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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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). Andrle (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 Oehlenschlager, 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
tests 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.
RESULTS

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

Seven species showed statistically significant declines during the sampling period: *Phaethornis striigularis*, *Xenops minutus*, *Glyphorynchus spirurus*, *Onychorhynchus coronatus*, *Myiobius sulphureipygius*, *Henicorhina leucosticta*, and *Eucometis penicillata* (Table 2). Of these taxa, four were captured throughout the sampling period: *P. striigularis*, *X. minutus*, *E. penicillata*, and *H. leucosticta*. *G. spirurus* was last captured in 1975, *O. coronatus* in 1986, and *M. sulphureipygius* in 1994, the last season of autumn netting. Four other species were captured in substantial numbers during early sampling periods but were not captured in later years: *Lepidocolaptes souleyetii*, *Ornithion semiflavum*, *Leptopogon amaurocephalus*, and *Coereba flaveola* (the latter may be an intratropical migrant in this region; Ramos, 1983); however, these species failed to show statistically significant declines in linear regression analyses, perhaps due to nonlinear declines. *L. souleyetii* was last captured in 1993-94, and the others were last captured in 1994-95. One species, *Hylomanes momotula*, was captured from 1986-1995 but not in the 1970s or in 2003-04. Though there were no captures in the 1970s, one individual was collected on 17 May 1974 a few km northeast of the station. A similar pattern occurred in *Anabacerthia variegaticeps*, with captures occurring only in the 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 guatimalensis*, 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. guatimalensis, 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. guatimalensis* 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
Deforestation in Los Tuxtlas as a whole (Fig. 1) may be too extensive even for these edge specialists. *L. souleyetii* prefers open forest and partially cleared areas (Howell & Webb, 1995). The habitat surrounding the station during the 1980s and 1990s was dominated by pasture scattered with isolated trees. In our later field seasons there was a noticeable decline in the number of isolated trees and fences constructed of living trees (Winker, pers. obs.). This loss may account for the extirpation of *L. souleyetii*. *G. spirurus* apparently disappeared from the station between the 1970s and 1986, the first of the documented extirpations. The majority of deforestation across the region took place during this period. This previously abundant species disappeared from our data in just over a decade. Interestingly, on the slopes of neighboring Volcán Santa Marta the species was present at least into the 1990s and probably still persists there (Winker, pers. obs.). Also, Estrada, Coates-Estrada, & Merritt (1997) had observational data of the species’ presence in the station area in 1990-1992, indicating at least a decline if not extirpation (Table 2). In Brazil, *G. spirurus* persisted in experimentally isolated fragments well after isolation (Stouffer & Bierregaard 1995), and the species persists in highly fragmented forest in southern Belize (Johnson & Winker, 2010). *H. momotula* was collected but not netted in 1974, was captured in substantial numbers during 1986 and 1992-94, but was absent in the last two seasons of sampling. This pattern is mysterious. This species has an elevational range extending to 1500 m and may persist in the forests of the upper slopes of Volcán San Martín. If so, we speculate that the station may serve as a sink for this species, where habitat is insufficient for a self-sustaining population but may occasionally be colonized by dispersing individuals (see also Winker et al., 1997). Continued sampling may provide more insight into its abundance patterns. It illustrates the need for improved understanding of species-specific dispersal behavior within and 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 guatimalensis, and Schifrnons 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 extripations (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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Figure captions

Figure 1. Comparative views of the Sierra de Los Tuxtolas 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).

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

Figure S2. Species accumulation curve for a representative year with below average net
hours (1992, 12,605 net hours).
Sample effort and periods during eight nonbreeding seasons across three decades in the Sierra de Los Tuxtlas, Veracruz, Mexico.

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Table 1. Sample effort and periods during eight nonbreeding seasons across three 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

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

$^a$ Species captured 1986-1995. See text.
Species showing an increase in abundance.
Species showing a significant decline.
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.

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| Species                          | Seasons Captured | Presence | Comments            |
|----------------------------------|------------------|----------|---------------------|
| Micrastur ruficollis             | 1                | Y        | observed            |
| Crypturellus boucardi            | 3                | Y        | observed            |
| Heliomaster longirostris         | 1                | ?        | hummingbird         |
| Florisuga mellivora             | 1                | ?        | hummingbird         |
| Chlorostilibon canivetii         | 2                | ?        | hummingbird         |
| Hylocharis eliciae               | 1, 2             | ?        | hummingbird         |
| Chloroceryle aenea               | 1, 2             | Y        | small streams       |
| Dryocopus lineatus               | 2                | Y        | observed            |
| Synallaxis erythrothorax         | 2                | Y        | observed            |
| Taraba major                     | 2                | N        | forest understory   |
| Formicarius analis               | 1                | N        | forest understory   |
| Grallaria guatimalensis         | 1, 3             | N        | forest understory   |
| Tityra inquisitor                | 1                | Y        | observed, canopy    |
| Cotinga amabilis                | 1                | ?        | canopy              |
| Schiffornis turdina              | 1                | N        | forest understory   |
| Polioptila plumbea              | 1                | Y        | observed            |
| Myadestes unicolor              | 1                | Y        | highlands           |
| Euphonia affinis                | 2                | ?        | none                |
| Species               | Count | Sex | Observed |
|----------------------|-------|-----|----------|
| Thraupis abbas       | 1     | Y   | observed |
| Thraupis episcopus   | 2     | Y   | observed |
| Saltator atriceps    | 1, 2  | Y   | observed |
| Molothrus aeneus     | 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).

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| Species                      | Habitat preference | Foraging guild | Elevational distribution (m) | Geographic distribution |
|------------------------------|-------------------|----------------|------------------------------|-------------------------|
| *Phaethornis striigularis*   | forest            | nectarivore    | 0-1500                       | periphery               |
| *Hylomanes momotula*         | forest            | frugivore      | 0-1500                       | periphery               |
| *Trogon collaris*            | forest            | frugivore      | 0-2400                       | core                    |
| *Xenops minutus*             | forest            | insectivore    | 0-1000                       | periphery               |
| *Xiphorhynchus flavigaster*  | forest            | insectivore    | 0-1500                       | core                    |
| * Glyphorynchus spirurus*    | forest            | insectivore    | 0-1200                       | periphery               |
| *Lepidocolaptes souleyetii*  | semi-open         | insectivore    | 0-1500                       | periphery               |
| *Taraba major*               | forest            | insectivore    | 0-1600                       | periphery               |
| *Formicarius analis*         | forest            | insectivore    | 0-750                        | periphery               |
| *Grallaria guatimalensis*    | forest            | insectivore    | 50-3500                      | core                    |
| *Ornithion semiflavum*       | edge              | insectivore    | 0-1500                       | periphery               |
| *Leptopogon amaurocephalus*  | edge              | insectivore    | 0-1300                       | periphery               |
| *Onychorhynchus coronatus*   | forest            | insectivore    | 0-1200                       | periphery               |
| *Myiobius sulphureipygius*   | forest            | insectivore    | 0-1000                       | periphery               |
| *Schiffornis turdina*        | forest            | frugivore      | 0-750                        | periphery               |
| *Henicorhina leucosticta*    | forest            | insectivore    | 0-1300                       | core                    |
| *Coereba flaveola*           | edge              | frugivore      | 0-1000                       | periphery               |
| *Eucometis penicillata*      | forest            | frugivore      | 0-750                        | periphery               |
* Presence/Absence data suggest species is extirpated.
Figure 1

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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.
