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PERSPECTIVES IN ORNITHOLOGY

EFFECTS OF DISTURBANCE OR LOSS OF TROPICAL RAINFOREST ON BIRDS

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EXTENSIVE TROPICAL DEFORESTATION is a major threat to bird biodiversity. Approximately 50% of the area originally covered by tropical forests has now been cleared, and much of what remains is being rapidly degraded (Wright 2005). This habitat loss is the primary cause of species endangerment and local extinctions (e.g., Brash 1987, Castelletta et al. 2000, Trainor 2007). Given that 70% of the world's threatened bird species occur in lowland and montane tropical forests (BirdLife International 2008), deforestation remains a major threat. It has been predicted that most of the currently threatened bird species could disappear by the end of this century if the present rate of deforestation continues (Pimm et al. 2006).

"Conserving large, continuous blocks of primary forest and extensive forest fragments is clearly imperative for conservation of tropical forest birds, many of which may be capable of using modified habitats only intermittently, if at all."

Although species disappearance is an expected consequence of outright habitat loss, much remains to be learned about the extinction process and how forest disturbance contributes to the decline of tropical birds. Here, we briefly highlight overall patterns of endangerment and extinction of bird species and discuss possible mechanisms (e.g., predation) and consequences (e.g., breakdown of ecosystem processes) of the loss of tropical forest species. We summarize current knowledge on the effects of deforestation and its associated drivers (e.g., fragmentation, agriculture) on forest birds. We end by identifying the conservation implications of the patterns we have highlighted and potential core areas for future research.

OVERALL PATTERNS

Forest loss and avian endangerment.—Humans have affected the structure and function of ecosystems around the world, but the threat to tropical forests is of primary conservation concern, because they contain at least half of the Earth's biodiversity (Dirzo and Raven 2003). Deforestation continues to accelerate in tropical countries, particularly in tropical Asia and Africa (Matthews 2001, Hansen and DeFries 2004). Countries with the largest annual net forest losses (e.g., Brazil and Indonesia) are located in the tropics, where collective losses averaged 8.2 million ha annually between 2000 and 2005 (Food and Agriculture Organization 2005). Global forest-loss trends over the past decade and a half reveal that deforestation has been more pronounced and widespread in the tropics, regardless of forest cover type examined (i.e., total, natural, or primary; left panels in Fig. 1, in green). There are also higher numbers of threatened and

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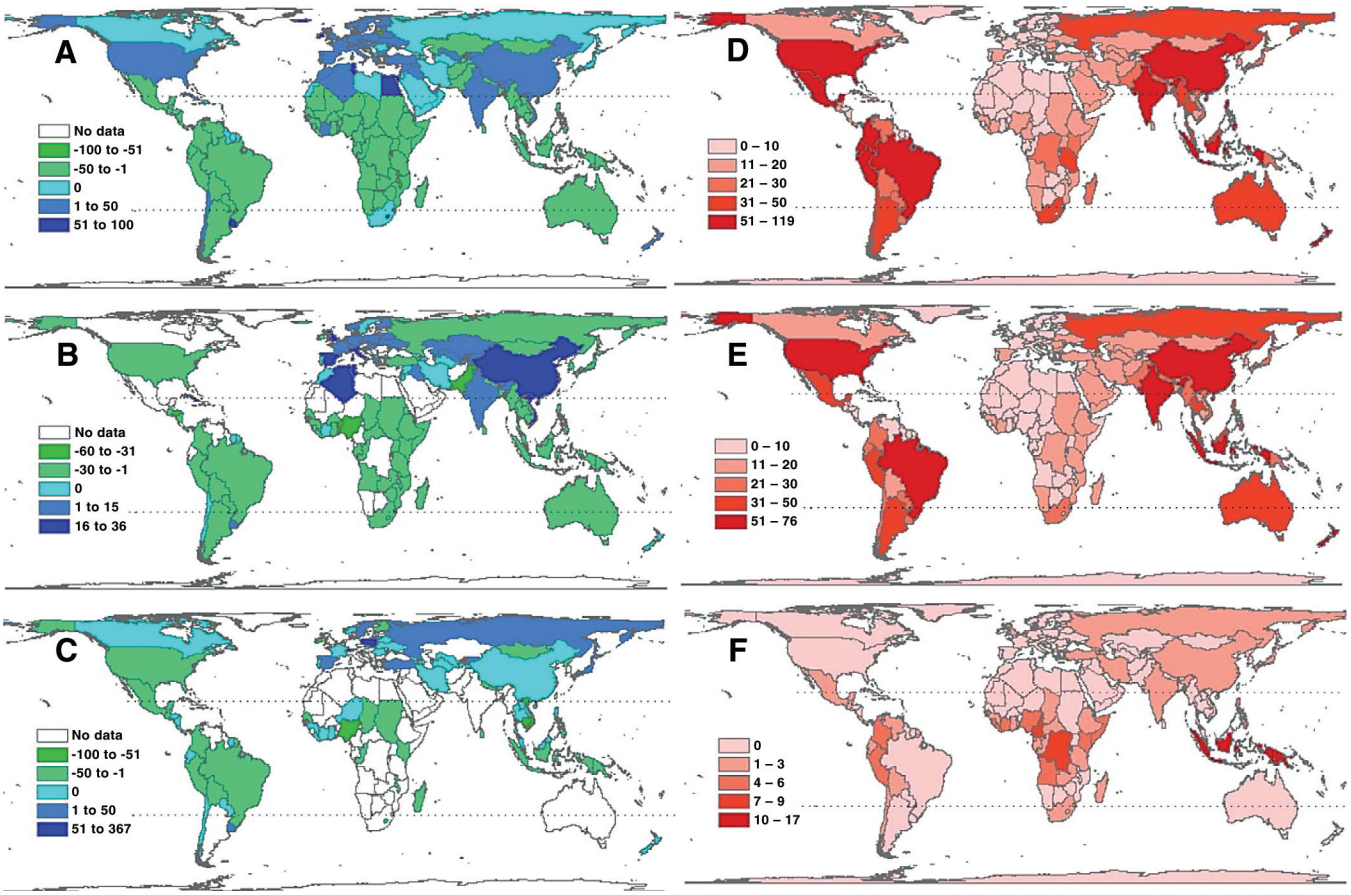

FIG. 1. Global distribution of average annual forest cover percent change (1990–2005) and richness of threatened and data-deficient terrestrial birds among countries. Data sources for rate of forest cover change and terrestrial birds were obtained from Global Forest Resources Assessment (Food and Agriculture Organization [FAO] 2005) and IUCN Red List of Threatened Species (International Union for the Conservation of Nature and Natural Resources 2007), respectively. Our definitions of (A) total, (B) natural, and (C) primary forest areas follow those of FAO (2005). Tropical countries are those in which all the land area is situated within ~23.5°N and ~23.5°S (indicated by the dotted lines). (D) Globally threatened species (i.e., those classified on the IUCN Red List as "critically endangered," "endangered," or "vulnerable"). (E) Globally threatened species as defined for D, but excluding those species listed under the Red List criteria A1c, B1b(iii), and B2b(iii) (i.e., criteria related to decline of the habitat area, in extent, quality, or both). (F) Data-deficient species (i.e., those classified on the Red List as "data-deficient").

data-deficient birds in the tropics, particularly in Southeast Asia (right panels in Fig. 1, in dark red). These results broadly reinforce the connection between high tropical deforestation and increased avian endangerment suggested by other studies (e.g., Brooks et al. 1997, BirdLife International 2008).

Avian extinctions.—Human actions have raised the rate of bird extinctions by several orders of magnitude, and rates are predicted to rapidly increase (Şekercioğlu et al. 2004, Pimm et al. 2006). As much as 67% of local tropical-forest avifauna has been reported to disappear following deforestation (Sodhi et al. 2004), though species often persist for long periods in forest remnants, which leads to a "time lag" between the deforestation event and extinction (Brooks et al. 1999). Bird communities in forest fragments are predicted to undergo half the total number of extinctions they are likely to experience within 50 years of isolation (Brooks et al. 1999). This time lag may also account for the lower-than-expected number of global extinctions attributable to deforestation that have been recorded thus far, particularly in continental systems (Brooks and Balmford 1996). However, analyses have shown that the number of bird species expected to become extinct from deforestation is similar to the actual numbers of species classified as threatened (Brooks and Balmford 1996, Brooks et al. 1997).

Extinction risk is not distributed equally among bird species (Bennett and Owens 1997, Şekercioğlu et al. 2004, Sodhi et al. 2004), but there has been little examination of which traits make tropical birds vulnerable. Various global analyses point to intrinsic biological traits (e.g., slow life history, large body size; Gaston and Blackburn 1995, Bennett and Owens 1997) and extrinsic factors that result in small populations (e.g., geographic range size; Blackburn and Gaston 2002) as being associated with high extinction risk. In addition, rare and specialized birds are particularly vulnerable to extinction following habitat loss (Owens and Bennett 2000, Şekercioğlu et al. 2004, Sodhi et al. 2004). Other analyses have, however, shown that even species that are flexible in their

habitat choice (e.g., can inhabit secondary forests) do not survive extensive deforestation (Harris and Pimm 2004).

Altered communities.—Disturbance and degradation alter forest communities and, thus, affect the survival of forest bird species in several ways. Increased access of open-country species to forests can lead to greater competition for resources and greater predation pressure (Yap and Sodhi 2004). Nest predation is also higher at the interface of forest and disturbed habitat (e.g., Gibbs 1991, Burkey 1993, Cooper and Francis 1998), where certain predators may be more efficient in detecting nests. The loss of large predatory species associated with overexploitation in deforested areas (Daily et al. 2003, Wright 2003) may increase populations of small and medium-sized mammals (i.e., mesopredator release) and, thus, exacerbate birds' vulnerability to predation. Typically, these mesopredators become more abundant following the decline of top predators and, thus, predation rates on avian young and eggs increase (Terborgh 1992, Crooks and Soulé 1999). Therefore, elevated mesopredator population densities may explain some species extinctions in forest fragments (Sieving 1992). Although some evidence points to predation pressure generally being lower in less disturbed forests (Cooper and Francis 1998, Wong et al. 1998), patterns across the tropics vary depending on the local fauna and the extent of disturbance (e.g., Carlson and Hartman 2001, Posa et al. 2007).

Altered processes.—Declining bird populations in the tropics have great implications for ecosystem processes, especially given that extinction threat is not uniformly distributed among avian functional groups, and some key groups such as scavengers, frugivores, and insectivores are more threatened than the global average (Şekercioğlu et al. 2004). Disruptions of ecological processes through species loss in degraded forests may also lead to cascading and catastrophic co-extinctions (Koh et al. 2004). For instance, frugivory, a key interaction linking plant reproduction and dispersal with animal nutrition, is placed in jeopardy by habitat degradation. Because many tropical trees have evolved to produce large, lipid-rich fruits adapted for animal dispersal (Howe 1984), the demise of avian frugivores may have serious consequences for forest regeneration. Several examples exist (Brash 1987; Cordeiro and Howe 2001, 2003) of fruiting tropical trees that either failed to become re-established after harvest or became less numerous in fragments where the frugivorous bird responsible for the dispersal of their seeds has declined or disappeared. In turn, the declining availability of fruits in disturbed tropical forests that results from disrupted avian-mediated seed dispersal may prevent colonization and persistence of certain frugivores in disturbed habitats (Lambert 1991, Zakaria and Nordin 1998). The biological control of herbivorous insects by birds may be of value in both anthropogenic and natural forest settings (Tscharntke et al. 2008). However, although it is clear that insectivorous birds play an important role in controlling outbreaks of herbivorous insects in agroforests (Perfecto et al. 2004), there are fewer studies with comparable results in natural forest stands (Van Bael et al. 2003, Sekercioglu 2006). Generally, insect herbivores inflict high damage in both the canopy and understory of forest stands that lack avian insectivores (Van Bael et al. 2003, Van Bael and Brawn 2005, Dunham 2008); this ability of birds to control herbivorous insects complements that of other insectivorous predators (Greenberg et al. 2000). As we discuss in more detail below, understory insectivores and frugivores are predicted to decline with increased disturbance and fragmentation of the tropical forest (Şekercioğlu et al. 2002); thus, the potential implications of the loss of birds of these two key trophic guilds for tropical forest productivity must be carefully examined. Although frugivory and insectivory are becoming better understood, more data are needed on how forest disturbance affects other avian functions such as pollination, vertebrate predation, and scavenging.

DEFORESTATION-RELATED DRIVERS

Forest fragmentation.—Currently, ~45 million ha of tropical forest exist as fragments (Achard et al. 2002) that are scattered among urban areas, pastures, agricultural areas, and other types of land uses. Numerous studies document avian losses and population declines in tropical fragments (reviewed in Turner 1996) and suggest that area, isolation, and quality of fragments all influence the rate and order of species disappearance. Also, several studies have found that traits related to population size and recovery rate, such as rarity (Newmark 1991), high population variability (Karr 1982), low annual survival rates, and low fecundity (Karr 1990, Sieving and Karr 1997), may predict or account for species loss in fragments.

Terrestrial insectivores are now widely recognized as a fragmentation-sensitive guild (Karr 1982, Kattan et al. 1994, Stouffer and Bierregaard 1995, Lambert and Collar 2002, Şekercioğlu et al. 2002, Sigel et al. 2006). Their limited dispersal abilities, high habitat-specificity, and dietary specialization are thought to underlie their propensity to disappear from fragments. For instance, Stratford and Stouffer (1999) found a 74% extinction rate for ground-foraging insectivores in Manaus, Brazil, even though some fragments were connected to contiguous forest by secondary growth. Species with specialized ecology, such as obligate ant-followers, are among the first to be lost from recently isolated fragments (Stouffer and Bierregaard 1995). Because they require a large foraging area, birds that forage in mixed-species flocks are also adversely affected (Stouffer and Bierregaard 1995, Sigel et al. 2006, Van Houtan et al. 2006).

Large-bodied frugivores are similarly fragmentation-sensitive, especially at higher elevations (Kattan et al. 1994, Renjifo 1999). Despite the typically high dispersal ability of canopy species, large frugivores are likely to depend on patchily distributed trees that fruit at different times, and the lowered vegetation diversity in small fragments may not support them (Willis 1979). Similarly, forest-interior raptors that require large tracts of forest are sensitive to fragmentation (Kattan et al. 1994, Thiollay 1996, Renjifo 1999). Moreover, large-bodied frugivores and forest raptors may also be subjected to human persecution in open habitats because of their size (Peres 2001).

Species persistence in fragmented landscapes is influenced by both patch-level and landscape-level factors. Forest-interior species are more affected by patch characteristics such as area, shape, plant species composition, vegetation structure, and extent of microclimatic change (Graham and Blake 2001). Edge-avoidance response has been found to be typical of Neotropical insectivores (Lindell et al. 2007), such that certain species are reluctant to cross even relatively narrow roads (Laurance 2004). For less restricted species, survival in fragments seems to be best predicted

by their presence in the matrix of modified habitats surrounding the fragments (Gascon et al. 1999, Renjifo 2001, Sekercioglu et al. 2002). The type and quality of the matrix, largely determined by the history and intensity of land use, can strongly influence processes within the fragments (Marzluff and Ewing 2001, Kupfer et al. 2006). Some matrices can provide foraging or breeding habitats (Sekercioglu et al. 2007); structurally complex natural or anthropogenic matrices (i.e., tree plantations) have been found to provide the best fragment-connectivity (Gascon et al. 1999, Renjifo 2001). If suitable connecting habitat is present, it can allow individuals to recolonize fragments and even restore pre-isolation abundance of some species (Stouffer et al. 2006). In remnants that are completely isolated, however, species richness erodes over time because of continued loss of species and lack of recolonization (Diamond et al. 1987, Robinson 1999, Sodhi et al. 2006).

Our understanding of the effects of tropical fragmentation is still incomplete, because temporal observations have been recorded only for relatively short periods (~20 years; Sodhi et al. 2005, Stouffer et al. 2006; but see Robinson 1999). Similarly, results inferred from comparing patches with contiguous forests do not paint a complete picture, because sensitive species may already have been extinct before the research was initiated (Graham and Blake 2001, Manu et al. 2007). To what degree fragmentation exacerbates outright habitat loss is not well understood, but it is theorized to have a greater effect in the tropics than in temperate systems (Andrén 1994, Fahrig 2003). Modeling the effects of area and isolation on extinction and colonization dynamics, Ferraz et al. (2007) found a stronger effect of area, suggesting that species are absent from small, isolated patches not because they are unable to colonize them but because they rarely occupy small patches, even in contiguous forest. Indeed, Van Houtan et al. (2007) showed that tropical forest birds may be better dispersers than assumed but also preferentially disperse from smaller to larger patches. It has been proposed that a critical threshold of 20–30% of habitat cover exists, below which the relative importance of habitat configuration for species persistence increases (Andrén 1994, Fahrig 2003). This is supported by a study that showed spatial organization to be important in sustaining source–sink dynamics and the retention of broader population structure in the face of some short-term local extinctions in the highly fragmented Brazilian Atlantic forest (Develey and Metzger 2006). Nonetheless, the general nature of this threshold needs to be verified, because minimum viable population sizes may depend on the level of connectivity in the landscape (Traill et al. 2007, Brook et al. 2008).

Timber harvesting practices.—Selective logging is practiced in many tropical countries, where gaps between successive harvests of timber species are meant to allow forests to regenerate, resulting in a forest structure with a mix of tree sizes and ages that mimics natural stands. Available data for tropical birds indicate that many forest species continue to survive in, or use, selectively logged forest. Although some species vacate an area when logging begins but return to it after it has been logged, this pattern is not universal (Thiollay 1992, Dranzoa 1998), and some communities remain distinct from the original for periods of 10–15 years (Johns 1996; Thiollay 1997, 1999). Logging can also result in significant changes in the relative abundance and composition of the avifauna, with an increase of widespread generalists or forest-edge species, compared with pristine forest (Johns 1996, Thiollay 1997, Dranzoa 1998, Aleixo 1999). This influx often accounts for the higher species richness in logged areas.

Selective logging affects various guilds differently. Some understory insectivores, as well as mixed-species flock members, are intolerant of the changes in microclimate and vegetation that occur after logging, because of their physiology and foraging-habitat specializations (Johns 1986, Mason 1996, Dranzoa 1998, Marsden 1998, Thiollay 1999). However, in other cases, such species can benefit from understory regrowth (Cleary et al. 2007). Guilds such as bark-associated insectivores and large-canopy frugivores (e.g., hornbills) decline after large trees are lost (Johns 1989, Cleary et al. 2007). On the other hand, some studies report that nectarivores, generalist frugivores, omnivores, and gap or edge specialists seem to benefit from logging-related changes in vegetation (Lambert 1992, Johns 1996, Mason 1996, Dranzoa 1998, Owiunji and Plumptre 1998, Thiollay 1999). A global meta-analysis showed that insectivores and frugivores decrease after moderate disturbance of tropical forest, but patterns for carnivores, omnivores, and nectarivores differ among tropical regions (Gray et al. 2007). There is little evidence that logging disproportionately threatens rare species or those with restricted ranges (Thiollay 1997, Marsden 1998). There are, however, indications that populations that do not experience natural disturbance (e.g., hurricanes) may be more sensitive to logging (Aleixo 1999).

Many logging concessions are in proximity to pristine forest from which birds can disperse, which may account for the minimal species loss and occurrence of some forest-dependent species in logged areas. The magnitude of impact on the avifauna can also depend on the management regime adopted by timber companies (Frumhoff 1995, Mason 1996, Sekercioglu 2002). If harvest regimes do not allow logged forests to regenerate naturally, isolate them from unlogged compartments, or change regeneration dynamics, bird communities are unlikely to regain their pre-logging composition. However, one of the serious consequences of logging is increased access through roads, which can lead to hunting and a higher probability of further forest clearance (Thiollay 1999, Asner et al. 2006, Sodhi and Brook 2006).

Agricultural practices.—The term "countryside habitat" has been used to encompass the diverse array of active agriculture, plantation or managed forests, fallow land, gardens, and small remnants of native vegetation in human-dominated landscapes (Daily et al. 2001). Surveys in these landscapes have indicated that they can harbor a substantial proportion of the regional avifauna, forest species included (Estrada et al. 1997, Daily et al. 2001, Hughes et al. 2002, Sodhi et al. 2005). However, the value of the different land uses for maintaining avian biodiversity varies considerably (Peh et al. 2005, Posa and Sodhi 2006, Soh et al. 2006).

Conversion of forest into pasture for cattle grazing has had the greatest impact, resulting in a near-total absence of birds in the heavily modified landscapes of some regions (Saab and Petit 1992, Estrada et al. 1997, Petit et al. 1999). Low species richness is also observed in other intensively managed plantations, especially in monocultures of non-arboreal annual crops (Estrada et al. 1997, Matlock et al. 2002, Waltert et al. 2004). Open-country species dominate these habitats, because forest birds are sensitive to the extreme climatic conditions there. Arboreal crops such as shade coffee (*Coffea* spp.), Cacao (*Theobroma cacao*), and Cardamom (*Elettaria cardamomum*) support a greater number of forest

bird species, particularly if natural vegetation is allowed to grow (Estrada et al. 1997, Greenberg et al. 1997, Shahabuddin 1997, Petit et al. 1999; but see Waltert et al. 2004). Remnant forest trees and riparian strips can be disproportionately important for forest birds persisting in tropical countryside (Sekercioglu et al. 2007). Some primary-forest birds can use older plantations of exotic trees that allow secondary growth (Mitra and Sheldon 1993) or traditional agroforests that are diverse and structurally complex (Thiollay 1995); however, species richness and diversity are still lower than in primary forest. Similarly, the successional vegetation that results from practices such as shifting cultivation (i.e., slash-and-burn) or from the abandonment of "permanent" agriculture can be colonized by forest birds. Species richness and abundance have been found to parallel recovery of vegetation (Bowman et al. 1990, Blankespoor 1991, Andrade and Rubio-Torgler 1994, Raman et al. 1998). Secondary forest regrowths from agricultural fallows can contain a significant proportion of forest avifauna, as well as secondary-growth specialists (Blankespoor 1991, Raman et al. 1998). However, these habitats are still suboptimal for forest-dependent species (Raman 2001), whereas traditional systems of shifting agriculture practiced on small scales, with long intervals between burning and recropping, may minimally affect the avifauna (Zhijun and Young 2003).

The degree of similarity between species assemblages in countryside habitats and in pristine forest appears to depend on land-use patterns and landscape context (Luck and Daily 2003). Pesticides adversely affect insectivores, as does the lack of leaf litter and low vegetational diversity in agriculture (Shahabuddin 1997), but the same birds benefit from insect pests in timber plantations (Mitra and Sheldon 1993). Although large frugivores generally do not benefit from the dominating crop trees of agroforests and are absent from plantations in some areas (Thiollay 1995, Shahabuddin 1997), they have been observed in other mixed rural habitats (Sodhi et al. 2005). However, such patterns may be attributable to the proximity of pristine forest to study areas (Barlow et al. 2007).

Infrastructure and urbanization.—Cities are expanding worldwide, and it is expected that more than half the world's total human population will be living in them by 2030 (Palmer et al. 2004). Unlike other land uses, urbanization makes natural successional recovery difficult or impossible; thus, the effects on biodiversity are long-term. Urbanization increases biological homogenization, causing the extirpation of native species and promoting the establishment of non-native, urban-adaptable species that are becoming increasingly widespread and locally abundant across the planet (McKinney 2006). There is a near-complete absence of forest species in tropical urban areas, and human commensals such as Rock Doves (*Columba livia*) and House Crows (*Corvus splendens*) can attain high densities (Sodhi et al. 1999, Lim and Sodhi 2004, Pauchard et al. 2006, Posa and Sodhi 2006). Some less sensitive native species, such as frugivores that can feed on fruit-bearing ornamental plants (Petit et al. 1999, Lim and Sodhi 2004, Posa and Sodhi 2006), are able to persist in city parks and low-density housing areas. The presence of remnant natural habitats may be the most important determinant of forest bird diversity in tropical cities (Sodhi et al. 1999, Lim and Sodhi 2004). Therefore, it is unfortunate that cities in developing tropical countries typically do not maintain natural elements in the urban environment (Pauchard et al. 2006, Posa and Sodhi 2006). Understanding of the effects of urbanization in regions of high avian diversity such as the tropics is still rudimentary (Chace and Walsh 2006), but measures for urban conservation will be crucial in the coming decades as urban sprawl is set to replace native and rural habitats.

FUTURE DIRECTIONS

Conserving large, continuous blocks of primary forest and extensive forest fragments is clearly imperative for conservation of tropical forest birds, many of which may be capable of using modified habitats only intermittently, if at all. With a large portion of the tropical landscape now deforested, it is critical to develop strategies that preserve the remaining forests' bird diversity and prevent further losses. On the basis of our review, we have identified the following research directions for tropical forest birds: (1) more research, especially in Oceanic, Asia and Africa, is needed to better understand the effects of forest disturbance on avian diversity, abundance, demographics, survivorship, and functionality (see Table 1); (2) better comprehension of the long-term persistence as well as habitat thresholds (minimum area requirements) is required with regard to forest bird populations in degraded tropical landscapes; and (3) the relative effects of different types of habitat disturbance (e.g., fragmentation vs. road construction) and synergies among different threats (e.g., fragmentation, fire, disease, invasive species, and global warming) need to be better studied. Among potential synergies, for instance, further work is needed to

TABLE 1. Comparison of land areas, threatened bird species, and publications in the various tropical regions

	Tropical regions			
	Americas	Africa	Asia	Oceania
Number of countries or territories	37	37	14	20
Approximate total land area (km^2)[a]	16,153,860	15,582,840	7,383,680	595,000
Number of bird species assessed by the 2007 IUCN Red List[b]	4,018	2,890	2,749	1,507
Number of threatened terrestrial bird species[b]	429	198	261	122
Number of papers published[c]	126	34	65	15

[a] Cumulative land area of countries that have most or all of their land area in the tropics.
[b] Number of extant native species obtained by running 2007 Red List searches including all tropical countries in each region. Threatened species are those classified as "critically endangered," "endangered," or "vulnerable."
[c] Results of searching of databases (Biosis, Current Contents Connect, Web of Science, and Zoological Records) for the period 1987–2007 using the key words (Tropic* OR Rainforest) AND (Avian OR Bird*) AND (Deforest* OR Logg* OR Fragment* OR Degrad*).

fully understand the link between forest disturbance and hunting and the susceptibility of rainforest bird populations to emerging infectious diseases and climate change in human-modified landscapes. Clearly, urgent actions are needed to mitigate human impacts on tropical forest birds.

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