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 local extinctions 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 extinctions 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; Robinson & Sherry 2012). Tropical forest species, which often occur in small, low-density populations, may be particularly vulnerable to local extinctions (Terborgh & Winter 1980; Pimm, Jones, & Diamond, 1988;

54   Stotz et al., 1996).

55   Relatively few studies have assessed changes through decades,

56   however (Ewers & Didham, 2006). And although deforestation and

57   fragmentation can occur over a short period, some time may pass before

58   species begin to disappear from an affected area (Leigh, 1975, 1981; Karr,

59   1982, Tilman et al., 1994; Brooks, Pimm, & Oyugi, 1999). Thus, to fully

60   document the impact of deforestation on a forest community, a site must be

61   studied for a substantial period of time after habitat alteration has occurred.

62   Detailing the process of local population decline and extinction over time

63   provides invaluable information about species' abilities to cope with habitat

64   fragmentation and how community composition itself stabilizes following this

65   disturbance.

66   Studies of species losses in birds have used a variety of methods,

67   including comparing species richness in different-sized fragments (Willis,

68   1979; Nemark, 1991; Blake, 1991), comparison of species composition at a

69   site pre- and post-fragmentation (Willis, 1974; Leck, 1979; Bierregaard &

70   Lovejoy, 1989; Kattan, 1994), and experimental fragmentation (Lovejoy et al.,

71   1986; Bierregaard & Lovejoy, 1988, 1989; Ferraz et al., 2003, 2007; Laurance

72   et al., 2011), and have often included scattered survey data prior to

73   fragmentation (Willis, 1974; Leck, 1979; Kattan, Halvarez-Lopez, & Giraldo,

74   1994; Robinson, 1999; Patten, Gómez de Silva, & Smith-Patten, 2010). Many

75   of these studies have relied on qualitative visual and audio survey

76   techniques, with multiple observers, though such techniques can allow

77   cryptic and low-density species to be overlooked (Whitman, Hagan, &

78 Brokaw, 1997). Additionally, observer skills and intensity of sampling may

79 vary among surveys.

80   Mist netting offers the most consistent and quantitative method

81 available to sample birds among years (Rappole, Winker, & Powell, 1998).

82 However, mist nets have documented weaknesses; the most relevant is the

83 limited stratum and size of birds they can effectively sample (Remsen &

84 Good, 1996; Whitman, Hagan, & Brokaw, 1997; Rappole, Winker, & Powell,

85 1998). This is particularly noticeable in structurally diverse habitats such as

86 tropical rainforests, where probability of detection using mist nets is unknown

87 for most species. Mist net studies in the Neotropics are therefore biased

88 toward understory, small- to mid-sized passerines. While mist nets, unlike

89 other methods, are less prone to observer bias and variability, we augmented

90 our analyses of netting data that suggested species losses with

91 presence-absence observational data (daily checklists in later years); this

92 becomes particularly important for low-density species and for those not

93 readily captured.

94   The Sierra de Los Tuxtlas of southern Veracruz, Mexico provides a

95 textbook case of deforestation. This small range of volcanic mountains is

96 home to the northernmost Neotropical rainforest (Pennington & Sarukhan,

97 1968; Dirzo & Miranda, 1991). The region has lost more than 90% of its

98 forests in the past century, with the majority of that loss occurring in the

99 lowlands over the past fifty years (Dirzo & Garcia, 1992; Rappole, Powell, and

100 Sader, 1994; Winker, 1997). Our study compares eight seasons of mist net

101 sampling from Los Tuxtlas over the course of more than thirty years. This

102 allows us to at least partly answer the question of how species composition

103 and relative abundance changed in and around a conserved core of local

104 rainforest habitat on a decadal scale.

105 **METHODS**

106 The Sierra de Los Tuxtlas is located in southern Veracruz, Mexico, 90

107 km southeast of Veracruz city. This range of mountains lies in the

108 northwestern portion of the Isthmus of Tehuantepec and is isolated from the

109 Sierra Madre Oriental by extensive lowlands. Los Tuxtlas encompass

110 approximately 4,200 km^2, and the range is dominated by Volcán San Martín

111 and Volcán Santa Marta, each reaching more than 1,500 m elevation. The

112 Gulf of Mexico lies a short distance from the mountains to the north and east.

113 The northernmost Neotropical evergreen rainforest formerly dominated the

114 habitat in the region (Andrle, 1966; Pennington & Sarukhan, 1968; Dirzo &

115 Miranda, 1991), but due to deforestation it is now a mosaic with a high

116 percentage of pasture, cropland, fencerows, and isolated trees (pers. obs.;

117 Dirzo & Garcia 1992; Estrada, Coates-Estrada, & Merritt 1997). Andrle (1966)

118 estimated that 50% of the region was forested in 1962. By 1975 Rappole &

119 Warner (1980) estimated that a third of the forests still stood. Just 15% of

120 forest remained in 1986 (Winker, Rappole, & Ramos, 1990; Dirzo & Garcia,

121 1992), and in 1994 only 7-10% of the region was forested (Winker, 1997).

122 Remaining forest occurs primarily in the highlands, and below 500 m forest is

123 scarce (Rappole, Powell, & Sader, 1994; Mendoza, Fay, & Dirzo, 2005; Figs. 1,

124 2).

125 The climate in Los Tuxtlas is warm and wet, with a mean annual

126 temperature of 25 C, and annual precipitation is 4,500-4,900 mm, with a

127 short dry season from March-May (Soto & Gama 1997). Canopy heights in

128 primary forest range from 30-35 m (Ibarra-Manriquez et al., 1997). Second

129 growth areas generally have variable canopy heights from 3-20 m (pers.

130 obs.).

131   In 1967 the Universidad Nacional Autónoma de México established the

132 Estación de Biología Los Tuxtlas, protecting a 640-ha tract of lowland

133 rainforest (18° 34'30"N, 95° 04'20"W; González-Soriano, Dirzo, & Vogt, 1997).

134 Over the following decades this site became largely isolated from other tracts

135 of forest, although a corridor of forest remains, connecting to the more

136 extensive upland forests on Volcán San Martín (Dirzo & Garcia, 1992; Fig. 1).

137 The first intensive sampling of birds in the region began in 1973, and data

138 from that effort are included here (see Winker, 1997).

139   During the non-breeding seasons of 1973-74 and 1974-75

140 Oehlenschlager, Ramos, Rappole, and Warner conducted the first intensive

141 mist-netting efforts in the area. Sites extended through what was then

142 contiguous rainforest from the biological station eastward to the coast (Fig.

143 3). In 1986, Rappole, Ramos, and Winker operated mist nets at the biological

144 station, and Winker and Escalante continued work there from 1992 to 1994.

145 In 2003-04 as part of a study of migrant birds, Shaw operated mist nets at

146 the same location as Winker and Escalante's work in the 1990s. This study

147 was approved by the University of Alaska Fairbanks IACUC (approval

148 numbers: #00-33 & #04-03). Fieldwork occurred primarily during the

149 non-breeding season. Effort was made to equally sample the available forest

150 types throughout the study period, although, in order to do this, habitat

151 changes precluded using the same sites across all years (see Winker 1995;

152 Fig. 3). Field effort as gauged by net hours also varied among years (Table 1).

153   Our earliest sampling occurred over a wider area than later seasons

154 (Fig. 3). During the earliest sampling, large tracts of contiguous forest

155 consisting of various microhabitats dominated the region and were sampled

156 accordingly (Fig. 3). This broader expanse of forest likely provided habitat to

157 more species than the current distribution of forest. This increased detection

158 probabilities for some species such as *S. turdina*, which was rare even during

159 our earliest sampling. Two general types of forest were present after

160 fragmentation: primary forest and acahual (second growth). Because our

161 sampling was forest-oriented, our efforts tracked the distribution of these

162 habitats. Primary rainforest and second growth habitats were sampled in all

163 efforts. We were unable to separate capture data by site for the early

164 sampling periods; our findings therefore include data from the somewhat

165 larger area from the station east to the coast. This sampling heterogeneity

166 leads us to be cautious and conservative in our analyses and interpretations.

167 Importantly, however, the same site and net lanes were used in the

168 1992-2004 efforts (sample periods 4-8 in Table 1).

169   Only resident species were used in our analyses due to seasonal

170 migration and the high levels of variance in abundance this causes among

171 obligate migrants. Changes in relative abundance were detected by

172 comparing capture rates (birds per 1000 net hours) from each year of

173 sampling. Species not captured in later sampling efforts and those with

174 apparently declining or increasing rates of capture were selected for more

175 detailed analyses (instead of applying statistical tests across all species).

176 Presence/absence patterns and observational data (daily checklists in later

177 years) were also considered to provide insight into changes in abundance in

178 low-density species that did not have sufficient samples for statistical testing.

179 Species were considered for examination for presence/absence if they had

180 not been captured since at least 1986-87. Vagrants, defined as those rarely

181 encountered species whose ranges do not normally include the Sierra de Los

182 Tuxtlas, were excluded (Winker et al., 1992; Howell & Webb, 1995). Only

183 first-time captures were used in statistical analyses. Simple linear regression

184 was used to detect changes in abundance for selected species. We looked for

185 newly appearing species using presence/absence netting, observational, and

186 specimen data. Daily checklists were used to augment mist-net data as a

187 check to determine whether absence from the mist-net data was indicative of

188 reality.

189   Species showing statistically significant declines and those not

190 captured or observed in later sampling periods were categorized by preferred

191 habitat (edge, forest, or semi-open), food preference (fruit/nectar or insects),

192 elevational range, and whether Los Tuxtlas was at the periphery or core of its

193 geographic range (Howell & Webb, 1995). These characteristics were used to

194 assess whether certain traits of the species increased their vulnerability to

195 local extirpation.

196 **RESULTS**

197   During this study we accumulated 165,083 net hours, equivalent to

198 37.7 net years if netting with a single net occurred twelve hours per day

199 (Table 1). A species accumulation curve for a representative year (1992) with

200 below-average net hours (12,605; mean = 20,220) showed that the avifauna

201 was effectively fully sampled during most field seasons (Fig. S1, though in

202 documenting a species' absence it is the among-season, aggregate sampling

203 that is important). In total, 122 nonmigratory species were captured

204 (Appendix).

205   Seven species showed statistically significant declines during the

206 sampling period: *Phaethornis striilgularis*, *Xenops minutus, Glyphorynchus*

207 *spirurus, Onychorhynchus coronatus, Myiobius sulphureipygius, Henicorhina*

208 *leucosticta,* and *Eucometis penicillata* (Table 2). Of these taxa, four were

209 captured throughout the sampling period: *P. striilgularis*, *X. minutus, E.*

210 *penicillata,* and *H. leucosticta*. *G. spirurus* was last captured in 1975, *O.*

211 *coronatus* in 1986, and *M. sulphureipygius* in 1994, the last season of autumn

212 netting. Four other species were captured in substantial numbers during early

213 sampling periods but were not captured in later years: *Lepidocolaptes*

214 *souleyetii, Ornithion semiflavum, Leptopogon amaurocephalus,* and *Coereba*

215 *flaveola* (the latter may be an intratropical migrant in this region; Ramos,

216 1983); however, these species failed to show statistically significant declines

217 in linear regression analyses, perhaps due to nonlinear declines. *L. souleyetii*

218 was last captured in 1993-94, and the others were last captured in 1994-95.

219 One species, *Hylomanes momotula,* was captured from 1986-1995 but not in

220 the 1970s or in 2003-04. Though there were no captures in the 1970s, one

221 individual was collected on 17 May 1974 a few km northeast of the station. A

222 similar pattern occurred in *Anabacerthia variegaticeps*, with captures

223 occurring only in the 1990s. Only two species (*Trogon collaris* and

224 *Xiphorhynchus flavigaster*) showed significant increases during the study

225 period.

226   Presence/absence mist-net capture data for low-density species not

227 captured after 1986-87 could be interpreted as suggesting that an additional

228 23 taxa were extirpated during the study (Table 3). However, we know from

229 observational data that not all of these species were absent. These taxa

230 included rarely captured species that are too large for effective mist-net

231 capture or that prefer the forest canopy (e.g., *Micrastur ruficollis, Cotinga*

232 *amabilis*), mixed/open habitat specialists (e.g., *Thraupis abbas* and *T.*

233 *episcopus*), a small-stream specialist (*Chloroceryle aenea*), and highland

234 species (e.g., *Myadestes unicolor*) that are either not prone to capture in mist

235 nets or at our site. Species such as *Tityra inquisitor,* both *Thraupis* tanagers,

236 and others were known to be present on the site or nearby but were not

237 captured in later sampling periods. Four species of hummingbirds are

238 included in Table 3, but due to inconsistent capture probabilities of

239 low-density hummingbird species and non-definitive observational data with

240 respect to accurate identification, we provide no hypotheses regarding their

241 possible extirpation or persistence at the site; further work focusing on these

242 species is warranted. There were six other species not in Tables 2 or 3 in

243 which mist net data alone might suggest declines or absences (Appendix)

244 during the entire study but which were present throughout from

245 observational data; netting is not an effective sampling tool for these taxa

246 because of body size or forest stratum occupied (e.g., *Glaucidium*

247 *brasilianum, Ciccaba virgata,* and *Celeus castaneus*) or because forest

248 understory is not preferred habitat (e.g., *Pitangus sulphuratus, Myiozetetes*

249 *similis,* and *Volatinia jacarina*; Appendix)*.* The first three of these species

250 require more focused study to determine abundances and possible declines.

251   Four lower-density species have likely been extirpated: *Taraba major*,

252 *Formicarius analis*, *Grallaria guatimalensis,* and *Schiffornis turdina* (Table 3).

253 One low-density species that might seem to have been extirpated from our

254 data, *Elaenia flavogaster*, is likely an intratropical migrant here (pers. obs.;

255 Howell & Webb, 1995; Table 3). Several species were captured only in later

256 sampling periods (Appendix) but were observed or collected throughout,

257 suggesting that there were no additions to the biological station's resident

258 avifauna during the study.

259   Based on all available data during the study (netting and observational

260 data), a minimum of 11 species of birds appear to have been extirpated from

261 the biological station over the past three decades. This translates into an

262 average loss of 3.7 species per decade or a local loss of 2.0% of the entire

263 Los Tuxtlas avifauna (561 spp.; Schaldach & Escalante, 1997), 4.1% of the

264 resident avifauna (269 spp.; Schaldach & Escalante, 1997), or 9.0% of the

265 resident species captured in our study (122 spp.; Appendix). All 16 species

266 showing significant declines or no longer present on the site prefer some

267 degree of forest cover (Table 4). Three species are edge specialists: *O.*

268 *semiflavum, O. mexicanus,* and *C. flaveola*. Twelve prefer closed canopy

269 forest: *P. striilgularis*, *H. momotula*, *X. minutus*, *G. spirurus, T. major, F. analis,*

270 *G. guatimalensis, L. amaurocephalus, M. sulphureipygius, S. turdina, H.*

271 *leucosticta,* and *E. penicillata. L. souleyetii* prefers semi-open or partly

272 cleared forest.

273   Eleven of 16, or 68.8%, of the species showing declines or extirpations

274 in this study are insectivores, whereas among all species captured 41% are

275 insectivores. This trend was not significant, however (*G*-test with Williams'

276 correction, $P > 0.1$).

277   The Sierra de Los Tuxtlas is the northernmost limit of the ranges of 13

278 of the 16 species showing declines. *G. guatimalensis* and *H. leucosticta* are

279 the only species with a distribution extending substantially to the north and

280 west of the study site. The field site is well within the elevational limits for all

281 16 species (Table 4).

282   The two species that significantly increased in abundance over the

283 sample period (Table 4) both occur here at the core of their ranges,

284 elevational distributions, and in their preferred forest habitat. *T. collaris* is a

285 frugivore, and *X. flavigaster* is an insectivore.

286 **DISCUSSION**

287   Although the absence of a species is not a clear indication of

288 extirpation, our sampling effort, despite its heterogeneity, does suggest that

289 at minimum a species' absence indicates a decline. It is possible that some of

290 the species now apparently gone from the station may persist in other,

291 unsampled fragments. If the data presented here and our interpretation of

292 them are accurate, the extirpation of species from the Estación de Biología

293 Los Tuxtlas has been ongoing since its isolation. Such an "extinction debt" is

294 a recognized component of deforestation, and models of empirical data show

295 that in birds this occurs across decades, but the species affected and the

296 mechanisms of species loss remain poorly understood (Tilman et al., 1994;

297 Ewers & Didham, 2003, Robinson & Sherry, 2012). Since 1973, 16 species

298 susceptible to capture in mist nets have either become locally extirpated or

299 are showing significant declines in abundance. The total number of losses

300 and declines is undoubtedly higher than presented, because species not

301 regularly captured in mist nets, such as large-bodied and canopy species,

302 were not adequately surveyed. Species known to have been extirpated from

303 Los Tuxtlas include *Sarcoramphus papa*, *Harpia harpyja*, and *Ara macao*.

304 Patten, Gómez de Silva, & Smith-Patten (2010) also documented the

305 extirpation of the latter two in Chiapas, Mexico. Many additional species have

306 also been categorized as endangered or threatened in the Sierra de Los

307 Tuxtlas (see Winker, 1997).

308   Our estimate of the average rate of avian losses from the station of 3.7

309 species per decade may not be directly comparable to other studies due to

310 differences in habitat and sampling, but it is similar to the rate of loss

311 observed at Barro Colorado Island by Robinson (1999) of 3.3 species per

312 decade. Our estimate, however, includes only those taxa captured in mist

313 nets, whereas Robinson's work included all species detected through

314 observation.

315   Of the eight species with data sufficient for statistical analysis that

316 showed local extirpation, six were lost between 1992 and 2004 (on the same

317 site), suggesting a continuing extirpation of species from the station.

318 Bierregaard & Lovejoy (1988, 1989) found that as surrounding habitat was

319 lost, species richness in remaining fragments increased as individuals

320 displaced from surrounding areas found their way to remaining forest

321 patches. This increased richness was limited by the lifespan of the individual

322 birds (Bierregaard & Lovejoy 1988, 1989). Unlike these studies, in which

323 forest patches were suddenly and completely isolated, the forest of the

324 Estación de Biología Los Tuxtlas was isolated gradually. Because extirpation

325 seems to be continuing, we expect declines and extinctions to continue for

326 some time at the station, even if no further deforestation occurs in the region

327 (Willis, 1974; Brooks, Pimm, & Oyugi, 1999, Robinson, 1999; Ferraz et al.,

328 2003).

329   Mechanisms for tropical bird species losses due to deforestation and

330 fragmentation probably include factors such as greater specialization as

331 compared to temperate birds, reduced dispersal abilities, lower population

332 densities, and patchy distributions (Robinson et al., 2004; Stratford &

333 Robinson, 2005; Moore et al., 2008; Rompré et al., 2007). Our assessment of

334 possible causes for the loss of these species reveals no definite patterns,

335 however, other than the predominant requirement of forested habitat. On

336 Barro Colorado Island in Lake Gatún, Panama, maturation of habitat and loss

337 of open areas was responsible for the decline in the island's avifauna (Willis,

338 1974; Karr, 1982). This is unlikely to be the case in Los Tuxtlas. Despite major

339 degradation of surrounding forests, the station has remained primary forest

340 with areas of second growth. A loss of sapling and seedling species has been

341 described (Dirzo & Miranda, 1990), but the overall structure of the forest

342   appears to have remained fairly stable. Vetter et al. (2011) found in a

343   meta-analysis of 30 studies that the effects of fragmentation are not subject

344   to simple generalities, and that they are highly site specific.

345   Los Tuxtlas is at the northernmost extent of the ranges of 13 of the 16

346   species we found to be declining or extirpated (Tables 3 and 4). Evidence is

347   mixed as to whether populations at the periphery of a species' range are

348   more vulnerable to extinction (Terborgh & Winter, 1980; Kattan,

349   Halvarez-Lopez, & Giraldo, 1994; Johnson, 1998). Los Tuxtlas is at the edge of

350   all species' geographic ranges endemic to Neotropical rainforest, so it is not

351   clear why this subset might be more subject to this phenomenon. The

352   elevational distribution of each of these species encompasses sea level to

353   750 m or more (Howell & Webb, 1995), and we consider this factor unlikely to

354   be responsible for the vulnerability of these particular taxa.

355   Although insectivores showed a trend toward being disproportionately

356   affected in our study, it was not significant. Elsewhere insectivores have been

357   shown to be particularly vulnerable to severe habitat change (e.g., Kattan,

358   Halvarez-Lopez, & Giraldo, 1994; Canaday, 1996; Johnson & Winker, 2010;

359   Vetter et al., 2011). Additionally, deforestation can negatively impact species

360   found in multi-species foraging flocks (Van Houtan et al., 2006), which are

361   important to many birds of tropical rainforest communities (Willis, 1966;

362   Morton, 1973; Buskirk, 1976; Rappole et al., 1983). Rappole & Morton (1985)

363   noted that *X. minutus,* one of the species showing a significant decline in our

364   study (Table 2) was a regular member of mixed flocks in the Sierra de Los

365   Tuxtlas.

366 We considered large-scale range shifts, perhaps from climate change,

367 as a possible cause for species loss, but this seems unlikely. At least some of

368 the species lost in our study appear to have persisted in the southern portion

369 of Los Tuxtlas near Volcán Santa Marta at least into the mid-1990s (Winker,

370 pers. obs.). If range shifts were the cause, species would likely have

371 disappeared region-wide and we would not expect only forest-related species

372 to be affected. Habitat loss and degradation seem to be the best

373 explanations for the losses observed, but exactly how these changes affected

374 each species remains unknown.

375 Another possible influence on mist-net captures, particularly in the

376 most recent, late winter/spring sampling periods, would be intra-tropical and

377 elevational movements in some of the study species (Ramos, 1983, 1988).

378 There is evidence that *C. flaveola* and *E. flavogaster* move seasonally within

379 the tropics, seemingly to breed in Los Tuxtlas then departing (Ramos &

380 Rappole, pers. obs.). Vega Rivera (1982) found probable elevational

381 movements in *M. sulphureipygius.* The local extinctions of seven of the 16

382 species are particularly notable. *C. flaveola* is a widely distributed species

383 known to thrive in manipulated habitats such as gardens and forest edges

384 and is a generalist frugivore and nectarivore (pers. obs.; Howell & Webb,

385 1995). This is not a species we would expect to decline due to forest

386 fragmentation; both its habitat and food preferences are well suited to

387 survival in a mosaic landscape, and it is known to persist in a fragmented

388 landscape elsewhere in northern Middle America (Johnson & Winker, 2010).

389 Intratropical migrations of *C. flaveola* may partially explain the changing

390   capture rates in this species (Ramos & Rappole, pers. obs.). *O. semiflavum*

391   and *L. amaurocephalus* are both edge specialists; thus, limited

392   fragmentation, creating an increase in edges, might *a priori* seem to benefit

393   these species. Though the habitat protected by the station has remained

394   relatively static, the intensity of lowland deforestation in Los Tuxtlas as a

395   whole (Fig. 2) may be too extensive even for these edge specialists. *L.*

396   *souleyetii* prefers open forest and partially cleared areas (Howell & Webb,

397   1995). The habitat surrounding the station during the 1980s and 1990s was

398   dominated by pasture scattered with isolated trees. In our later field seasons

399   there was a noticeable decline in the number of isolated trees and fences

400   constructed of living trees (Winker, pers. obs.). This loss may account for the

401   extirpation of *L. souleyetii. G. spirurus* apparently disappeared from the

402   station between the 1970s and 1986, the first of the documented

403   extirpations. The majority of deforestation across the region took place

404   during this period. This previously abundant species disappeared from our

405   data in just over a decade. Interestingly, on the slopes of neighboring Volcán

406   Santa Marta the species was present at least into the 1990s and probably still

407   persists there (Winker, pers. obs.). Also, Estrada, Coates-Estrada, & Merritt

408   (1997) had observational data of the species' presence in the station area in

409   1990-1992, indicating at least a decline if not extirpation (Table 2). In Brazil,

410   *G. spirurus* persisted in experimentally isolated fragments well after isolation

411   (Stouffer & Bierregaard 1995), and the species persists in highly fragmented

412   forest in southern Belize (Johnson & Winker, 2010). *H. momotula* was

413   collected but not netted in 1974, was captured in substantial numbers during

414 1986 and 1992-94, but was absent in the last two seasons of sampling. This

415 pattern is mysterious. This species has an elevational range extending to

416 1500 m and may persist in the forests of the upper slopes of Volcán San

417 Martín. If so, we speculate that the station may serve as a sink for this

418 species, where habitat is insufficient for a self-sustaining population but may

419 occasionally be colonized by dispersing individuals (see also Winker et al.,

420 1997). Continued sampling may provide more insight into its abundance

421 patterns. It illustrates the need for improved understanding of

422 species-specific dispersal behavior within and among forest fragments (e.g.,

423 Van Houtan et al., 2007; Moore et al., 2008; Ibarra-Macias, Robinson, &

424 Gaines 2011), which may be an important driver for patterns such as those

425 we observed.

426   Two other studies provide comparative value to our results. The four

427 species we consider likely extirpated (*Taraba major*, *Formicarius analis*,

428 *Grallaria guatimalensis,* and *Schiffornis turdina*) were not detected in the

429 much broader census surveys of Estrada, Coates-Estrada, & Merritt (1997) in

430 1990-1992. Patten, Gómez de Silva, & Smith-Patten (2010) conducted the

431 geographically closest long-term study to ours in their analysis of avian

432 declines at Palenque, Chiapas, Mexico. Their results showed only three

433 species that overlapped our results. They found *Eucometis penicillata*

434 extirpated (to our decline) and two others that declined as our populations

435 did (*Xenops minutus* and *Leptopogon amaurocephalus*). Indeed, the

436 species-level heterogeneity between our studies is noteworthy.

437   Our analyses suggest that the Estación de Biología Tropical Los Tuxtlas

438 is too small to maintain its full, historic complement of bird species. If

439 deforestation accelerated region-wide, eliminating other forest refugia, the

440 station alone (640 ha) would be unable to maintain the historical avian

441 diversity of the region or to provide source populations for restored forest

442 habitats for many of its present bird species. Given the scale of deforestation

443 in the region, it is surprising that there are not more species showing

444 declines. Indeed, we may consider it good news that important forest seed

445 dispersers such as *Habia* tanagers (Puebla & Winker, 2004) did not show

446 significant declines. The overall size of the remaining forests, particularly in

447 the highlands, may be ameliorating the effects of lowland deforestation.

448 However, increasing or continued isolation of the station will probably limit

449 recolonization from elsewhere, and species losses will likely continue.

450   In our study, although several species seemed to quickly succumb to

451 local and regional deforestation, others showed delayed declines and

452 extirpations, a phenomenon also known to happen at larger scales (Tilman et

453 al., 1994, Pimm et al., 2006). Moreover, the effects of deforestation were

454 remarkably heterogeneous among forest-related species, with no single clear

455 pattern of why some species experienced declines or extirpation. Our

456 long-term data suggest that predicting which species will be most affected by

457 deforestation in the northern Neotropics, and thus effectively working to

458 ameliorate the effects of forest loss, will be particularly challenging.

459 Nevertheless, as similar long-term datasets accrue, subtle patterns may

460 reveal how species-specific responses reflect underlying commonalities that

461 can be exploited for effective management and conservation.

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Figure captions

Figure 1. 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 arrow (image from GoogleEarth, 2005).

Figure 2. Comparative views of Volcán Santa Marta and San Martin Pajapan in

the southern Sierra de Los Tuxtlas from 1973 (top; NASA/Skylab) and 2005

(bottom; GoogleEarth) showing extent of deforestation, particularly severe in

the lowlands.

Figure 3. Maps of the study area in the northern lowlands of the Sierra de Los

Tuxtlas 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.

Figure S1. Species accumulation curve for a representative year with below

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

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737   Fig. 1

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742   Fig. 2

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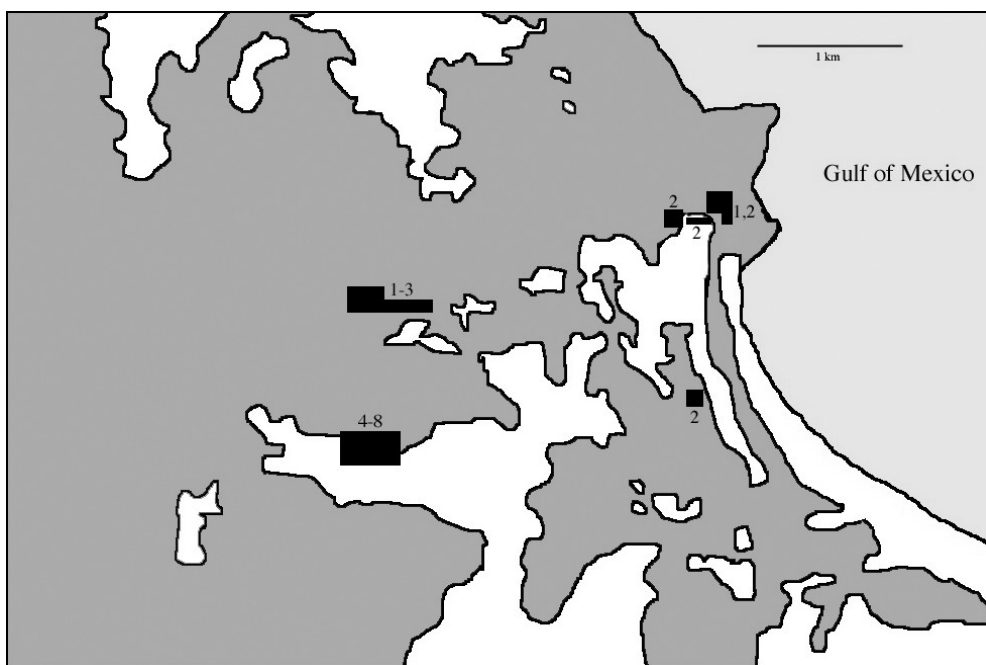
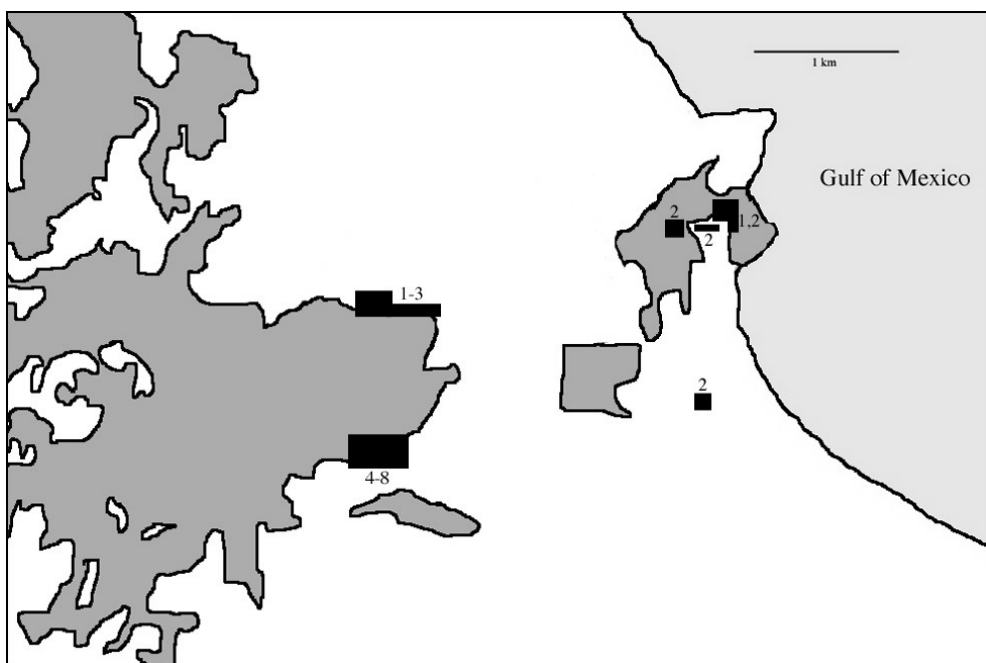
747   Fig. 3

Tables 1 through 4

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. 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 α = 0.05.

Species	*F*	*P*	R^2	Last captured
Phaethornis striilgularis [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 souleyetii [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.

^b Species showing an increase in abundance.

^c Species showing a significant decline.

^d Species not captured in later sampling periods.

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

Species	Seasons Captured	Presence	Comments
Micrastur ruficollis	1	Y	observed
Crypturellus boucardi	3	Y	observed
Heliomaster longirostris	1	?	hummingbird
Florisuga mellivora	1	?	hummingbird
Chlorostilbon 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
Thraupis abbas	1	Y	observed
Thraupis episcopus	2	Y	observed
Saltator atriceps	1, 2	Y	observed
Molothrus aeneus	1	Y	observed

Table 4. 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).

Species	Habitat preference	Foraging guild	Elevational distribution (m)	Geographic distribution
Phaethornis striilgularis	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.