentage of cavity-nesting bee and wasp species richness per habitat type based on resource use by each functional group in coastal Ecuador (habitat types are rice and pasture as open land, coffee agroforestry, Ab coffee [abandoned coffee resembling young secondary forest], and forest remnants) and Central Sulawesi, Indonesia (H.I.Af, M.I.Af, and L.I.Af = High-, medium-, and low-intensity cacao agroforests, respectively, and continuous rain forest). Different letters within a functional group indicate significant differences (see *Insect functional diversity in tropical agroecosystems* for more details).

overall distribution of bird functional groups, based on dietary guilds, did not differ between forest and agriculture–forest species ($\chi^2 = 11.9, P = 0.16$), but both differed from agricultural species ($\chi^2 > 94.2, P <$

0.0001). There were substantial differences in some categories (Fig. 1a), often in agreement with the patterns observed in field studies. Nearly a quarter of agriculture–forest species are primarily frugivorous, which

represent <4% of agricultural bird species. Nectarivores show a similar pattern, doubling in proportion among agriculture–forest species when compared to forests, and quadrupling when compared to those in agricultural areas. Granivores increase with decreasing tree cover, comprising a third of all agricultural bird species, four or five times greater than their share of agriculture–forest or forest bird species respectively. In contrast, the proportion of tropical insectivorous species declines by about 25% in both agriculture–forest and agricultural communities (Fig. 1a).

The combination of previous studies and our global analysis suggests that replacing forests and agroforests with simplified agricultural systems results in shifts toward less specialized bird communities with altered proportions of functional groups. This may affect the ecosystem services provided by birds in agroforests and other agricultural landscapes. The proportion of insect predators is lower among agroforest and agricultural birds. The proportions of frugivores and nectarivores, which act as important seed dispersers and pollinators, respectively, increase among birds that prefer agroforests, especially compared to agricultural birds that exhibit a much higher proportion of granivores, potentially major seed predators. While reduced or increased species richness does not necessarily mean there will be parallel changes in abundance, biomass or function (Greenberg et al. 2000, Perfecto et al. 2004), due to the “sampling effect” (Huston 1997), higher species richness increases the probability of having species that are particularly effective in their ecological functions (Perfecto et al. 2004). Given the complex community dynamics involved, there is an urgent need for detailed field studies comparing avian function and functional diversity between forests, agroforests, and simplified agricultural systems (Van Bael et al. 2008). Studies that rigorously compare and manipulate relative abundance and biomass of avian functional groups in tropical agroecosystems, 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.

Insect functional diversity in tropical agroecosystems

Land use intensity in the tropics also has strong effects on the diversity and abundance of functionally important insects such as ants, parasitoids, dung beetles, pollinating bees, predacious wasps and phytophagous insects including crop pests (Schulze et al. 2004, Tylianakis et al. 2005, 2006, 2007, Klein et al. 2006, Wilby et al. 2006, Perfecto et al. 2007). However, different arthropod feeding groups can respond differently to land use changes (Wilby et al. 2006), while the diversity of each of these trophic groups has been shown to affect rates of ecosystem processes such as pollination (Kremen et al. 2002), biological control (Snyder et al. 2006), or parasitism of beneficial species (Tylianakis et

al. 2006). Here we use trap-nest data from Ecuador and Indonesia to analyze diversity responses to land-use changes at local and landscape scales of four major trophic groups: (1) pollinators (bees), (2) first-order predators (e.g., eumenid wasps, which feed on caterpillars and are potential biocontrol agents), (3) second-order predators (e.g., pompilid wasps, which feed on spiders and have a negative effect on biocontrol, because they feed on potential biocontrol agents), and (4) parasitoids (which were reared from the above functional groups, so will generally have a negative effect on potential ecosystem services). In Ecuador, we studied five land use types, representing a gradient of decreasing modification: rice, pasture, coffee agroforests, abandoned coffee (resembling secondary forest), and forest (see Tylianakis et al. 2005, 2006). In Indonesia, we used a more subtle gradient of habitat modification, with three management intensities of cacao agroforestry (high intensity [low diversity of planted shade trees], medium intensity [higher diversity of planted shade trees], and low intensity [shade canopy consisting of mostly native forest trees]) and forests (for details, see Bos et al. 2007). Data from standardized trap-nests were pooled for each site and diversity of functional groups was compared across habitat types using ANOVA for the Indonesian species and a GLM (ANCOVA with proportion natural habitat included) for the Ecuadorian species (see Appendix B). Results of proportional diversity are given in Fig. 1b, while the statistical results for proportional diversity (and raw diversity) are in Appendix B (Table B1).

A total of 42 species were recorded in Ecuador and 52 in Indonesia. Increasing habitat modification showed significant negative effects on first-order predator richness (GLM, $F_{4,35} = 3.56$, $P = 0.016$) and proportionate richness (GLM, $F_{4,35} = 3.78$, $P = 0.012$) in Ecuador, with rice and pasture having fewer species than the remaining forested habitats. Loss of tree cover in the intensive systems of Ecuador was therefore the critical determinant of first-order predator loss. If predator diversity correlates with predation rates (Snyder et al. 2006) in this region, intensive management may be harmful to biocontrol services. In Indonesia, richness ($F_{3,12} = 13.08$, $P < 0.001$), but not the proportion ($F_{3,12} = 0.65$, $P = 0.598$) of first-order predator species also decreased with cacao management intensity. Management intensity did not significantly affect bees in Ecuador, whereas in Indonesia, richness ($F_{3,12} = 5.73$, $P = 0.011$) and proportionate richness ($F_{3,12} = 3.85$, $P = 0.038$) of bees increased along the land-use intensification gradient, with significantly higher richness in medium-intensity than low intensity agroforests or forests, and a significantly higher proportion of bees in forests than high-intensity agroforests. Second-order predators showed no response in Ecuador, and in Indonesia, just a weakly significant variance in richness ($F_{3,12} = 4.00$, $P = 0.034$) but not the proportion of richness was found. Habitat modification increased

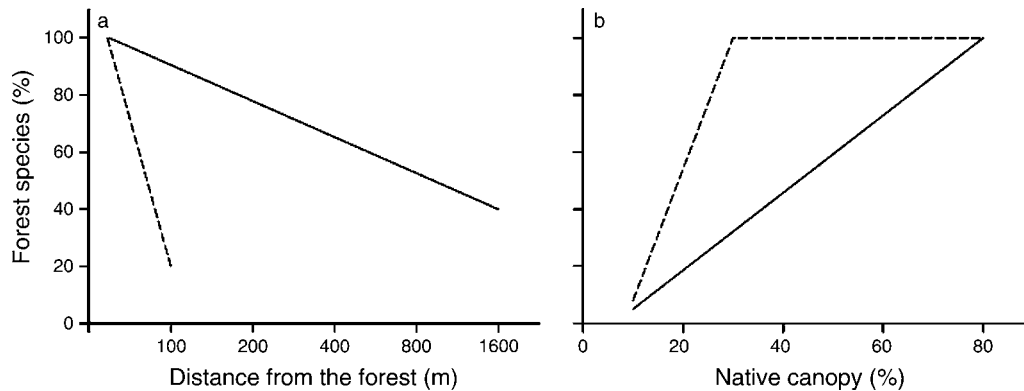


FIG. 2. (a) The percentage of forest species in agricultural areas decreases with increased distance from a nearby forest. (b) Native forest cover in agricultural areas can attract the forest species. However, some forest communities may be more resilient than others. To illustrate this, we graphically present two extreme scenarios (dashed and solid lines; see Klein et al. [2003, 2006], Sodhi et al. [2004, 2005], Soh et al. [2006], and Laurance [2007] for more details).

parasitoid richness (GLM: Ecuador, $F_{4,35} = 2.66$, $P = 0.049$; Indonesia, $F_{3,12} = 11.46$, $P < 0.001$) and their proportion (GLM: Ecuador, $F_{4,35} = 4.16$, $P = 0.007$; Indonesia, $F_{3,12} = 5.60$, $P = 0.012$), and percentage parasitism on first-order predators and bees increased significantly with parasitoid diversity (Tylianakis et al. 2006).

For landscape effects, we focused on Ecuador and used the proportion of natural or near natural vegetation (agroforests, forests, and abandoned forests), calculated from GIS maps made from satellite images for a 500 m radius around each site. Species richness of bees and first-order predators showed a slight tendency to increase with the proportion of forest cover in a 500 m radius (as may be expected from the enhanced availability of nesting sites), whereas second-order predators and parasitoids showed a tendency to decrease, but the effect was significant only for parasitoids (GLM, $F_{1,35} = 12.9$, $P = 0.001$, $r^2 = 0.198$). The latter was probably due to the increased abundance of hosts and prey in the non-forested agroecosystems. It should also be noted that all of our sites had at least some tree cover nearby, and there may be a threshold level of landscape modification (Tscharntke et al. 2002, 2005) beyond which higher trophic levels cease to benefit from increased prey abundance, and begin to suffer from a deficit of refuges and nesting sites.

LANDSCAPE CONFIGURATION AND SPILLOVER ACROSS HABITATS

Survival of functional groups in agricultural landscapes may depend upon the configuration of forested and non-forested patches. Metapopulation theory suggests that populations can be maintained in lower quality habitat patches by influxes of individuals from source populations, and this movement is facilitated by a high quality matrix (Vandermeer and Carvajal 2001). Biocontrol agents, pollinating bees, seed-dispersing frugivores and other functionally important species

survive in many land-use systems within tropical mosaic landscapes only when these are connected to natural habitats (Elmqvist et al. 2003, Klein et al. 2003, Schroth et al. 2004, Bianchi et al. 2006). Less mobile organisms may be more constrained by mobility than quality of the matrix and require low-intensity agroecosystems as suitable habitat (e.g., belowground decomposers [Hedlund et al. 2004]). Ricketts et al. (2001) found that diversity of phytophagous moths formed “halos” of relatively high species richness and abundance extending over 1 km around forest patches irrespective of the land management. Such an effect has not yet been demonstrated for pollinating bees and parasitoids (Klein et al. 2006).

Kareiva and Wennergren (1995) argue that the spatial arrangement of habitat fragments may mitigate extinction risk, while Harrison and Bruna (1999) find only habitat loss to be of major importance. Landscape ecology, but not metapopulation theory, considers the details of the landscape context and the impact of the matrix on processes between and within patches (Tscharntke and Brandl 2004). In agriculture-dominated tropical landscapes, distance to the nearest forest (a main species source) has been shown to be a major configuration effect (Fig. 2a), with a number of examples from functionally important birds and insects (see results from Ecuador for pollinating bees and predatory wasps above [Klein et al. 2006, Perfecto et al. 2007]). Enhanced arthropod species richness in agricultural systems adjacent to forests, particularly of pollinators and predators, can ultimately result in increased crop yields (Kremen et al. 2002, Klein et al. 2003, 2006, Ricketts et al. 2004, Olschewski et al. 2006). Even isolated fruiting trees in agricultural areas can provide important resources for frugivorous birds (Sekercioglu et al. 2007). Neighboring large forest tracts again can also enhance the use of these fruiting trees by a wide range of frugivores (Luck and Daily 2003), and as little as 5% native canopy cover can attract 100% of bird

species that use forest edges (Peh et al. 2006). Therefore, retaining native canopy cover (Fig. 2b) in agricultural areas can promote not only seed dispersal but also pollination activities. Similar scenarios are applicable to arthropods and their effects on ecosystem functioning (Klein et al. 2003, 2006, Schulze et al. 2004, Bos et al. 2007). The reduction in shade tree cover from 80% to 40% causes only minor changes in arthropod biodiversity and supports ecosystem functions such as decomposition, herbivory, or parasitism, while doubling the farmers' net income (Steffan-Dewenter et al. 2007). Balancing such trade-offs, small-loss-big-gain or even win-win approaches for a compromise of economic and ecological benefit are important areas for future research (de Fries et al. 2004).

Most populations and communities are not restricted to defined habitat types, including predatory species from natural habitats colonizing agroecosystems (Cronin and Reeve 2005, Bianchi et al. 2006). In contrast, some functional groups of animals (e.g., pollinators, seed feeders, predators) may also profit from agroecosystems, because of the often higher productivity and greater food resources of agroecosystems (e.g., fruits and nectar), and then spill over into natural habitats (Tscharntke et al. 2005, Rand et al. 2006). Different taxa may experience differential permeability across habitats, which have been shown for low-dispersal solitary vs. high-dispersal social bees (Klein et al. 2003, Ricketts et al. 2004, Rand et al. 2006). If more farmers adopt less-intensive management methods (Dietsch 2005), increases in matrix habitat quality may reduce threshold effects by improving overall connectivity and reducing fragmentation (Tscharntke et al. 2002, 2005). Forest-associated species may then be less constrained by dispersal abilities and distance from source populations in reserves, which may have important benefits for the yields of crops such as coffee (Ricketts et al. 2004, Olschewski et al. 2006). Edge effects can penetrate 200 m into tropical forests, effectively reducing the acreage of primary forest habitat (Laurance 2007), while the use of less intensive agricultural practices, such as shade coffee, along habitat boundaries and in buffer zones can ameliorate the environmental characteristics that produce the edge effect (Perfecto et al. 2007).

In managed landscapes, patch size (i.e., grain or resolution) of the landscape mosaic is another important consideration affecting matrix quality (Fischer and Lindenmayer 2005). In temperate farming landscapes of Sweden, small organic farms had a higher diversity of birds, pollinators, and plants than large organic farms (Belfrage et al. 2005). Similarly, farm size may help explain some biodiversity patterns in tropical agroforestry systems. If large plantation owners use the same management practices across the entire plantation, for example in their choice of shade trees, then there may be enhanced biodiversity in a similar sized landscapes composed of small farms, including the added habitat value from boundary vegetation between farms. This

heterogeneity in management may create a greater range of habitat, each with distinct and characteristic communities allowing an accumulation of functionally important species in mosaic landscapes (Perfecto et al. 2004, 2007).

Even though species richness of forest taxa usually declines dramatically in small forest fragments (Laurance 2007), these fragments sometimes have high turnover and contribute considerably to overall landscape richness (Fischer and Lindenmayer 2005). This diversity includes functionally important groups such as parasitoids, which show a close connection between richness and parasitism rates (Tscharntke et al. 2002, Tylianakis et al. 2006). Turnover of species through space and time can contribute significantly to landscape and regional biodiversity (Thiollay 2006), and beta diversity is usually higher in natural than managed systems, as known from bees, predatory wasps and parasitoids (Tylianakis et al. 2005). Management should take into account such landscape-wide species turnover, because high diversity of functionally important species has been suggested to provide insurance under conditions of environmental change, such that formerly "insignificant" species can respond to a disturbance and maintain ecosystem functioning (Bengtsson et al. 2003, Elmquist et al. 2003, Loreau et al. 2003).

CONCLUSIONS AND OUTLOOK

Understanding the ecology of human-dominated landscapes provides critical insights into functional diversity in the tropics, because most species experience their surroundings at spatial scales beyond the plot level, and a spillover across natural and managed ecosystems is common. Given this importance for ecology and conservation biology, we provide an overview of important considerations shaping bird and insect functional groups in human-dominated tropical landscapes. Based on our analyses, bird communities of agroforests, in comparison to forests, are comprised of a greater proportion of frugivorous and nectarivorous, but fewer insectivorous species, thereby affecting seed dispersal, pollination, and biological control (Sekercioğlu 2006). Similarly, insect predators of plant-feeding arthropods were more diverse in low-intensity agroforest and forest compared to rice and pasture, while in Indonesia bee diversity was also higher in forested habitats. Hence, diversity of bird and insect predators as well as bee pollinators declines with agricultural habitat transformation, contrasting with the increase in avian seed dispersers. Such patterns are little known, but important predictors of changing response diversity and resilience of landscapes that may affect the capacity of the communities to reorganize after disturbance and to sustain ecological functions such as biological control, pollination and seed dispersal (Bengtsson et al. 2003, Elmquist et al. 2003, Tscharntke et al. 2005, Snyder et al. 2006). As similarity of functionally important bird and insect communities in agricultural systems is higher than

that in natural areas, diversity assessments that do not incorporate beta diversity may be biased (Tylianakis et al. 2005). Furthermore, scale of management is an underappreciated determinant of functional biodiversity and higher in small than large farmer landscapes, due to higher management heterogeneity. Proximity of agroforests to forests, which is an important aspect of landscape configuration, also influences functional diversity and may drive successful biological control and pollination (Perfecto et al. 2007), while patches of fruit trees may already serve as stepping stones or corridors for frugivores (Luck and Daily 2003).

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APPENDIX A

Methods for the review and meta-analysis of avian functional diversity (*Ecological Archives* E089-055-A1).

APPENDIX B

Analyses of cavity-nesting bees, wasps, and their natural enemies (*Ecological Archives* E089-055-A2).