

Decadal changes and delayed avian species losses due to deforestation in the northern Neotropics

How avifauna respond to the long-term loss and fragmentation of tropical forests is a critical issue in biodiversity management. We use data from over 30 years to gain insights into such changes in the northernmost Neotropical rainforest in the Sierra de Los Tuxtlas of southern Veracruz, Mexico. This region has been extensively deforested over the past half-century. The Estación de Biología Tropical Los Tuxtlas, of the Universidad Nacional Autónoma de México (UNAM), protects a 640 ha tract of lowland forest. It became relatively isolated from other forested tracts between 1975 and 1985, but it retains a corridor of forest to more extensive forests at higher elevations on Volcán San Martín. Most deforestation in this area occurred during the 1970s and early 1980s. Forest birds were sampled on the station and surrounding areas using mist nets during eight non-breeding seasons from 1973 to 2004 (though in some seasons netting extended into the local breeding season for some species). Our data suggested extirpations or declines in 12 species of birds subject to capture in mist nets. Six of the eight species no longer present were captured in 1992-95, but not in 2003-2004. Presence/absence data from netting and observational data suggested that another four low-density species also disappeared since sampling began. This indicates a substantial time lag between the loss of habitat and the apparent extirpation of these species. Delayed species loss and the heterogeneous nature of the species affected will be important factors in tropical forest management and conservation.

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2 David W. Shaw^{1,2}, Patricia Escalante³, John H. Rappole⁴, Mario A. Ramos⁵,
3 Richard J. Oehlenschläger⁶, Dwain W. Warner⁵, and Kevin Winker¹

4

5 ¹University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775 USA.

6

7 ²Current Address: 1540 Jones Road, Fairbanks Alaska 99709 USA.

8

9 ³Colección Nacional de Aves, Instituto de Biología, Universidad Nacional Autónoma de
10 México, Circuito Exterior s/n, Ciudad Universitaria, Copilco, Coyoacan, A. P. 70-233
11 Mexico, Distrito Federal. C. P. 14510 MEXICO.

12

13 ⁴Smithsonian's National Zoological Park, Conservation and Research Center, 1500
14 Remount Road, Front Royal, VA 22630 USA.

15

16 ⁵Deceased.

17

18 ⁶Science Museum of Minnesota, 120 W. Kellogg Blvd. St. Paul, MN 55102 USA.

19

20 Corresponding Author:

21 Kevin Winker

22 University of Alaska Museum

23 907 Yukon Drive

24 Fairbanks, AK 99775

25 kevin.winker@alaska.edu

26 907-474-7027

27

INTRODUCTION

Deforestation is one of the main threats to biodiversity conservation. Forest loss and fragmentation have caused declines or local extinctions among animal species at many locations (Turner, 1996; Fahrig, 2003; Dirzo & Raven, 2003). Local population declines and extirpations may be the most important leading indicators of biodiversity loss (Ceballos & Ehrlich, 2002; O'Grady et al., 2004). Bird losses have been documented in many forest systems (e.g., Willis, 1974, 1979; Leck, 1979; Karr, 1982; Bierregaard & Lovejoy, 1989; Kattan, Halvarez-Lopez, & Giraldo, 1994; Robinson, 1999; Sodhi, Liow, & Bazzaz, 2004; Ferraz et al., 2007; Patten, Gómez de Silva, & Smith-Patten, 2010; Laurance et al., 2011). Perhaps nowhere has this phenomenon been more noticeable than among tropical forests, where species losses have been documented in numerous taxonomic groups (e.g., Zimmerman & Bierregaard, 1986; Powell & Powell, 1987; Malcolm, 1988; Pahl, Winter, & Heinsohn 1988; Becker, Moure, & Peralta, 1991; Daily & Ehrlich, 1995; Brook, Sodhi, & Ng, 2003, Dirzo & Raven, 2003, Stuart et al. 2004; Robinson & Sherry, 2012). Species losses can occur at the landscape or patch levels and depend on the intensity of the change in forest cover, the distance to and size of other forest fragments, shape and size of the fragment, and other factors (Robbins, 1980; Lovejoy et al., 1984, 1986, Rolstad, 1991; Andrén, 1994; Faaborg et al., 1995; Lees & Peres, 2006; Barlow et al., 2006; Patten & Smith-Patten, 2011; Robinson & Sherry 2012). Tropical forest species, which often occur in small, low-density populations, may be particularly vulnerable to extirpation (Terborgh & Winter 1980; Pimm, Jones, & Diamond, 1988; Stotz et al., 1996).

Relatively few studies have assessed changes through decades, however (Ewers & Didham, 2006). And although deforestation and fragmentation can occur over a short period, some time may pass before species begin to disappear from an affected area

(Leigh, 1975, 1981; Karr, 1982, Tilman et al., 1994; Brooks, Pimm, & Oyugi, 1999). Thus, to fully document the impact of deforestation on a forest community, a site must be studied for a substantial period of time after habitat alteration has occurred. Detailing the process of local population decline and extirpation over time provides invaluable information about species' abilities to cope with habitat fragmentation. It also informs us about how community composition itself may be resistant to change, its degree of resilience following change, and how or if it stabilizes following this disturbance.

Studies of species losses in birds have used a variety of methods, including comparing species richness in different-sized fragments (Willis, 1979; Nemark, 1991; Blake, 1991), comparison of species composition at a site pre- and post-fragmentation (Willis, 1974; Leck, 1979; Bierregaard & Lovejoy, 1989; Kattan, 1994; Patten & Smith-Patten, 2011), and experimental fragmentation (Lovejoy et al., 1986; Bierregaard & Lovejoy, 1988, 1989; Ferraz et al., 2003, 2007; Laurance et al., 2011), and have often included scattered survey data prior to fragmentation (Willis, 1974; Leck, 1979; Kattan, Halvarez-Lopez, & Giraldo, 1994; Robinson, 1999; Patten, Gómez de Silva, & Smith-Patten, 2010; Patten & Smith-Patten, 2011). Many of these studies have relied on qualitative visual and audio survey techniques, with multiple observers, though such techniques can allow cryptic and low-density species to be overlooked (Whitman, Hagan, & Brokaw, 1997). Additionally, observer skills and intensity of sampling may vary among surveys.

Mist netting offers the most consistent and quantitative method available to sample birds among years (Rappole, Winker, & Powell, 1998). However, mist nets have documented weaknesses; the most relevant is the limited stratum and size of birds they can effectively sample (Remsen & Good, 1996; Whitman, Hagan, & Brokaw, 1997; Rappole, Winker, & Powell, 1998). This is particularly noticeable in structurally diverse

habitats such as tropical rainforests, where probability of detection using mist nets is unknown for most species. Mist net studies in the Neotropics are therefore biased toward understory, small- to mid-sized passerines. While mist nets, unlike other methods, are less prone to observer bias and variability, we augmented our analyses of netting data that suggested species losses with presence-absence observational data (daily checklists in later years); this becomes particularly important for low-density species and for those not readily captured.

The Sierra de Los Tuxtlas of southern Veracruz, Mexico provides a textbook case of deforestation. This small range of volcanic mountains is home to the northernmost Neotropical rainforest (Pennington & Sarukhan, 1968; Dirzo & Miranda, 1991). The region has lost more than 90% of its forests in the past century, with the majority of that loss occurring in the lowlands over the past fifty years (Dirzo & Garcia, 1992; Rappole, Powell, and Sader, 1994; Winker, 1997). Our study compares eight seasons of mist net sampling from Los Tuxtlas over the course of more than thirty years. This allows us to at least partly answer the question of how species composition and relative abundance changed in and around a conserved core of local rainforest habitat on a decadal scale.

METHODS

The Sierra de Los Tuxtlas is located in southern Veracruz, Mexico, 90 km southeast of Veracruz city. This range of mountains lies in the northwestern portion of the Isthmus of Tehuantepec and is isolated from the Sierra Madre Oriental by extensive lowlands. Los Tuxtlas encompass approximately 4,200 km², and the range is dominated by Volcán San Martín and Volcán Santa Marta, each reaching more than 1,500 m elevation. The Gulf of Mexico lies a short distance from the mountains to the north and east. The northernmost Neotropical evergreen rainforest formerly dominated the habitat in the region (Andrle, 1966; Pennington & Sarukhan, 1968; Dirzo & Miranda, 1991), but

due to deforestation it is now a mosaic with a high percentage of pasture, cropland, fencerows, and isolated trees (pers. obs.; Dirzo & Garcia 1992; Estrada, Coates-Estrada, & Merritt 1997). Andrie (1966) estimated that 50% of the region was forested in 1962. By 1975 Rappole & Warner (1980) estimated that a third of the forests still stood. Just 15% of forest remained in 1986 (Winker, Rappole, & Ramos, 1990; Dirzo & Garcia, 1992), and in 1994 only 7-10% of the region was forested (Winker, 1997). Remaining forest occurs primarily in the highlands, and below 500 m forest is scarce (Rappole, Powell, & Sader, 1994; Mendoza, Fay, & Dirzo, 2005; Figs. 1, 2, S1).

The climate in Los Tuxtlas is warm and wet, with a mean annual temperature of 25 C, and annual precipitation is 4,500-4,900 mm, with a short dry season from March-May (Soto & Gama 1997). Canopy heights in primary forest range from 30-35 m (Ibarra-Manriquez et al., 1997). Second growth areas generally have variable canopy heights from 3-20 m (pers. obs.).

In 1967 the Universidad Nacional Autónoma de México established the Estación de Biología Los Tuxtlas, protecting a 640-ha tract of lowland rainforest (González-Soriano, Dirzo, & Vogt, 1997). Over the following decades this site became largely isolated from other tracts of forest, although a corridor of forest remains, connecting to the more extensive upland forests on Volcán San Martín (Dirzo & Garcia, 1992; Fig. 2). The first intensive sampling of birds in the region began in 1973, and data from that effort are included here (see Winker, 1997).

During the non-breeding seasons of 1973-74 and 1974-75 Oehlenschläger, Ramos, Rappole, and Warner conducted the first intensive mist-netting efforts in the area. Sites extended through what was then contiguous rainforest from the biological station eastward to the coast (Fig. 3). In 1986, Rappole, Ramos, and Winker operated mist nets at the biological station, and Winker and Escalante continued work there from 1992 to

1994. In 2003-04 as part of a study of migrant birds, Shaw operated mist nets at the same location as Winker and Escalante's work in the 1990s. This study was approved by the University of Alaska Fairbanks IACUC (approval numbers: #00-33 & #04-03). Fieldwork occurred primarily during the non-breeding season. Effort was made to equally sample the available forest types throughout the study period, although, in order to do this, habitat changes precluded using the same sites across all years (see Winker 1995; Fig. 3). Field effort as gauged by net hours also varied among years (Table 1).

Our earliest sampling occurred over a wider area than later seasons (Fig. 3). During the earliest sampling, large tracts of contiguous forest consisting of various microhabitats dominated the region and were sampled accordingly (Fig. 3). This broader expanse of forest likely provided habitat to more species than the current distribution of forest. This increased detection probabilities for some species such as *Schiffornis turdina*, which was rare even during our earliest sampling. Two general types of forest were present after fragmentation: primary forest and acahual (second growth). Because our sampling was forest-oriented, our efforts tracked the distribution of these habitats. Primary rainforest and second growth habitats were sampled in all efforts. We were unable to separate capture data by site for the early sampling periods; our findings therefore include data from the somewhat larger area from the station east to the coast. Our sampling was also uneven with respect to season, with wet and dry season sampling being unevenly distributed among years; we attempt to account for this, especially in relation to seasonal movements, when considering the results. This sampling heterogeneity leads us to be cautious and conservative in our analyses and interpretations. Importantly, however, the same site (18° 34'50"N, 95° 04'20"W) and net lanes were used in the 1992-2004 efforts (sample periods 4-8 in Table 1).

Only resident species were used in our analyses due to seasonal migration and the

high levels of variance in abundance this causes among obligate migrants. Changes in relative abundance were detected by comparing capture rates (birds per 1000 net hours) from each year of sampling. Through visual inspection of data (Appendix) we chose species absent in later samples and those with trends of apparently declining or increasing rates of capture for more detailed analyses. Neither gaps nor monotonic changes were necessary for inclusion, just suggestion of a possible trend. We did this instead of applying statistical tests across all 122 species to minimize Type I and Type II errors either by applying a very large number of tests or a conservative correction (e.g., Bonferroni). Presence/absence patterns and observational data (daily checklists in later years) were also considered to provide insight into changes in abundance in low-density species that did not have sufficient samples for statistical testing. Species were considered for examination for presence/absence if they had not been captured since at least 1986-87. Vagrants, defined as those rarely encountered species whose ranges do not normally include the Sierra de Los Tuxtlas, were excluded (Winker et al., 1992; Howell & Webb, 1995). Only first-time captures (within a season) were used in statistical analyses. Ordinary least squares regression was used to detect changes in abundance for selected species. We looked for newly appearing species using presence/absence netting, observational, and specimen data. Daily checklists were used to augment mist-net data as a check to determine whether absence from the mist-net data was indicative of reality.

Species showing statistically significant declines and those not captured or observed in later sampling periods were categorized by preferred habitat (edge, forest, or semi-open), food preference (fruit/nectar or insects), elevational range, and whether Los Tuxtlas was at the periphery or core of its geographic range (Howell & Webb, 1995). These characteristics were used to assess whether certain traits of the species increased their vulnerability to local extirpation.

178 RESULTS

179 During this study we accumulated 165,083 net hours, equivalent to 37.7 net years
 180 if netting with a single net occurred twelve hours per day (Table 1). A species
 181 accumulation curve for a representative year (1992) with below-average net hours
 182 (12,605; mean = 20,220) showed that the avifauna was effectively fully sampled during
 183 most field seasons (Fig. S2, though in documenting a species' absence it is the among-
 184 season, aggregate sampling that is important). In total, 122 nonmigratory species were
 185 captured (Appendix).

186 Seven species showed statistically significant declines during the sampling period:
 187 *Phaethornis striigularis*, *Xenops minutus*, *Glyphorhynchus spirurus*, *Onychorhynchus*
 188 *coronatus*, *Myiobius sulphureipygius*, *Henicorhina leucosticta*, and *Eucometis*
 189 *penicillata* (Table 2). Of these taxa, four were captured throughout the sampling period:
 190 *P. striigularis*, *X. minutus*, *E. penicillata*, and *H. leucosticta*. *G. spirurus* was last
 191 captured in 1975, *O. coronatus* in 1986, and *M. sulphureipygius* in 1994, the last season
 192 of autumn netting. Four other species were captured in substantial numbers during early
 193 sampling periods but were not captured in later years: *Lepidocolaptes souleyetii*,
 194 *Ornithion semiflavum*, *Leptopogon amaurocephalus*, and *Coereba flaveola* (the latter
 195 may be an intratropical migrant in this region; Ramos, 1983); however, these species
 196 failed to show statistically significant declines in linear regression analyses, perhaps due
 197 to nonlinear declines. *L. souleyetii* was last captured in 1993-94, and the others were last
 198 captured in 1994-95. One species, *Hylomanes momotula*, was captured from 1986-1995
 199 but not in the 1970s or in 2003-04. Though there were no captures in the 1970s, one
 200 individual was collected on 17 May 1974 a few km northeast of the station. A similar
 201 pattern occurred in *Anabacerthia variegaticeps*, with captures occurring only in the
 202 1990s. Only two species (*Trogon collaris* and *Xiphorhynchus flavigaster*) showed

significant increases during the study period.

Presence/absence mist-net capture data for low-density species not captured after 1986-87 could be interpreted as suggesting that an additional 23 taxa were extirpated during the study (Table 3). However, we know from observational data that not all of these species were absent. These taxa included rarely captured species that are too large for effective mist-net capture or that prefer the forest canopy (e.g., *Micrastur ruficollis*, *Cotinga amabilis*), mixed/open habitat specialists (e.g., *Thraupis abbas* and *T. episcopus*), a small-stream specialist (*Chloroceryle aenea*), and highland species (e.g., *Myadestes unicolor*) that are either not prone to capture in mist nets or at our site. Species such as *Tityra inquisitor*, both *Thraupis* tanagers, and others were known to be present on the site or nearby but were not captured in later sampling periods. Four species of hummingbirds are included in Table 3, but due to inconsistent capture probabilities of low-density hummingbird species and non-definitive observational data with respect to accurate identification, we provide no hypotheses regarding their possible extirpation or persistence at the site; further work focusing on these species is warranted. There were six other species not in Tables 2 or 3 in which mist net data alone might suggest declines or absences (Appendix) during the entire study but which were present throughout from observational data; netting is not an effective sampling tool for these taxa because of body size or forest stratum occupied (e.g., *Glaucidium brasilianum*, *Ciccaba virgata*, and *Celeus castaneus*) or because forest understory is not preferred habitat (e.g., *Pitangus sulphuratus*, *Myiozetetes similis*, and *Volatinia jacarina*; Appendix). The first three of these species require more focused study to determine abundances and possible declines.

Four lower-density species have likely been extirpated: *Taraba major*, *Formicarius analis*, *Grallaria guatemalensis*, and *Schiffornis turdina* (Table 3). One

low-density species that might seem to have been extirpated from our data, *Elaenia flavogaster*, is likely an intratropical migrant here (pers. obs.; Howell & Webb, 1995; Table 3). Several species were captured only in later sampling periods (Appendix) but were observed or collected throughout, suggesting that there were no additions to the biological station's resident avifauna during the study.

Based on all available data during the study (netting and observational data), a minimum of 11 species of birds appear to have been extirpated from the biological station over the past three decades. This translates into an average loss of 3.7 species per decade or a local loss of 2.0% of the entire Los Tuxtlas avifauna (561 spp.; Schaldach & Escalante, 1997), 4.1% of the resident avifauna (269 spp.; Schaldach & Escalante, 1997), or 9.0% of the resident species captured in our study (122 spp.; Appendix). All 16 species showing significant declines or no longer present on the site prefer some degree of forest cover (Table 4). Three species are edge specialists: *O. semiflavum*, *O. mexicanus*, and *C. flaveola*. Eleven prefer closed canopy forest: *P. striigularis*, *H. momotula*, *X. minutus*, *G. spirurus*, *F. analis*, *G. guatemalensis*, *L. amaurocephalus*, *M. sulphureipygius*, *S. turdina*, *H. leucosticta*, and *E. penicillata*. *T. major* prefers primary forest edge, second growth, and riparian thickets, while *L. souleyetii* prefers semi-open or partly cleared forest.

Eleven of 16, or 68.8%, of the species showing declines or extirpations in this study are insectivores, whereas among all species captured 41% are insectivores. This trend was not significant, however (*G*-test with Williams' correction, $P > 0.1$).

The Sierra de Los Tuxtlas is the northernmost limit of the ranges of 13 of the 16 species showing declines. *G. guatemalensis* and *H. leucosticta* are the only species with a distribution extending substantially to the north and west of the study site. The field site is well within the elevational limits for all 16 species (Table 4).

The two species that significantly increased in abundance over the sample period (Table 4) both occur here at the core of their ranges, elevational distributions, and in their preferred forest habitat. *T. collaris* is a frugivore, and *X. flavigaster* is an insectivore.

DISCUSSION

Although the absence of a species is not a clear indication of extirpation, our sampling effort, despite its heterogeneity, does suggest that at minimum a species' absence indicates a decline. It is possible that some of the species now apparently gone from the station may persist in other, unsampled fragments. If the data presented here and our interpretations of them are accurate, the extirpation of species from the Estación de Biología Los Tuxtlas has been ongoing since its isolation. Such an "extinction debt" is a recognized component of deforestation, and models of empirical data show that in birds this occurs across decades, but the species affected and the mechanisms of species loss remain poorly understood (Tilman et al., 1994; Ewers & Didham, 2003, Robinson & Sherry, 2012). Since 1973, 16 species susceptible to capture in mist nets have either become locally extirpated or are showing significant declines in abundance. The total number of losses and declines is undoubtedly higher than presented, because species not regularly captured in mist nets, such as large-bodied and canopy species, were not adequately surveyed. Species known to have been extirpated from Los Tuxtlas include *Sarcoramphus papa*, *Harpia harpyja*, and *Ara macao*. Patten, Gómez de Silva, & Smith-Patten (2010) also documented the extirpation of the latter two in Chiapas, Mexico. Many additional species have also been categorized as endangered or threatened in the Sierra de Los Tuxtlas (see Winker, 1997).

Our estimate of the average rate of avian losses from the station of 3.7 species per decade may not be directly comparable to other studies due to differences in habitat and

sampling, but it is similar to the rate of loss observed at Barro Colorado Island by Robinson (1999) of 3.3 species per decade. Our estimate, however, includes only those taxa captured in mist nets, whereas Robinson's work included all species detected through observation.

Of the eight species with data sufficient for statistical analysis that showed local extirpation, six were lost between 1992 and 2004 (on the same site), suggesting a continuing extirpation of species from the station. Bierregaard & Lovejoy (1988, 1989) found that as surrounding habitat was lost, species richness in remaining fragments increased as individuals displaced from surrounding areas found their way to remaining forest patches. This increased richness was limited by the lifespan of the individual birds (Bierregaard & Lovejoy 1988, 1989). Unlike these studies, in which forest patches were suddenly and completely isolated, the forest of the Estación de Biología Los Tuxtlas was isolated gradually. Because extirpation seems to be continuing, we expect declines and extirpations to continue for some time at the station, even if no further deforestation occurs in the region (Willis, 1974; Brooks, Pimm, & Oyugi, 1999, Robinson, 1999; Ferraz et al., 2003).

Mechanisms for tropical bird species losses due to deforestation and fragmentation probably include factors such as greater specialization as compared to temperate birds, reduced dispersal abilities, lower population densities, and patchy distributions (Robinson et al., 2004; Stratford & Robinson, 2005; Moore et al., 2008; Rompré et al., 2007). Our assessment of possible causes for the loss of these species reveals no definite patterns, however, other than the predominant requirement of forested habitat. On Barro Colorado Island in Lake Gatún, Panama, maturation of habitat and loss of open areas was responsible for the decline in the island's avifauna (Willis, 1974; Karr, 1982). This is unlikely to be the case in Los Tuxtlas. Despite major

degradation of surrounding forests, the station has remained primary forest with areas of second growth. A loss of sapling and seedling species has been described (Dirzo & Miranda, 1990), but the overall structure of the forest appears to have remained fairly stable. Vetter et al. (2011) found in a meta-analysis of 30 studies that the effects of fragmentation are not subject to simple generalities, and that they are highly site specific. Patten & Smith-Patten (2011) pointed to the need to understand extirpations at local scales because responses can differ from predictions made at larger scales.

Los Tuxtlas is at the northernmost extent of the ranges of 13 of the 16 species we found to be declining or extirpated (Tables 3 and 4). Evidence is mixed as to whether populations at the periphery of a species' range are more vulnerable to extirpation (Terborgh & Winter, 1980; Kattan, Halvarez-Lopez, & Giraldo, 1994; Johnson, 1998). Los Tuxtlas is at the edge of all species' geographic ranges endemic to Neotropical rainforest, so it is not clear why this subset might be more subject to this phenomenon. The elevational distribution of each of these species encompasses sea level to 750 m or more (Howell & Webb, 1995), and we consider this factor unlikely to be responsible for the vulnerability of these particular taxa.

Although insectivores showed a trend toward being disproportionately affected in our study, it was not significant. Elsewhere insectivores have been shown to be particularly vulnerable to severe habitat change (e.g., Kattan, Halvarez-Lopez, & Giraldo, 1994; Canaday, 1996; Johnson & Winker, 2010; Vetter et al., 2011). Additionally, deforestation can negatively impact species found in multi-species foraging flocks (Van Houtan et al., 2006), which are important to many birds of tropical rainforest communities (Willis, 1966; Morton, 1973; Buskirk, 1976; Rappole et al., 1983). Rappole & Morton (1985) noted that *X. minutus*, one of the species showing a significant decline in our study (Table 2) was a regular member of mixed flocks in the Sierra de Los Tuxtlas.

We considered large-scale range shifts, perhaps from climate change, as a possible cause for species loss, but this seems unlikely. At least some of the species lost in our study appear to have persisted in the southern portion of Los Tuxtlas near Volcán Santa Marta at least into the mid-1990s (Winker, pers. obs.). If range shifts were the cause, species would likely have disappeared region-wide and we would not expect only forest-related species to be affected. Habitat loss and degradation seem to be the best explanations for the losses observed, but exactly how these changes affected each species remains unknown.

Another possible influence on mist-net captures, particularly in the most recent, late winter/spring sampling periods, would be seasonal intra-tropical and elevational movements in some of the study species (Ramos, 1983, 1988). There is evidence that *C. flaveola* and *E. flavogaster* move seasonally within the tropics, seemingly to breed in Los Tuxtlas then departing (Ramos & Rappole, pers. obs.). Vega Rivera (1982) found probable elevational movements in *M. sulphureipygius*. The extirpations of seven of the 16 species are particularly notable. *C. flaveola* is a widely distributed species known to thrive in manipulated habitats such as gardens and forest edges and is a generalist frugivore and nectarivore (pers. obs.; Howell & Webb, 1995). This is not a species we would expect to decline due to forest fragmentation; both its habitat and food preferences are well suited to survival in a mosaic landscape, and it is known to persist in a fragmented landscape elsewhere in northern Middle America (Johnson & Winker, 2010). Intratropical migrations of *C. flaveola* may partially explain the changing capture rates in this species (Ramos & Rappole, pers. obs.). *O. semiflavum* and *L. amaurocephalus* are both edge specialists; thus, limited fragmentation, creating an increase in edges, might *a priori* seem to benefit these species. Though the habitat protected by the station has remained relatively static, the intensity of lowland

353 deforestation in Los Tuxtlas as a whole (Fig. 1) may be too extensive even for these edge
 354 specialists. *L. souleyetii* prefers open forest and partially cleared areas (Howell & Webb,
 355 1995). The habitat surrounding the station during the 1980s and 1990s was dominated
 356 by pasture scattered with isolated trees. In our later field seasons there was a noticeable
 357 decline in the number of isolated trees and fences constructed of living trees (Winker,
 358 pers. obs.). This loss may account for the extirpation of *L. souleyetii*. *G. spirurus*
 359 apparently disappeared from the station between the 1970s and 1986, the first of the
 360 documented extirpations. The majority of deforestation across the region took place
 361 during this period. This previously abundant species disappeared from our data in just
 362 over a decade. Interestingly, on the slopes of neighboring Volcán Santa Marta the species
 363 was present at least into the 1990s and probably still persists there (Winker, pers. obs.).
 364 Also, Estrada, Coates-Estrada, & Merritt (1997) had observational data of the species'
 365 presence in the station area in 1990-1992, indicating at least a decline if not extirpation
 366 (Table 2). In Brazil, *G. spirurus* persisted in experimentally isolated fragments well after
 367 isolation (Stouffer & Bierregaard 1995), and the species persists in highly fragmented
 368 forest in southern Belize (Johnson & Winker, 2010). *H. momotula* was collected but not
 369 netted in 1974, was captured in substantial numbers during 1986 and 1992-94, but was
 370 absent in the last two seasons of sampling. This pattern is mysterious. This species has
 371 an elevational range extending to 1500 m and may persist in the forests of the upper
 372 slopes of Volcán San Martín. If so, we speculate that the station may serve as a sink for
 373 this species, where habitat is insufficient for a self-sustaining population but may
 374 occasionally be colonized by dispersing individuals (see also Winker et al., 1997).
 375 Continued sampling may provide more insight into its abundance patterns. It illustrates
 376 the need for improved understanding of species-specific dispersal behavior within and
 377 among forest fragments (e.g., Van Houtan et al., 2007; Moore et al., 2008; Ibarra-

Macias, Robinson, & Gaines 2011), which may be an important driver for patterns such as those we observed.

Two other studies provide comparative value to our results. The four species we consider likely extirpated (*Taraba major*, *Formicarius analis*, *Grallaria guatemalensis*, and *Schiffornis turdina*) were not detected in the much broader census surveys of Estrada, Coates-Estrada, & Merritt (1997) in 1990-1992. Patten, Gómez de Silva, & Smith-Patten (2010) conducted the geographically closest long-term study to ours in their analysis of avian declines at Palenque, Chiapas, Mexico. Their results showed only three species that overlapped our results. They found *Eucometis penicillata* extirpated (to our decline) and two others that declined as our populations did (*Xenops minutus* and *Leptopogon amaurocephalus*). Indeed, the species-level heterogeneity between our studies is noteworthy. A key similarity between our studies, however, is the importance of forest in explaining declines and extirpations (Patten & Smith-Patten, 2011).

Our analyses suggest that the Estación de Biología Tropical Los Tuxtlas is too small to maintain its full, historic complement of bird species. If deforestation accelerated region-wide, eliminating other forest refugia, the station alone (640 ha) would be unable to maintain the historical avian diversity of the region or to provide source populations for restored forest habitats for many of its present bird species. Given the scale of deforestation in the region, it is surprising that there are not more species showing declines. Indeed, we may consider it good news that important forest seed dispersers such as *Habia* tanagers (Puebla & Winker, 2004) did not show significant declines. The overall size of the remaining forests, particularly in the highlands, may be ameliorating the effects of lowland deforestation. However, increasing or continued isolation of the station will probably limit recolonization from elsewhere, and species losses will likely continue.

In our study, although several species seemed to quickly succumb to local and regional deforestation, others showed delayed declines and extirpations, a phenomenon also known to happen at larger scales (Tilman et al., 1994, Pimm et al., 2006). Moreover, the effects of deforestation were remarkably heterogeneous among forest-related species, with no single clear pattern of why some species experienced declines or extirpation. Our long-term data suggest that predicting which species will be most affected by deforestation in the northern Neotropics, and thus effectively working to ameliorate the effects of forest loss, will be particularly challenging. Nevertheless, as similar long-term datasets accrue, subtle patterns may reveal how species-specific responses reflect underlying commonalities that can be exploited for effective management and conservation.

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LITERATURE CITED

- Andrén H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355-366.
- Andrle RF. 1966. North American migrants in the Sierra de Tuxtla of southern Veracruz, Mexico. *Condor* 68:177-184.
- Barlow J, Peres CA, Henriques LMP, Stouffer PC, Wunderle JM. 2006. The responses of understorey birds to forest fragmentation, logging and wildfires: An Amazonian synthesis. *Biological Conservation* 128:182-192.
- Becker P, Moure JS, Peralta FJA. 1991. More about euglossine bees in

- 428 Amazonian forest fragments. *Biotropica* 23:586-591.
- 429 Bierregaard RO, Lovejoy TE. 1988. Birds in Amazonian forest fragments: Effects of
430 insularization. Pages 1564-1579 in: *Acta XIX Congressus Internationalis*
431 *Ornithologici* (H. Oellet, ed.). University of Ottawa Press, Ottawa, Canada.
- 432 Bierregaard RO, Lovejoy TE. 1989. Effects of forest fragmentation on Amazonian
433 understory bird communities. *Acta Amazonica* 19:215-241.
- 434 Blake JG. 1991. Nested subsets and the distribution of birds in isolated woodlots.
435 *Conservation Biology* 5:58-86.
- 436 Brook BW, Sodhi NS, Ng PKL. 2003. Catastrophic extinctions follow deforestation in
437 Singapore. *Nature* 424:420-423.
- 438 Brooks TM, Pimm SL, Oyugi JO. 1999. Time lag between deforestation and bird
439 extinction in tropical forest fragments. *Conservation Biology* 13:1140-1150.
- 440 Buskirk WH. 1976. Social systems in a tropical forest avifauna. *American Naturalist*
441 110:293-310.
- 442 Canaday C. 1996. Loss of insectivorous birds among a gradient of human impact in
443 Amazonia. *Biological Conservation* 77:63-77.
- 444 Ceballos G, Ehrlich PR. 2002. Mammal population losses and the extinction crisis.
445 *Science* 296:904-907.
- 446 Daily GC, Ehrlich PR. 1995. Preservation of biodiversity in small rainforest
447 patches: rapid evaluations using butterfly trapping. *Biodiversity and*
448 *Conservation* 4: 35-55.
- 449 Dirzo R, Garcia MC. 1992. Rates of deforestation in Los Tuxtlas, a Neotropical area in
450 southeast Mexico. *Conservation Biology* 6:84-90.
- 451 Dirzo R, Miranda A. 1990. Contemporary Neotropical defaunation and forest structure,
452 function, and diversity, a sequel to John Terborgh. *Conservation Biology* 4:444-

- 453 447.
- 454 Dirzo R, Miranda A. 1991. Altered patterns of herbivory and diversity in the forest
- 455 understory: a case study of the possible consequences of contemporary
- 456 defaunation. Pages 273-287 in: *Plant-Animal Interactions: Evolutionary ecology*
- 457 *in tropical and temperate regions* (Price PW, Lewinsohn TM, Fernandes GW,
- 458 Benson WW, eds.). Wiley and Sons, Inc., New York.
- 459 Dirzo R, Raven PH. 2003. Global state of biodiversity and loss. *Annual Review of*
- 460 *Environment and Resources* 28:137-167.
- 461 Estrada A, Coates-Estrada R, Merritt Jr DA. 1997. Anthropogenic landscape changes and
- 462 avian diversity at Los Tuxtlas, Mexico. *Biodiversity and Conservation* 6:19-43.
- 463 Ewers RM, Didham RK. 2006. Confounding factors in the detection of species responses
- 464 to fragmentation. *Biological Reviews* 81:117-142.
- 465 Faaborg J, Brittingham M, Donovan T, Blake J. 1995. Habitat fragmentation in the
- 466 temperate zone. Pages 357-380 in: *Ecology and management of Neotropical*
- 467 *migratory birds: a synthesis and review of the critical issues* (Finch DM, Martin
- 468 TE, eds.). Oxford University Press, Cambridge, United Kingdom.
- 469 Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of*
- 470 *Ecology Evolution and Systematics* 34:487-515.
- 471 Ferraz G, Russell GJ, Stouffer PC, Bierregaard RO, Pimm SL, Lovejoy TE. 2003. Rates of
- 472 species loss from Amazonian forest fragments. *Proceedings of the National*
- 473 *Academy of Sciences USA* 100:14069-14073.
- 474 Ferraz G, Nichols JD, Hines JE, Stouffer PC, Bierregaard RO, Lovejoy TE. 2007. A large-
- 475 scale deforestation experiment: Effects of patch area and isolation on Amazon
- 476 birds. *Science* 315:238-241.
- 477 González-Soriano E, Dirzo R, Vogt RC, eds. 1997. *Historia Natural de Los Tuxtlas*.

- 478 Universidad Nacional Autónoma de México, México, D.F.
- 479 Howell S, Webb S. 1995. *A guide to the birds of Mexico and northern Central America*.
- 480 Oxford University Press, New York.
- 481 Ibarra-Macias A, Robinson WD, Gaines MS. 2011. Experimental evaluation of bird
- 482 movements in a fragmented Neotropical landscape. *Biological Conservation*
- 483 144:703-712.
- 484 Ibarra-Manríquez G, Martinez-Ramos M, Dirzon R, Núñez-Farfán J. 1997 La vegetación.
- 485 Pages 61–74 in *Historia Natural de Los Tuxtlas* (González-Soriano E, Dirzo R,
- 486 Vogt RC, Eds). Universidad Nacional Autónoma de México, México, D.F.
- 487 Johnson AB, Winker K. 2010. Short-term hurricane impacts on a Neotropical
- 488 community of marked birds. *PLoS ONE* 5:e15109.
- 489 Johnson CN. 1998. Species extinction and the relationship between distribution and
- 490 abundance. *Nature* 394:272-274.
- 491 Kattan GH, Halvarez-Lopez H, Giraldo M. 1994. Forest fragmentation and bird
- 492 extinctions: San Antonio eighty years later. *Conservation Biology* 8:138-146.
- 493 Karr JR. 1982. Population variability and extinction in a tropical land-bridge island.
- 494 *Ecology* 63:1975-1978.
- 495 Laurance WF, et al. 2011. The fate of Amazonian forest fragments: A 32-year
- 496 investigation. *Biological Conservation* 144:56-67.
- 497 Leck CF. 1979. Avian extinctions in an isolated tropical wet-forest preserve, Ecuador.
- 498 *Auk* 96:343-352.
- 499 Lees AC, Peres CA. 2006. Rapid avifaunal collapse along the Amazonian deforestation
- 500 frontier. *Biological Conservation* 133:198-211.
- 501 Leigh EG, Jr. 1975. Population fluctuations, community stability, and environmental
- 502 variability. Pages 52-73 in: *Ecology and evolution of communities* (Cody ML,

- Diamond JM, eds.). Belknap Press, Cambridge, Massachusetts.
- Leigh EG, Jr. 1981. The average lifetime of a population in a varying environment. *Journal of Theoretical Biology* 90:213-239.
- Lovejoy TE, Rankin JM, Bierregaard RO, Brown KS, Jr., Emmons LH, Van Der Voort ME. 1984. Ecosystem decay of Amazon forest remnants. Pages 295-325 in: *Extinctions* (Nitecki MH, ed.). University of Chicago Press, Chicago, Illinois.
- Lovejoy TE, Bierregaard RO, Rylands AB, Malcolm JR, Quintela CE, Harper LH, Brown KS, Powell AH, Powell GVN, Schubart HOR, Hays MB. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 in: *Conservation biology: The science of scarcity of diversity* (Soule ME, ed.). Sinauer Associates, Sunderland, Massachusetts.
- Malcolm JR. 1988. Small mammal abundances in isolated and non-isolated primary forest reserves near Manaus, Brazil. *Acta Amazonica* 18: 67-83.
- Mendoza E, Fay J, Dirzo R. 2005. A quantitative analysis of forest fragmentation in Los Tuxtlas, southeast Mexico: patterns and implications for conservation. *Revista Chilena de Historia Natural* 78:451-467.
- Moore RP, Robinson WD, Lovette IJ, Robinson TR. 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters* 11: 960-968.
- Morton ES. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *American Naturalist* 107:8-22.
- Nemark WD. 1991. Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara Mountains, Tanzania. *Conservation Biology* 5:67-78.
- O'Grady JJ, Reed DH, Brook BW, Frankham R. 2004. What are the best correlates of predicted extinction risk? *Biological Conservation* 118:513-520.

- 526 Pahl LI, Winter JW, Heinsohn G. 1988. Variation in responses of arboreal marsupials to
527 fragmentation of tropical rainforest in north eastern Australia. *Biological*
528 *Conservation* 46:71-82
- 529 Patten MA, Gomez de Silva H, Smith-Patten BD. 2010. Long-term changes in the bird
530 community of Palenque, Chiapas, in response to rainforest loss. *Biodiversity and*
531 *Conservation* 19:21-36.
- 532 Patten MA, Smith-Patten BD. 2011. Predictors of occupancy trend across spatial scale.
533 *Conservation Biology* 6:1203-1211.
- 534 Pennington TD, Sarukhan J. 1968. *Arboles Tropicales de Mexico*. Instituto Nacional de
535 Investigaciones Forestales, D.F., Mexico.
- 536 Pimm SL, Jones HH, Diamond J. 1988. On the risk of extinction. *American Naturalist*
537 132:757-785.
- 538 Pimm SL, Raven P, Peterson A, Şekercioğlu Ç, Ehrlich PR. 2006. Human impacts on the
539 rates of recent, present, and future bird extinctions. *Proceedings of the National*
540 *Academy of Sciences USA* 103:10941-10946.
- 541 Powell AH, Powell GVN. 1987. Population dynamics of male euglossine bees in
542 Amazonian forest fragments. *Biotropica* 19: 176-179.
- 543 Puebla F, Winker K. 2004. Dieta y dispersión de semillas de dos especies de tangara
544 (*Habia*) en dos tipos de vegetación en Los Tuxtlas, Veracruz, México. *Ornitología*
545 *Neotropical* 15:53-64.
- 546 Ramos MA. 1983. *Seasonal movements of bird populations at a Neotropical study site*
547 *in southern Veracruz, Mexico*. Ph.D. dissertation. University of Minnesota,
548 Minneapolis.
- 549 Ramos MA. 1988. Eco-evolutionary aspects of bird movements in the northern
550 Neotropical region. Pages 251-293 in: *Acta XIX Congressus Internationalis*

- 551 *Ornithologici*, Vol. I, (Ouellet H, ed.). University of Ottawa Press, Ottawa,
- 552 Canada.
- 553 Rappole JH, Warner DW. 1980. Ecological aspects of migrant bird behavior in Veracruz,
- 554 Mexcio. Pages 353-393 in: *Migrant Birds in the Neotropics: Ecology, Behavior,*
- 555 *Distribution, and Conservation*, (Keast A, Morton ES, eds.). Smithsonian
- 556 Institution Press, Washington, D. C.
- 557 Rappole JH, Morton ES, Lovejoy TE, III, Ruos JL. 1983. *Nearctic avian migrants in the*
- 558 *Neotropics*. United States Fish and Wildlife Service, Washington D.C.
- 559 Rappole JH, Powell GVN, Sader SA. 1994. Remote-sensing assessment of tropical
- 560 habitat availability for a Nearctic migrant: the Wood Thrush. Pages 91-103 in:
- 561 *Mapping the diversity of nature* (Miller RI, ed.). Chapman and Hall, London.
- 562 Rappole JH, Winker K, Powell GVN. 1998. Migratory bird habitat use in southern
- 563 Mexico: mist nets versus point counts. *Journal of Field Ornithology* 69:635-643.
- 564 Remsen JV Jr., Good DA. 1996. Misuse of data from mist-net captures to assess relative
- 565 abundance in bird populations. *Auk* 113: 381-398.
- 566 Robbins CS. 1980. Effect of forest fragmentation on breeding bird populations in the
- 567 piedmont of the mid-Atlantic region. *Atlantic Naturalist* 33:31-36.
- 568 Robinson WD. 1999. Long-term changes in the avifauna of Barro Colorado
- 569 Island, Panama, a tropical forest isolate. *Conservation Biology* 13:85-97.
- 570 Robinson WD, Sherry TW. 2012. Mechanisms of avian population decline and species
- 571 loss in tropical forest fragments. *Journal of Ornithology* 153:S141-S152.
- 572 Robinson WD, Angehr GR, Robinson TR, Petit LJ, Petit DR, Brawn JD. 2004.
- 573 Distribution of bird diversity in a vulnerable Neotropical landscape. *Conservation*
- 574 *Biology* 18:510-518.
- 575 Rolstad J. 1991. Consequences of forest fragmentation for the dynamics of bird

- 576 populations: conceptual issues and the evidence. *Biological Journal of the*
- 577 *Linnean Society* 42:149-163.
- 578 Rompré G, Robinson WD, Desrochers A, Angehr G. 2007. Environmental correlates of
- 579 avian diversity in lowland Panama rainforests. *Journal of Biogeography* 34:802-
- 580 815.
- 581 Schaldach W, Escalante P. 1997. Lista de Aves. Pages 571-573 in: *Historia Natural de*
- 582 *Los Tuxtlas* (González-Soriano E, Dirzo R, Vogt RC, eds.). Universidad Nacional
- 583 Autonoma de Mexico. D.F., Mexico.
- 584 Sodhi NS, Liow LH, Bazzaz FA. 2004. Avian extinctions from tropical and subtropical
- 585 forests. *Annual Review of Ecology Evolution and Systematics* 35:323-345.
- 586 Soto M, Gama L. 1997. Climas. Pages 7-23 In: *Historia Natural de Los Tuxtlas*
- 587 (González-Soriano E, Dirzo R, Vogt RC, eds.). Universidad Nacional Autonoma de
- 588 Mexico. D.F., Mexico.
- 589 Stotz DF, Fitzpatrick JW, Parker TA, Moskovits DK. 1996. *Neotropical birds: ecology*
- 590 *and conservation*. University of Chicago Press, Chicago.
- 591 Stouffer PC, Bierregaard RO. 1995. Effects of forest fragmentation on understory
- 592 insectivorous birds. *Ecology* 76:2429-45.
- 593 Stratford JA, Robinson WD. 2005. Gulliver travels to the fragmented tropics: geographic
- 594 variation in mechanisms of avian extinction. *Frontiers in Ecology and the*
- 595 *Environment* 3:85-92.
- 596 Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, Waller RW.
- 597 2004. Status and trends of amphibian declines and extinctions worldwide.
- 598 *Science* 306:1783-1786.
- 599 Terborgh J, Winter B. 1980. Some causes of extinction. Pages 119-133 In: *Conservation*
- 600 *biology: an evolutionary-ecological perspective* (Soule ME, Wilcox BA, eds.).

Sinauer Associates, Sunderland, Massachusetts.

Tilman D, May RM, Lehman CL, Nowak MA. 1994. Habitat destruction and the extinction debt. *Nature* 371:65-66.

Turner IM. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* 33:200-209.

Van Houtan KS, Pimm SL, Bierregaard RO, Jr., Lovejoy TE, Stouffer PC. 2006. Local extinctions in flocking birds in Amazonian forest fragments. *Evolutionary Ecology Research* 8:129-148.

Van Houtan KS, Pimm SL, Halley JM, Bierregaard RO Jr., Lovejoy TE. 2007. Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology Letters* 10:219-229.

Vega Rivera JH. 1982. Aspectos biológicos de *Myiobius sulphureipygius* (Aves: Tyrannidae) en el área de Santa Marta region de “Los Tuxtlas,” Veracruz, Mexico. Professional thesis. Universidad Nacional Autónoma de México.

Vetter D, Hansbauer MM, Végvári Z, Storch I. 2011. Predictors of forest fragmentation sensitivity in Neotropical vertebrates: a quantitative review. *Ecography* 34:1-8.

Whitman AA, Hagan JM III, Brokaw NVL. 1997. A comparison of two survey techniques used in a subtropical forest. *Condor* 99:955-965.

Willis EO. 1966. The role of migrant birds at swarms of army ants. *Living Bird* 5:187-231.

Willis EO. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecological Monographs* 44:153-169.

Willis EO. 1979. The composition of avian communities in remanescent woodlots in southern Brazil. *Papeis Avulsos de Zoolgia* 33:1-25.

Winker K. 1995. Habitat selection in woodland Nearctic-Neotropical migrants on the

626 Isthmus of Tehuantepec. I. Autumn migration. *Wilson Bulletin* 107:26-39.

627 Winker K. 1997. Introduction to the birds of Los Tuxtlas. Pages 535-541 in: *Historia*

628 *Natural de Los Tuxtlas* (González-Soriano E, Dirzo R, Vogt RC, Eds.).

629 Universidad Nacional Autonoma de Mexico. D.F., Mexico.

630 Winker K, Rappole JH, Ramos MA. 1990. Population dynamics of the Wood Thrush

631 (*Hylocichla mustelina*) on its wintering grounds in southern Veracruz, Mexico.

632 *Condor* 92:444-460.

633 Winker K, Oehlenschlager RJ, Ramos MA, Zink RM, Rappole JH, Warner DW. 1992.

634 Avian distribution and abundance records for the Sierra de Los Tuxtlas, Veracruz,

635 Mexico. *Wilson Bulletin* 104:699-718.

636 Winker K, Escalante P, Rappole JH, Ramos MA, Oehlenschlager RJ, Warner DW. 1997.

637 Periodic migration and lowland forest refugia in a sedentary Neotropical bird,

638 Wetmore's bush-tanager. *Conservation Biology* 11:692-697.

639 Zimmerman BL, Bierregaard RO. 1986. Relevance of the equilibrium theory of

640 island biogeography and species-area relations to conservation with a case from

641 Amazonia. *Journal of Biogeography* 13:133-143.

642

643 **Figure captions**

644 Figure 1. Comparative views of the Sierra de Los Tuxtlas from an artificially colorized
645 1979 Landsat image (top) and a 2010/11 Google Earth image (bottom) showing the
646 extent of deforestation in the region. Remaining forest has become concentrated at
647 higher elevations on the slopes of the region's three volcanoes, San Martín, Santa Marta,
648 and San Martín Pajápan (the forested areas remaining, from left to right).

649

650 Figure 2. Satellite view of Volcán San Martín, the northernmost volcano in the Sierra de
651 Los Tuxtlas, showing the distribution of forests (dark areas). The study area is indicated
652 by the white box, which corresponds to the area in Fig. 3 (image from Google Earth,
653 2010).

654

655 Figure 3. Maps of the study area in the northern lowlands of the Sierra de Los Tuxtlas
656 (this is the area in the white box in Fig. 2) showing a rough outline of all forests types
657 (dark gray areas) in 1979 (top, from Landsat image), in 2005 (bottom, from
658 GoogleEarth), and netting sites (black polygons). Numbers indicate field season(s) site
659 was used and correspond to rows in Table 1.

660

661 Figure S1. A series of satellite images depicting deforestation in Los Tuxtlas, focusing in
662 on the volcanoes Santa Marta (left) and San Martín Pajápan (right), starting with a
663 1973/4 Skylab image (upper left) and progressing through a series of Landsat images,
664 from 1999 (upper right), 2003 (lower left), and 2011 (lower right).

665

666 Figure S2. Species accumulation curve for a representative year with below average net

667 hours (1992, 12,605 net hours).

Table 1 (on next page)

Sample effort and periods during eight nonbreeding seasons across three decades in the Sierra de Los Tuxtlas, Veracruz, Mexico.

Sample effort and periods during eight nonbreeding seasons across three decades in the Sierra de Los Tuxtlas, Veracruz, Mexico.

2 Table 1. Sample effort and periods during eight nonbreeding seasons across three
3 decades in the Sierra de Los Tuxtlas, Veracruz, Mexico.

Nonbreeding season	Net hours	Sampling period
1) 1973-74	33,976	15 Aug-26 May
2) 1974-75	36,512	7 Aug-29 May
3) 1986-87	4,310	17 Nov-16 Jan
4) 1992-93	12,605	5 Sep-15 Nov
5) 1993-94	41,142	25 Aug-20 May
6) 1994-95	22,509	15 Aug-15 Nov
7) 2002-03	8,395	21 Feb-27 Apr
8) 2003-04	2,312	5 Apr-29 Apr

Table 2_(on next page)

Outcomes of regression analyses for 14 species showing changes in abundance (capture rates; captures and rates are given in the Appendix) and those not detected in the later sampling periods. Those P-values presented in bold are significant at $\alpha = 0.0$

Outcomes of regression analyses for 14 species showing changes in abundance (capture rates; captures and rates are given in the Appendix) and those not detected in the later sampling periods. Those P-values presented in bold are significant at $\alpha = 0.05$.

- 1 Table 2. Outcomes of regression analyses for 14 species showing changes in abundance
- 2 (capture rates; captures and rates are given in the Appendix) and those not detected in
- 3 the later sampling periods. Those *P*-values presented in bold are significant at $\alpha = 0.05$.

Species	<i>F</i>	<i>P</i>	<i>R</i> ²	Last captured
<i>Phaethornis striigularis</i> ^c	6.337	0.045	0.514	2002-03
<i>Hylomanes momotula</i> ^a	0.210	0.890	0.003	1994-95
<i>Trogon collaris</i> ^b	7.041	0.038	0.540	n/a
<i>Xiphorhynchus flavigaster</i> ^b	6.941	0.039	0.536	n/a
<i>Xenops minutus</i> ^c	7.578	0.033	0.558	2003-04
<i>Glyphorhynchus spirurus</i> ^{c,d}	7.529	0.034	0.557	1974-75
<i>Lepidocolaptes souleyetii</i> ^d	3.265	0.121	0.352	1992-93
<i>Ornithion semiflavum</i> ^d	0.327	0.588	0.052	1994-95
<i>Leptopogon amaurocephalus</i> ^d	2.814	0.144	0.319	1994-95
<i>Onychorhynchus coronatus</i> ^{c,d}	6.861	0.040	0.533	1986-87
<i>Myiobius sulphureipygius</i> ^{c,d}	10.555	0.019	0.629	1994-95
<i>Henicorhina leucosticta</i> ^{c,d}	6.740	0.041	0.529	2003-04
<i>Coereba flaveola</i> ^d	2.164	0.192	0.265	1994-95
<i>Eucometis penicillata</i> ^c	18.725	0.005	0.757	2002-03

- 4 ^a Species captured 1986-1995. See text.

- 5 ^b Species showing an increase in abundance.
- 6 ^c Species showing a significant decline.
- 7 ^d Species not captured in later sampling periods.

Table 3(on next page)

Species not captured or observed from 1992-2004, seasons captured (from Appendix), presence on the field site in later sampling periods, and comments.

Species not captured or observed from 1992-2004, seasons captured (from Appendix), presence on the field site in later sampling periods, and comments.

- 1 Table 3. Species not captured or observed from 1992-2004, seasons captured (from
- 2 Appendix), presence on the field site in later sampling periods, and comments.

Species	Seasons Captured	Presence	Comments
<i>Micrastur ruficollis</i>	1	Y	observed
<i>Crypturellus boucardi</i>	3	Y	observed
<i>Heliomaster longirostris</i>	1	?	hummingbird
<i>Florisuga mellivora</i>	1	?	hummingbird
<i>Chlorostilbon canivetii</i>	2	?	hummingbird
<i>Hylocharis eliciae</i>	1, 2	?	hummingbird
<i>Chloroceryle aenea</i>	1, 2	Y	small streams
<i>Dryocopus lineatus</i>	2	Y	observed
<i>Synallaxis erythrothorax</i>	2	Y	observed
<i>Taraba major</i>	2	N	forest understory
<i>Formicarius analis</i>	1	N	forest understory
<i>Grallaria guatemalensis</i>	1, 3	N	forest understory
<i>Tityra inquisitor</i>	1	Y	observed, canopy
<i>Cotinga amabilis</i>	1	?	canopy
<i>Schiffornis turdina</i>	1	N	forest understory
<i>Polioptila plumbea</i>	1	Y	observed
<i>Myadestes unicolor</i>	1	Y	highlands
<i>Euphonia affinis</i>	2	?	none

<i>Thraupis abbas</i>	1	Y	observed
<i>Thraupis episcopus</i>	2	Y	observed
<i>Saltator atriceps</i>	1, 2	Y	observed
<i>Molothrus aeneus</i>	1	Y	observed

Table 4 (on next page)

Habitat, foraging preference, elevational range, and position within geographical distribution for 18 species of birds at the Estación de Biología Los Tuxtlas (from Howell and Webb, 1995).

Habitat, foraging preference, elevational range, and position within geographical distribution for 18 species of birds at the Estación de Biología Los Tuxtlas (from Howell and Webb, 1995).

- 1 Table 4. Habitat, foraging preference, elevational range, and position within
- 2 geographical distribution for 18 species of birds at the Estación de Biología Los Tuxtlas
- 3 (from Howell and Webb, 1995).

Species	Habitat preference	Foraging guild	Elevational distribution (m)	Geographic distribution
<i>Phaethornis striigularis</i>	forest	nectarivore	0-1500	periphery
<i>Hylomanes momotula</i>	forest	frugivore	0-1500	periphery
<i>Trogon collaris</i>	forest	frugivore	0-2400	core
<i>Xenops minutus</i>	forest	insectivore	0-1000	periphery
<i>Xiphorhynchus flavigaster</i>	forest	insectivore	0-1500	core
<i>Glyphorhynchus spirurus</i> *	forest	insectivore	0-1200	periphery
<i>Lepidocolaptes souleyetii</i>	semi-open	insectivore	0-1500	periphery
<i>Taraba major</i> *	forest	insectivore	0-1600	periphery
<i>Formicarius analis</i> *	forest	insectivore	0-750	periphery
<i>Grallaria guatemalensis</i> *	forest	insectivore	50-3500	core
<i>Ornithion semiflavum</i>	edge	insectivore	0-1500	periphery
<i>Leptopogon amaurocephalus</i>	edge	insectivore	0-1300	periphery
<i>Onychorhynchus coronatus</i>	forest	insectivore	0-1200	periphery
<i>Myiobius sulphureipygius</i>	forest	insectivore	0-1000	periphery
<i>Schiffornis turdina</i> *	forest	frugivore	0-750	periphery
<i>Henicorhina leucosticta</i>	forest	insectivore	0-1300	core
<i>Coereba flaveola</i>	edge	frugivore	0-1000	periphery
<i>Eucometis penicillata</i>	forest	frugivore	0-750	periphery

4 * Presence/Absence data suggest species is extirpated.

Figure 1

Comparative views of the Sierra de Los Tuxtlas from an artificially colorized 1979 Landsat image (top) and a 2010/11 Google Earth image (bottom) showing the extent of deforestation in the region. Remaining forest has become concentrated at higher elevatio

Comparative views of the Sierra de Los Tuxtlas from an artificially colorized 1979 Landsat image (top) and a 2010/11 Google Earth image (bottom) showing the extent of deforestation in the region. Remaining forest has become concentrated at higher elevations on the slopes of the region's three volcanoes, San Martín, Santa Marta, and San Martín Pajápan (the forested areas remaining, from left to right).



Figure 2

Satellite view of Volcán San Martín, the northernmost volcano in the Sierra de Los Tuxtlas, showing the distribution of forests (dark areas). The study area is indicated by the white box, which corresponds to the area in Fig. 3 (image from Google Earth, 2

Satellite view of Volcán San Martín, the northernmost volcano in the Sierra de Los Tuxtlas, showing the distribution of forests (dark areas). The study area is indicated by the white box, which corresponds to the area in Fig. 3 (image from Google Earth, 2010).



Figure 3

Maps of the study area in the northern lowlands of the Sierra de Los Tuxtlas (this is the area in the white box in Fig. 2) showing a rough outline of all forests types (dark gray areas) in 1979 (top, from Landsat image), in 2005 (bottom, from GoogleEarth)

Maps of the study area in the northern lowlands of the Sierra de Los Tuxtlas (this is the area in the white box in Fig. 2) showing a rough outline of all forests types (dark gray areas) in 1979 (top, from Landsat image), in 2005 (bottom, from GoogleEarth), and netting sites (black polygons). Numbers indicate field season(s) site was used and correspond to rows in Table 1.

