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Long-term changes in the bird community of Palenque, Chiapas, in response to rainforest loss

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Abstract With increased human populations and subsequent pressure to develop or farm land, the rate of fragmentation of tropical rainforests has accelerated in the past several decades. How native organisms respond to such fragmentation has been the subject of intense study in temperate ecosystems and at several tropical sites in Central and South America, but there has been little study of this phenomenon in Mexico, the country bridging the Neotropics and temperate North America. A reason for this neglect is an apparent lack of long-term data; however, such data can be obtained from "non-traditional" sources, such as birders and tour leaders. We make innovative use of such data, combining them with more traditional data (e.g., museum specimens) to create a record of occurrence for Palenque, Mexico, from 1900 to 2009, including a near-continuous presence–absence record since 1970. We analyzed these data using logistic regression and, importantly, recent statistical advances expressly for sighting records. As recently as the 1960s Palenque's forest was contiguous with that of Selva Lacandona to the east, but the protected area surrounding the famous ruins is now a forested island. As a result, various species formerly known from the site have disappeared, including species both large (*Crax rubra*, *Penelope purpurascens*, and *Ara macao*) and small (*Notharchus hyperrhynchos*, *Malacoptila panamensis*, *Microrhopias quixensis*, and *Pachyramphus cinnamomeus*). By contrast, several species of open areas or second growth have apparently colonized the area

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(e.g., *Thryothorus modestus*, *Mimus gilvus*, *Euphonia affinis*). Some species turnover has occurred within particular families, such as Columbidae, Trochilidae, and Troglodytidae. Losses and declines we documented at Palenque correspond with those reported from other sites in Mesoamerica, suggesting the soundness of our approach and the general vulnerability of certain species. Compilation and analysis of sighting record data holds great promise for tracking trends in many regions and across many taxa for which long-term census data are lacking.

Keywords Colonization · Community turnover · Deforestation · Extirpation · Neotropics · Sighting record

Introduction

It is axiomatic that reductions in forested habitats will lead to reductions in population densities and species richness of forest birds (e.g., Brook et al. 2003). Richness falls as habitat area shrinks, as predicted by species–area relationships (Pimm et al. 1995; Pimm and Raven 2000; Sodhi et al. 2004). This pattern is especially alarming because, for many decades now, tropical forests have been absorbing two blows: they are being felled worldwide at a high rate, estimated recently at ~6,000,000 ha/year (Achard et al. 2002), and little remaining forest is undisturbed (Willis et al. 2004; Lewis 2006). Tropical deforestation generally has occurred as a result of agricultural and pastoral expansion (Gaston et al. 2003; Carr 2004)—forest is being traded for field. As a result, “weedy” species of open-country and second growth might be expected to replace forest-dependent species, many of which are threatened with extirpation (Turner 1996; Laurance and Bierregaar 1997), and species loss can occur rapidly (Lees and Peres 2006). Clearly, an understanding of the long-term effects of deforestation is needed if we hope to preserve natural habitats and their species into the distant future.

A suite of empirical data show that extirpation and extinction is non-random (Purvis et al. 2000; Bennett et al. 2005; Gray et al. 2007)—some species or groups are more vulnerable, others more resilient. Detecting patterns can be challenging, especially when comparing among avifaunas (Stratford and Robinson 2005); nonetheless, correlates of vulnerability have emerged often enough to have reached a kind of consensus. Species with a large body size and (typically correlated) low annual fecundity are particularly prone to extinction (Bennett et al. 2005), as are species with low mobility, an indication of limited dispersal ability and low population density (Turner 1996; Reed 1999; Moore et al. 2008). Another key correlate of vulnerability is the degree of habitat specialization (Sodhi et al. 2004). A species restricted to a particular habitat, that requires a particular resource, or otherwise has specific social needs—such as leks or mixed-species flocks—is at higher risk than a species with a wider habitat range or more plastic behavior (Reed 1999).

Determining to what extent these patterns hold requires data from geographically diverse sites. Much of the data comes from the Americas: from 1970 to 2000 over half (54.3%) of research on biotic effects of tropical deforestation was conducted in the Neotropics (Rudel et al. 2000). A disproportionate amount of that research, however, is from a single (albeit excellent) long-term study, the Biological Dynamics of Forest Fragments Project at Manaus, Brazil (Turner 1996). In the northern Neotropics, studies have been published from, for example, southern Mexico (Estrada et al. 1997), Costa Rica (Sigel et al. 2006), Panama (Willis 1974; Robinson 2001), and Colombia (Renjifo 1999), but additional data are needed from different sites if we hope to recognize and test the generality of posited patterns. Attempts to accomplish this task face an apparently intractable limitation: most potential study sites do not have long-term data available. Some sites, such as Los Tuxtlas in Mexico, La Selva in Costa Rica, and Barro Colorado Island in Panama, have established biological stations with extensive records, yet, obviously, most sites do not have such stations.

Herein we make use of a vast source of largely untapped data. Birders (and other natural history enthusiasts) frequent numerous sites, with some sites visited annually, and most keep notes of what they saw, even if only a species list. In the Neotropics, one such heavily visited site is the Mayan ruins at Palenque, Mexico. Despite being discovered well over a century ago and now residing in a national park, no biological station has been established at or near Palenque and no long-term, systematic effort to keep track of its avifauna has been undertaken. Even so, data collected from birders and from museums provides a nearly continuous record of presence–absence over the past three and a half decades, with additional coverage back to May 1900, when E. W. Nelson and E. A. Goldman first surveyed the site's avifauna for the Smithsonian Institution, part of their multi-year expedition throughout Mexico (see Goldman 1951). Using statistical techniques designed for sighting records and presence–absence data and the aforementioned non-traditional data sources, we construct a detailed portrait of species turnover at Palenque over the past century.

Methods

Study site

Palenque (~17.5°N, 92.0°W) lies in the northeastern portion of Chiapas, Mexico's southernmost state. The study site consists of the Mayan ruins located ~8 km from the town of the same name. Although some have argued that much of the lowland forest of the region was disturbed by the Maya (e.g., Whitmore et al. 1990), the forest appears to have recovered in the >700 years that elapsed between the Maya collapse (circa A.D. 800) and arrival of the Spanish (Denevan 1992), and it certainly had recovered by the time the ruins were "re-discovered" by Westerners in the mid-nineteenth century (Stephens 1841). At that time, and until at least the 1950s (Goodnight and Goodnight 1956), Palenque sat amid a vast expanse of rainforest that stretched eastward and southward through much of the Petén in northern Guatemala, and Palenque is part of this biogeographic region (Patten and Smith-Patten 2008). This rainforest has been deforested and fragmented heavily since the 1970s (De Jong et al. 2000). Average deforestation rates in Mexico of 1.1–2.4% yield a minimum loss of 631,000 ha/yr (Arizpe et al. 1996; (FAO-UN) 2001). The situation is worse in the south. The Palenque region is at the northern tip of Selva Lacandona, a vast tract of rainforest being lost at rates of 3.5–12.4% per year (O'Brien 1998; De Jong et al. 2000; Estrada et al. 2002). Nearby areas in the southern Yucatán peninsula have similar rates of 2.0–4.5% (Cortina Villar et al. 1999; Mas Caussel 1996). Palenque National Park now constitutes an island of rainforest separated from the bulk of the remaining Lacandona by pastures and roads (De Jong et al. 2000). Factors contributing to forest loss in the Lacandona include timber extraction, cattle ranching, agricultural clearing (Fig. 1), growing human population, and road construction (O'Brien 1998). Rainforest habitat has been lost even within the protected area of the national park (Fig. 2), where major excavations began in the 1970s.

Fig. 1 A recent (May 2006) example of “slash and burn” clearing of rainforest at a site near the eastern boundary of Palenque National Park, Chiapas, Mexico. With continued clearing, the park itself becomes more and more isolated from Selva Lacandona, a vast swath of rainforest to the south

Fig. 2 Clearing of rainforest within Palenque National Park, Chiapas, Mexico, here around the Temple of the Foliated Cross, as seen in 1949 (*left*; from Goodnight and Goodnight 1956, © Ecological Society of America, reproduced with permission) and in 2006 (*right*)

Data collection

We compiled a baseline list of species—those species that occurred or were presumed to occur at Palenque prior to 1970—from Brodkorb (1943), Friedmann et al. (1950), Tashian (1952), Miller et al. (1957), and Alvarez del Toro (1964) and collections at the following institutions: American Museum of Natural History (New York), Field Museum of Natural History (FM; Chicago), Florida Museum of Natural History (FMNH; Gainesville), Louisiana State University Museum of Natural Science (Baton Rouge), Macaulay Library (Cornell Lab of Ornithology, Ithaca, New York), Moore Laboratory of Zoology (MLZ; Occidental College, Los Angeles), Museum of Vertebrate Zoology (University of California, Berkeley), National Museum of Natural History (USNM; Washington, D.C.), Natural History Museum of Los Angeles County (Los Angeles, California), Royal Ontario Museum (Ottawa), Universidad Nacional Autónoma de México (México, D.F.), University of Kansas Museum of Natural History (Lawrence), University of Michigan Museum of Zoology (UMMZ; Ann Arbor), and Yale Peabody Museum (New Haven, Connecticut). Data compiled from specimens collected in May 1900 (USNM) were supplemented by field notes from E. W. Nelson, housed at the Smithsonian Institution Archives in Washington, D.C. Baseline data also included 1967 field notes from Ernest P. Edwards and 1969 sound recordings from Ben B. Coffey, Jr. (FMNH).

We compiled data from 1970 through 2009 from our own field observations (22 visits for $\sim$50 field days), from those of other observers who responded to our requests for assistance or to direct mailings (see Acknowledgments), and from 16 site visits posted in eBird (http://ebird.org/). We also obtained some data from audio recordings made between the early 1970s and mid-1980s. Few observers estimated abundances of species they observed, so we constructed a matrix from 1970 to 2009 in which we marked species as either present (“1”) or absent (“0”) for any given year. We were careful to vet all reports that seemed unusual (per Patten, Gómez de Silva, Smith-Patten, and Ibarra,” An annotated list of the avifauna of Palenque, Chiapas,” in prep.) and queried observers on them. We discarded questionable species, often with consent of the observer. Throughout taxonomy and nomenclature follow the American Ornithologists’ Union (1998) as amended through Banks et al. (2008), although we recognize the family Tityridae, including the genera *Schiffornis*, *Pachyramphus*, and *Tityra*, after Barber and Rice (2007).

Statistical analyses

We excluded from the study all Neotropical migrants and wide-ranging waterbirds (e.g., Anseriformes, Pelenicaniformes, Ciconiiformes), although we analyzed several species of tropical waterfowl and herons. Our final list of species included resident breeders at Palenque, species that breed at Palenque and winter farther south, or species that breed near Palenque and occur at the site on a regular basis (e.g., altitudinal migrants). We analyzed data in two ways. For each species, we first conducted a logistic regression (proc logistic; SAS 9.1, SAS Institute, Cary, North Carolina) over 1970–2009. Any species in our baseline data set was marked as present in 1970. Because survey effort was uneven across years, we weighted the score for each year by the ($\log_{10}$) number of species recorded in that year. We chose this weighting instead of the number of field days because species richness will asymptote despite continued field work. When data permitted, we conducted logistic regressions over 1900–2009 to verify trends detected in the shorter-term data set. We could not rely on many apparent 1900–2009 trends, however, because almost all data before 1967 are from specimens—chiefly from 1900 (USNM), 1939 (Brodkorb 1943; UMMZ), 1946 (MLZ), and 1949 (Tashian 1952; FM)—so certain species are grossly under represented; e.g., large raptors, parrots, swifts, and hummingbirds are difficult to collect, meaning an absence in those years meant little about a species’ true status at Palenque. We thus placed greater confidence in the 1970–2009 trends.

For species either with a significant negative trend or that had not been recorded in 10 years, we determined the probability that a species was extirpated at Palenque on the basis of its sighting record (Solow 2005; McInerny et al. 2006). Solow (1993) developed a parametric runs test that can be modified easily to incorporate clumped data, such a multiple sightings within a given year (Burgman et al. 1995). This model assumes a stationary Poisson process. Stochastic count data are modeled well with this process; nevertheless, we preferred the more conservative non-parametric tests based on the jackknife and on Weibull's extreme value distribution (Solow 2005). Regarding the Weibull test, Solow (2005) reported that "this method works reasonably well when k [the number of most recent sightings] is at least five." Accordingly, we chose $k = 6$ for all Weibull tests; if 6 years of record were not available, we conducted only the jackknife test. We likewise estimated time (year) of extirpation using a non-parametric approach (Robson and Whitlock 1964). We calculated results for all tests and estimates in a spreadsheet (Quattro Pro 10, Corel Corporation, Ottawa). Because the jackknife and Weibull tests are conservative, we set α to 0.10; for either test a statistically significant result ($P < 0.10$) means the null hypothesis of not extinct (i.e., no change in status) can be rejected. Both methods work well when sampling effort does not decline over time (Rivadeneira et al. 2009), fitting well sampling effort at Palenque.

For species with a significant positive trend revealed by the logistic regression, we modified ("inverted") the Weibull test to estimate probability of colonization. We used 1950 as an arbitrary start date for these tests because the overwhelming majority (96%) of museum specimens, the principal source of early records, predate 1950. (We note, however, that use of 1970 as a start date does not change statistical outcomes.)

Regardless of approach, the test statistics above assume independence of observations. Given the potential lack of independence of multiple sightings by the same observer within a short time (e.g., a week-long visit), we treated all data as presence–absence within a given year. However, we treated visits in different years, regardless of observer, as independent. We feel that this treatment is appropriate: birders who visit Palenque do so to see tropical species, even if common ones, and there is no "rarity hunting" per se (such as associated with birding hotlines and internet listservs), meaning the same individual birds are unlikely to be reported year-after-year.

Results

Extirpation and decrease

Slightly over 350 species of birds have been recorded at Palenque, of which 240 breed at or near the site. Of the breeders, the status of two-thirds (165) did not change detectably. Of the remaining 75 species, at least 26 of them apparently are extirpated at Palenque (Table 1). For these species, despite near annual effort—data are missing for just 1 year in the past two decades—in each case the species has not been recorded reliably in at least 14 years, and in many cases the last record is far older. Palenque has no specific records for two of these species, the Harpy Eagle and Scarlet Macaw, but each species was widespread in lowland rainforest of southeastern Mexico and was recorded near the site. Each almost certainly occurred historically at Palenque, and E. W. Nelson, in his May 1900 field notes, remarked that the eagle and macaw were "said to occur" in the area.

An additional 20 species have declined significantly at Palenque (Table 2). In some cases the species may be extirpated already, but the statistics are such that we cannot be certain. The Plain-breasted Ground-Dove and Piratic Flycatcher may present exceptions. The former has not been reported at Palenque *per se* since 1993, but it still occurs in nearby tropical savannah (e.g., M. A. Patten pers. obs., 2004, 2006, and 2008) and thus, in our judgement, may yet occur at the site. The latter has not been reported at Palenque since 1983, but it is a low-density summer visitor to southern Mexico that occurs in open forest, savannah, and edge. The majority of birders who visit Palenque do so during winter or early spring, especially from December to mid-March (>50% of post-1983 field days in

Table 1 Species apparently extirpated at Palenque, Chiapas, Mexico. For post-1970 losses, the probability of extirpation was assessed, when possible, with non-parametric Weibull and jackknife tests (Solow 2005)

Scientific name	English name	Probability		Last record	$\hat{T}_E$
		Weibull	Jackknife		
Penelope purpurascens	Crested Guan	–	–	1939	1978
Crax rubra	Great Curassow	–	–	1991	2002
Colinus virginianus	Northern Bobwhite	0.03	0.04	1982	1994
Claravis pretiosa	Blue Ground-Dove	0.03	0.04	1982	1984
Lophornis helenae	Black-crested Coquette	–	0.09	1977	1980
Eupherusa eximia	Stripe-tailed Hummingbird	0.02	0.08	1985	1987
Heliothryx barroti	Purple-crowned Fairy	0.07	–	1992	1994
Notharchus hyperrhynchos	White-necked Puffbird	–	0.07	1984	2001
Malacoptila panamensis	White-whiskered Puffbird	–	0.05	1949	1952
Automolus ochrolaemus	Buff-throated Foliage-gleaner	–	0.06	1993	1994
Microrhopias quixensis	Dot-winged Antwren	0.02	0.04	1982	1984
Pachyramphus cinnamomeus	Cinnamon Becard	–	–	1991	1999
Lipaugus unirufus	Rufous Piha	–	–	1995	1999
Hylophilus ochraceiceps	Tawny-crowned Greenlet	0.02	0.04	1982	1985
Cistothorus platensis	Sedge Wren	–	–	1946	1953
Uropsila leucogastra	White-bellied Wren	0.01	0.04	1983	1984
Microcerculus philomela	Nightingale Wren	0.03	0.04	1984	1985
Turdus assimilis	White-throated Robin	–	–	1983	1993
Granatellus sallaei	Gray-throated Chat	–	–	1946	1953
Eucometis penicillata	Gray-headed Tanager	–	–	1982	1989
Lanio aurantius	Balck-throated Shrike-Tanager	0.05	0.08	1985	1987
Piranga leucoptera	White-winged Tanager	–	0.04	1983	1984
Sicalis luteola	Grassland Yellow-Finch	–	–	1939	1978

No species has been recorded at Palenque in >15 years, a period over which a near-continuous sighting record is available (from 1988 to 2009, data only for 1998 are missing). Two species, the Harpy Eagle (*Harpyia harpyja*) and Scarlet Macaw (*Ara macao*), also likely occurred at Palenque historically, but there are no definite records since ornithological exploration began in May 1900. Estimated year of extinction ($\hat{T}_E$) is from the non-parametric formula of Robson and Whitlock (1964)

our data set), when the Piratic Flycatcher is on its wintering grounds in South America (American Ornithologists' Union 1998). Given its habitat needs and seasonality, we feel the species may still occur despite the dearth of recent records. However, we have been unable to locate the species despite >30 days of field effort in May, June, and July.

Colonization and increase

Several species occur commonly or regularly at Palenque that were unknown in our baseline data (i.e., prior to 1970). We conclude that at least 14 of these species have colonized (Table 3). The Lesser Yellow-headed Vulture has been reported several times in recent years, but it may be too early to state conclusively (i.e., with full statistical confidence) if the species has moved into the area. An additional 16 species have increased markedly at Palenque (Table 4). One of these species, the House Wren, has more likely colonized recently: two collected in March 1946 (MLZ 44121, MLZ 44124) furnished the

Table 2 Species exhibiting a significant ($P < 0.05$) negative trend in occurrence at Palenque, Chiapas, Mexico, on the basis of a presence–absence sighting record from 1970 to 2009

Scientific name	English name	Slope (SE)	Intercept (SE)	r^2
Odontophorus guttatus	Spotted Wood-Quail	−0.072 (0.029)	141.3 (57.4)	0.18
Nyctanassa violacea	Yellow-crowned Night-Heron	−0.098 (0.047)	192.9 (93.9)	0.15
Sarcoramphus papa	King Vulture	−0.051 (0.016)	99.4 (31.9)	0.29
Patagioenas nigrirostris	Short-billed Pigeon	−0.061 (0.023)	121.0 (45.5)	0.20
Columbina minuta	Plain-breasted Ground-Dove	−0.153 (0.037)	303.7 (73.5)	0.55
Hylomanes momotula	Tody Motmot	−0.052 (0.026)	102.7 (52.5)	0.11
Xenops minutus	Plain Xenops	−0.126 (0.037)	248.8 (73.9)	0.38
Leptopogon amaurocephalus	Sepia-capped Flycatcher	−0.107 (0.036)	210.5 (71.6)	0.28
Todirostrum cinereum	Common Tody-Flycatcher	−0.065 (0.024)	128.8 (47.6)	0.21
Platyrinchus cancrominus	Stub-tailed Spadebill	−0.068 (0.026)	134.4 (51.8)	0.19
Legatus leucophaius	Piratic Flycatcher	−0.130 (0.055)	255.9 (108.6)	0.22
Pachyramphus aglaiae	Rose-throated Becard	−0.068 (0.023)	135.0 (45.9)	0.24
Cotinga amabilis	Lovely Cotinga	−0.088 (0.029)	173.6 (58.3)	0.27
Vireolanius pulchellus	Green Shrike-Vireo	−0.064 (0.023)	127.9 (45.3)	0.22
Campylorhynchus zonatus	Band-backed Wren	−0.060 (0.023)	120.0 (45.4)	0.22
Polioptila plumbea	Tropical Gnatcatcher	−0.078 (0.028)	153.9 (54.7)	0.19
Oryzoborus funereus	Thick-billed Seed-Finch	−0.044 (0.022)	86.3 (43.1)	0.11
Molothrus aeneus	Bronzed Cowbird	−0.078 (0.031)	153.8 (62.4)	0.19
Icterus prosthemelas	Black-cowled Oriole	−0.045 (0.022)	89.6 (43.9)	0.12
Icterus mesomelas	Yellow-tailed Oriole	−0.045 (0.022)	89.9 (42.9)	0.12

The approximate r^2 is an indication of the extent that year explains the trend. This list excludes species now extirpated from Palenque (Table 1)

only records for Palenque until 1991, after which it became numerous. We are less sure about the status of two forest or second growth species that apparently have increased (Table 4): neither the Collared Trogon nor the Black-headed Saltator was recorded during any of the extensive collecting trips in 1900, 1939, 1946, or 1949, and neither was reported at Palenque until 1967 (E. P. Edwards). It is possible that both species were overlooked previously; still, both are now common.

We uncovered only a single instance of a species that was either extirpated or had declined markedly but later appeared to recolonize Palenque: the Rufous-tailed Jacamar was detected on each of the major collecting expeditions in the first half of the twentieth century (1900, 1939, 1946, 1949), during which 24 specimens were collected. Thereafter, apart from single records from 1967 (E. P. Edwards) and 1972 (R. A. Rowlett), the species was not detected again until 1990. It is now observed frequently, with records from 15 of the 21 years from 1990 to 2009.

Discussion

Patterns of species loss

Ecological theory predicts that large-bodied species are more prone to extirpation, and this pattern has been documented in birds (Bennett et al. 2005). Accordingly, the loss from

Table 3 Species that apparently have colonized Palenque, Chiapas, Mexico, since 1970

Scientific name	English name	Probability	First record
Dendrocygna autumnalis	Black-bellied Whistling-Duck	0.01	1989
Tigrisoma mexicanum	Bare-throated Tiger-Heron	0.01	2001
Cathartes burrovianus	Lesser Yellow-headed Vulture	–	2004
Buteo brachyurus	Short-tailed Hawk	0.02	1972
Aramus guarauna	Limpkin	0.02	1984
Patagioenas flavirostris	Red-billed Pigeon	0.03	1973
Zenaida asiatica	White-winged Dove	0.05	1984
Nyctibius jamaicensis	Northern Potoo	0.03	1977
Heliomaster longirostris	Long-billed Starthroat	0.01	1992
Picoides scalaris	Ladder-backed Woodpecker	0.01	1979
Thryothorus modestus	Plain Wren	0.02	1991
Mimus gilvus	Tropical Mockingbird	0.03	1983
Sporophila corvina	Variable Seedeater	0.02	1972
Euphonia affinis	Scrub Euphonia	0.01	1981

The probability of colonization was assessed with a modified non-parametric Weibull (see text). A probability for *Cathartes burrovianus* could not be estimated because there are not yet enough data for that species (although it was recorded again as recently as March 2009)

Table 4 Species exhibiting a significant ($P < 0.05$) positive trend in occurrence at Palenque, Chiapas, Mexico, on the basis of a presence–absence sighting record from 1970 to 2009

Scientific name	English name	Slope (SE)	Intercept (SE)	r^2
Buteogallus anthracinus	Common Black-Hawk	0.077 (0.024)	−154.5 (48.6)	0.28
Falco rufigularis	Bat Falcon	0.092 (0.034)	−181.0 (67.7)	0.23
Patagioenas cayennensis	Pale-vented Pigeon	0.083 (0.025)	−164.3 (49.0)	0.31
Pionus senilis	White-crowned Parrot	0.090 (0.028)	−177.6 (55.9)	0.30
Amazona albifrons	White-fronted Parrot	0.097 (0.029)	−191.9 (57.2)	0.33
Campylopterus hemileucurus	Violet Sabrewing	0.072 (0.024)	−143.7 (48.3)	0.25
Anthracothorax prevostii	Green-breasted Mango	0.063 (0.024)	−124.7 (47.6)	0.19
Chlorostilbon canivetii	Canivet's Emerald	0.067 (0.026)	−134.1 (52.7)	0.18
Trogon collaris	Collared Trogon	0.063 (0.030)	−122.6 (59.5)	0.13
Myiarchus tyrannulus	Brown-crested Flycatcher	0.054 (0.023)	−108.3 (44.9)	0.16
Troglodytes aedon	House Wren	0.159 (0.035)	−317.0 (70.1)	0.70
Chlorophanes spiza	Green Honeycreeper	0.071 (0.030)	−139.3 (60.0)	0.16
Cyanerpes cyaneus	Red-legged Honeycreeper	0.122 (0.043)	−240.7 (84.7)	0.29
Saltator atriceps	Black-headed Saltator	0.072 (0.037)	−141.1 (72.5)	0.12
Quiscalus mexicanus	Great-tailed Grackle	0.062 (0.032)	−122.0 (62.5)	0.12
Psarocolius wagleri	Chestnut-headed Oropendola	0.093 (0.027)	−185.1 (52.6)	0.35

The approximate r^2 is an indication of the extent that year explains the trend. This list excludes species that have colonized recently (Table 3)

Palenque of large gamebirds like the Crested Guan and Great Curassow is not surprising. To these species we may add the Northern Bobwhite and, to say nothing of the decline of the Spotted Wood-Quail. Other large-bodied species extirpated from Palenque include the

Harpy Eagle and Scarlet Macaw. The eagle is nearly extirpated from Mexico (Vargas et al. 2006), and macaw populations have been reduced greatly (Wiedenfeld 1994), from many thousands across southern Mexico to perhaps a few hundred now confined to the relatively undisturbed heart of Selva Lacandona. By contrast, we found no evidence that any of three species of tinamous have declined.

Two additional non-random patterns of extirpation or decline appear in the long-term data from Palenque. Many mid-sized frugivores or insectivores of the forest canopy have disappeared or declined, including the Blue Ground-Dove and Short-billed Pigeon, two species of puffbirds (Bucconidae), and the Tody Motmot, Rufous Piha, Cinnamon Becard, Lovely Cotinga, Green Shrike-Vireo, and Black-throated Shrike-Tanager (Tables 1, 2). Some disappearances are particularly striking. Tashian (1952) stated that the White-whiskered Puffbird was "encountered often in the forest understory" and there are seven specimens from the 1940s (MLZ, FM), but there are no records for Palenque since the 1949 excursion. Loss of the Cinnamon Becard is also remarkable, given that both Tashian (1952) and Miller et al. (1957:61) considered this species to be "abundant" at Palenque. A few still occurred in the 1970s, but there are only scattered records in the early 1980s and the species was last observed in 1991. The Lovely Cotinga suffered a similar fate, although one not as final. Although we have not located the specimens, Miller et al. (1957:59) reported that 27 were collected at Palenque in 1936, a remarkable number considering the general furtiveness and scarcity of members of this genus. The species continued to be recorded sporadically through the 1980s, but we know of but a single post-1991 record: an immature male in January 2007 (M. Carmody). Likewise, three calling Tody Motmots in spring 2002 (R. C. Hoyer) provided the only record of the species for the Palenque area since 1991.

The third non-random pattern involves small-bodied insectivores of the forest interior, particularly those species associated with foraging flocks. Judging from historical field notes, foraging flocks were the norm at Palenque through the 1970s but declined thereafter. This decline likely corresponds to loss of the Buff-throated Foliage-gleaner, Dot-winged Antwren, Tawny-crowned Greenlet, and Gray-headed Tanager, each of which joins mixed-species flocks in the understorey. Other groups in the insectivorous guild of the forest interior with a prevalence of extirpations or declines include various wrens (Troglodytidae; see below) and small flycatchers (Tyrannidae), including three small species in subfamilies Elaeniinae (the Sepia-capped Flycatcher) and Platyrinchinae (the Common Tody-Flycatcher and Stub-tailed Spadebill).

The timing of extirpation and colonization is varied (Tables 1, 3); however, some general statements can be made. Regional deforestation began chiefly in the early 1970s (De Jong et al. 2000), in large part coinciding with construction of a paved highway to Ocosingo to the south–southwest, but also because of marked expansion of cattle ranching (Howard 1998). Accordingly, we might predict that faunal turnover became noticeable shortly thereafter. We find preliminary support for this prediction by noting that mean year for colonizations is 1982 and for extirpations is 1981. Similarly, mean inflection points for species exhibiting a significant trend (Tables 2, 4) are 1977 for declining species and 1980 for increasing species. The extent to which any of the declining species will persist is unknown, but given the recency of large-scale disturbance coupled with ongoing deforestation (Fig. 1), it would be surprising if faunal relaxation (Diamond 1972) has run its course. Instead, it is likely that extirpation of forest birds will continue until a new, lower richness is reached, which may take a century (Brooks et al. 1999). Species declining sharply probably will be the next to go, as extirpation tends to follow a period of decline (Foote et al. 2007) rather than occurring abruptly (or rather than a population reaching a new, lower stable level).

Tit for tat

Hummingbirds (Trochilidae) and wrens present interesting instances of species turnover within a family. Three hummingbirds extirpated from Palenque—the Black-crested Coquette, Stripe-tailed Hummingbird, and Purple-crowned Fairy—are forest species, whereas three species that have increased markedly or colonized—the Green-breasted Mango, Canivet's Emerald, and Long-billed Starthroat—occur in savannah or second growth. Thus, in terms of richness the hummingbird community has remained stable, but there has been turnover from forest to savannah species. The wrens repeated this pattern: two forest species, the White-bellied Wren and Nightingale Wren, have disappeared (Table 1), and the Band-backed Wren has declined significantly (Table 2). In their place the Plain Wren and, probably, House Wren have invaded the site (Tables 3, 4); each of these species occurs in open habitats or second growth.

Pigeons and doves (Columbidae) provide another example of intra-familial turnover: forest species have been extirpated (the Blue Ground-Dove) or have declined significantly (the Short-billed Pigeon), whereas three species of open habitats have either colonized (the Red-billed Pigeon and White-winged Dove) or increased markedly (the Pale-vented Pigeon). The Red-billed Pigeon is particularly interesting in that this species is widespread and common in the lowlands of eastern Mexico, but Nelson, in his May 1900 field notes, expressly remarked of this species that none were found "anywhere in the district"; instead, the Pale-vented Pigeon "replaced" it in the Palenque area. The Red-billed Pigeon was first noted at Palenque in 1973, and it is now found there abundantly and presumably breeds.

A further example may be evident within the genus *Leptotila*, phenotypically similar doves found in undergrowth of primary or secondary forest. Although a trend is not apparent since 1970, from 1900 to 2007 the White-tipped Dove (*L. verreauxi*) has increased ($\beta = 0.050$, $r^2 = 0.26$, $P < 0.002$). The species was missed entirely on three of the four historical expeditions (1900, 1939, 1949) and during some extended site visits by experienced observers in the early 1970s. Conversely, the Gray-headed Dove (*L. plumbeiceps*) has held steady, whereas the Gray-chested Dove (*L. cassini*) was observed regularly in the 1970s and 1980s but is noted only sporadically now. The increasing species tolerates disturbance and readily occupies second growth, but the declining species depends on primary forest.

Correlated response?

It may come as a surprise that a cowbird—a brood parasite known to tolerate open habitats and human settlements—is among those species to have declined, but the sighting record for the Bronzed Cowbird suggests just that. In this case there may be a biological explanation. Although this cowbird is modestly generalized in its use of hosts (Rothstein et al. 2002), it is said to preferentially parasitize orioles (Friedmann 1929). Yet both the Black-cowled and Yellow-tailed Orioles, for many years the only two species of orioles known to breed at Palenque, have declined significantly (Table 2). Although data are scarce, the Altamira Oriole (*Icterus gularis*) may be increasing at Palenque ($\beta = 0.110$, $r^2 = 0.24$, $P < 0.01$); however, this species apparently rejects cowbird eggs (Carter 1986), unlike its smaller congeners. It thus may be that with the decline of its favored hosts the Bronzed Cowbird has declined as well.

Habitat associations

A species of wren (the Sedge Wren) and dove (the Plain-breasted Ground-Dove) have disappeared or declined even though each occurs in grassland or savannah, not forest, and the Northern Bobwhite and Grassland Yellow-Finch have also disappeared. These species are exceptions, perhaps because they require relatively undisturbed native grassland or tropical savannah and thus do not tolerate heavily grazed pasture—i.e., bird species that depend on tropical grasslands may face threats similar to those faced by temperate grasslands (see Vickery et al. 1999).

In general, however, as noted above species that occur in open habitats have increased or colonized Palenque at the expense of species dependent on forested habitats (Fig. 3). The loss of tropical rainforest—the trading of forest for field—has led to a concomitant pattern of species occurrence at the site. Species such as the Red-billed Pigeon, White-winged Dove, Ladder-backed Woodpecker, Tropical Mockingbird, and Scrub Euphonia, exemplify the tendency for open-country species to colonize, as does the potential on-going colonization by the Lesser Yellow-headed Vulture, a species essentially confined to tropical savannah in Mexico (Howell and Webb 1995).

Species lost or declining are, by contrast, birds of the forest. As noted above, losses tend to fall in three general categories: large-bodied forest species, mid-sized frugivores of the canopy or heavy forest, and small-bodied insectivores of the forest interior, particularly species that occur in mixed-species flocks. Although the species involved may not be the same, these same patterns have been detected in studies conducted elsewhere in Middle America (Estrada et al. 1997; Robinson 2001; Sigel et al. 2006). Among shared species, for example, the Short-billed Pigeon, Rufous Piha, and Green Shrike-Vireo were among the species that have declined sharply at Barro Colorado Island, Panama (Robinson 2001), as did a coquette, two puffbirds, and a becard. Likewise, Sigel et al. (2006) reported declines

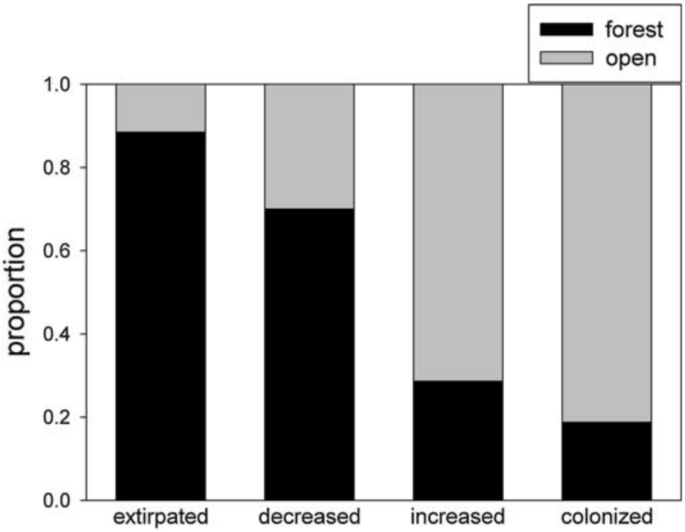

Fig. 3 Turnover of the avifauna at Palenque, Chiapas, Mexico, 1900–2009, with respect to broad habitat type. Species that are extirpated or have decreased are those dependent of forest, whereas species that have increased or colonized occur in open habitat such as tropical savannah and scrubby second growth

or disappearances of the White-whiskered Puffbird, Dot-winged Antwren, Green Shrike-Vireo, and Band-backed Wren at La Selva, Costa Rica.

Constructing a sighting record

Tapping into the vast wealth of data kept by birders and field ornithologists is not only possible but relatively straightforward in the internet age. Numerous newsletters, listservs, and on-line groups are available for requesting information, and many birders are happy to share. Additional sites need to be tackled; for example, some sites in the northern Neotropics visited frequently by birders include Tikal in Guatemala, Chan Chich in Belize, and Copán in Honduras. As we have shown, the effort will be worthwhile and resultant data will be amenable to statistical analyses; however, data compilation is time consuming and can be frustrating.

A better long-term solution would be to establish a sighting database. In the Neotropics that could be accomplished best under the auspices of the Organization for Tropical Studies, Smithsonian Tropical Research Institute, or other party or parties. Such a database could be modeled after the one maintained by Birds Australia, which compiles a vast store of presence–absence data across the country for use in trend analyses (see Cunningham and Olsen 2009). We envision such a database storing information from any persons willing to submit notes, whether historical or current. At the outset, the effort would require proper advertising to make people aware of the database’s existence and importance, and perhaps a small incentive could be offered to encourage contribution. Over time, the database would need regular upkeep and would need a system of vetting unusual or questionable reports. The latter would require administrators familiar enough with avian status and distribution in the Neotropics to recognize and flag such reports and request additional documentation where appropriate. For example, eBird may provide an existing platform for amassing such data. As it stands, however, on the basis of our making use of Palenque data in this burgeoning on-line archive, it is evident that a great deal of vetting will be necessary if eBird data are to be incorporated into a study—there are numerous misidentifications. In any event, the database we envision would also require a substantial “start up” effort to compile and enter historical records from museums and older field notes. Once a sufficient amount of data were archived, researchers could access these data to examine trends at a particular site or to compare status changes within a species across sites. In effect, the end product would be a database akin to GenBank but for species rather than genes.

We emphasize that this sort of study is hardly limited to birds given that, for example, butterfly and herpetile enthusiasts abound, and even mammals, dragonflies, and ferns could be tracked, in some areas, given the attention they receive from naturalists and tour groups. Moreover, in advocating a sighting database we do not mean to imply that “casual” sightings are a substitute for long-term, well-planned censuses, which are much more likely to be amenable to more robust statistical analyses (e.g., see Chap. 4 of MacKenzie et al. 2006). But for many locations a sighting record is all we have. We argue that it is better to make use of imperfect data—particularly in this age of the biodiversity crisis—than to await the perfect study or, worse, proceed as if no data exist.

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