1 LRH: Mayhew *et al.*

2 RRH: BIRD COMMUNITIES IN SECONDARY FOREST

3

4

5

6 **Connectivity with primary forest determines the value of secondary tropical forests for**

7 **bird conservation**

8

9

10 Rebekah J. Mayhew[1, 4], Joseph A. Tobias[2], Lynsey Bunnefeld[1], and Daisy H. Dent[1, 3]

11

12

13 [1]Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, UK.

14 [2]Department of Life Sciences, Imperial College London, Silwood Park, Buckhurst Road, Ascot,

15 Berkshire, SL5 7PY, UK.

16 [3]Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Panama.

17

18 [4]Corresponding author; email: rebekah.j.mayhew@gmail.com

19

24 **ABSTRACT**

25

26 Species extinctions caused by the destruction and degradation of tropical primary forest may be

27 at least partially mitigated by the expansion of regenerating secondary forest. However, the

28 conservation value of secondary forest remains controversial, and potentially underestimated,

29 since most previous studies have focused on young, single-aged, or isolated stands. Here we use

30 point count surveys to compare tropical forest bird communities in 20–120-yr-old secondary

31 forest with primary forest stands in central Panama, with varying connectivity between

32 secondary forest sites and extensive primary forest. We found that species richness and other

33 metrics of ecological diversity, as well as the combined population density of all birds, reached a

34 peak in younger (20-yr-old) secondary forests, and appeared to decline in older secondary forest

35 stands. This counter-intuitive result can be explained by the greater connectivity between

36 younger secondary forests and extensive primary forests at our study site, compared with older

37 secondary forests that are either (1) more isolated, or (2) connected to primary forests that are

38 themselves small and isolated. Our results suggest that connectivity with extensive primary

39 forest is a more important determinant of avian species richness and community structure than

40 forest age, and highlight the vital contribution secondary forests can make in conserving tropical

41 bird diversity, so long as extensive primary habitats are adjacent and spatially connected.

42

43

ABSTRACT IN SPANISH

La extinción de especies causada por la destrucción y la degradación del bosque tropical primario puede ser mitigada, en cierta parte, por la expansión del bosque secundario. Sin embargo, la importancia del bosque secundario para la conservación es un tema controversial y potencialmente subestimado ya que la mayoría de los estudios previos se han centrado en bosques muy jóvenes de una sola edad, o aislados de bosques con diferentes edades. En este estudio utilizamos puntos de conteo para comparar las comunidades de aves en bosques secundarios de 20 a 120 años de edad y en bosques primarios en Panamá, y con conectividad variable entre los bosques secundarios y los bosques primarios. Encontramos que la riqueza de especies, y otras métricas de la diversidad ecológica, alcanzaron su máximo en los bosques secundarios más jóvenes (20 años de edad) y parecieron disminuir en los bosques secundarios más antiguos. Este resultado aparentemente contradictorio se puede explicar por la mayor conectividad entre los bosques secundarios más jóvenes y los bosques primarios de gran extensión, y porque los bosques secundarios más antiguos están (1) más aislados o (2) están conectados a bosques primarios aislados y de menor extensión. Nuestros resultados indican que la riqueza de especies y la estructura de la comunidad de aves dependen más de la conectividad entre bosques primarios extensos que de la edad del bosque. Así mismo, nuestros resultados resaltan la importancia de los bosques secundarios para la conservación de las aves tropicales, especialmente estos son contiguos y están conectados a bosques primarios extensos.

68 BETWEEN 2010 AND 2015 THERE WAS AN ANNUAL LOSS OF APPROXIMATELY 7.6 MILLION HA of

69 forest globally, with most of this deforestation occurring in the tropics (FAO 2015). Most of the

70 world's biodiversity is found in the tropics (Dirzo & Raven 2003), and the continued loss and

71 degradation of tropical forests is likely to cause mass species extinctions (Dent & Wright 2009,

72 Wright & Muller-Landau 2006). It has been proposed that primary forest (PF) losses may be

73 offset by the planting and natural regeneration of secondary forests (SF) on previously deforested

74 land (Wright 2005). However, the long-term conservation value of SF depends on whether these

75 habitats can maintain similar species composition and ecosystem functions as PF (Chazdon *et al.*

76 2009, Dent & Wright 2009).

77   Many studies that assess the conservation value of tropical SF have focused on birds, one

78 of the best studied faunal groups in the tropics (e.g. Barlow *et al.* 2007b, Lees & Peres 2006,

79 Robinson 1999, Stotz *et al.* 1996, Willis 1974). Birds provide important ecosystem services, such

80 as pollination and seed dispersal (Sekercioglu 2006, Whelan *et al.* 2008), and their diverse

81 habitat and dietary requirements often lead to species-specific responses to habitat disturbance

82 (Hughes *et al.* 2002, Petit & Petit 2003). Birds are also convenient indicators for ecological

83 assessments because they are relatively easy to identify and survey.

84   Studies comparing avian species richness and community structure in SF and PF report

85 inconsistent results. Some studies have found equivalent or higher species richness in SF

86 compared to PF (Andrade & Rubio-Torgler 1994, Blake & Loiselle 2001, Borges 2007, O'Dea

87 & Whittaker 2007, Schulze & Waltert 2004), while other studies report reduced species richness

88 in SF (Barlow *et al.* 2007b, Bowman *et al.* 1990, Gibson *et al.* 2011, Terborgh & Weske 1969,

89 Tvardíková 2010). These conflicting results may stem from three key factors: the age of SF

90 studied, the landscape context, and the responses of different avian groups to habitat change.

91   In terms of SF age, most studies examining avian diversity in tropical SF have only

92   included relatively young, and single-aged stands (less than 35 yr; e.g. Barlow *et al.* 2007b,

93   Blake & Loiselle 2001, Borges 2007, Terborgh & Weske 1969). With increasing forest age, SF

94   typically develops greater structural complexity, resembling PF over time (Guariguata &

95   Ostertag 2001, Pena-Claros 2003). More complex forest structure offers an increased breadth of

96   ecological niches for forest birds (DeWalt *et al.* 2003, Zahawi *et al.* 2015). Thus, the structural

97   complexity that develops over SF succession should provide habitats for increasingly diverse and

98   complex bird communities (MacArthur & MacArthur 1961, Casas *et al*. 2016). Studies focusing

99   on young SF may therefore underestimate the longer-term value of SF for bird conservation.

100   While estimates of avian species richness in young SF are often inflated by non-forest species,

101   species composition in young tropical SF tends to differ from PF (Barlow *et al.* 2007a, Borges

102   2007, Tvardíková 2010). With increasing time since abandonment both forest structure and bird

103   communities become more similar to those of PF (Andrade & Rubio-Torgler 1994, Borges 2007,

104   Raman 1998). Thus estimates of conservation value need to consider the recovery of forest

105   species composition and abundance rather than richness alone.

106   The landscape context of SF, defined by connectivity to PF source populations and

107   isolation within the countryside matrix, plays a critical role in determining avian community

108   reassembly (Chazdon *et al.* 2009, Dent & Wright 2009, Wolfe *et al.* 2015). Many tropical forest

109   birds are highly dispersal limited with poor gap-crossing abilities, and may not be able to

110   colonise SF unless it is contiguous with PF (Van Houtan *et al.* 2007, Lees & Peres 2009, Moore

111   *et al.* 2008, Tobias *et al.* 2013). In addition, bird species occurring in isolated SF embedded

112   within a non-forest matrix may be more sensitive to random population fluctuations and local

113   extinction. Connectivity to PF is an important factor in SF recovery, and the species composition

114   of bird communities in isolated SF may never fully converge with that of PF (Jones *et al.* 2016,

115   Wolfe *et al.* 2015).

116   Finally, the response of bird species to forest succession may be mediated by their degree

117   of ecological specialisation. It has been suggested that generalist, migratory or forest-edge

118   species proliferate in SF as their wider niche breadth makes them better adapted to the conditions

119   found in younger forest (Barlow *et al.* 2007b, Stotz *et al.* 1996). By contrast, forest specialists

120   are likely to require foraging and nesting resources only found in more mature forest (Barlow *et*

121   *al.* 2007b, DeWalt *et al.* 2003). Forest isolation has also been shown to adversely affect forest-

122   dependent, understorey insectivore species more severely than other functional groups (Bradfer-

123   Lawrence *et al.* 2018, Barlow *et al.* 2006, Ferraz *et al.* 2007, Stouffer *et al.* 2006). Thus, the

124   conservation value of SF for birds is affected by species-specific responses mediated by both site

125   and landscape factors, including habitat age, and level of isolation and connectivity to PF.

126   Here, we examine the species richness and composition of bird communities in central

127   Panama across the longest SF chronosequence studied to date, spanning forest ages from 20 to

128   120 yr, as well as PF controls (see Fig. 1). Across this age gradient, we sampled forests that were

129   either isolated from or connected to extensive PF. This landscape presents an opportunity to

130   examine how bird communities change across both successional and isolation gradients, and to

131   investigate the relative importance of forest age versus isolation in determining the conservation

132   value of SF. Including forest age and landscape context introduces a new level of complexity to

133   classical forest fragmentation studies, which arguably reflects the reality of most human-

134   modified tropical forest landscapes.

135   In this context, we assessed the relative role of secondary forest age versus connectivity

136   with primary forest in determining bird diversity – estimated as (1) bird species richness and

137   other diversity metrics, (2) bird population density, and (3) the similarity of avian community

138   composition to PF. In all cases, we examined the extent to which variation in bird communities is

139   mediated by landscape context, such as isolation by water barriers.

140

141   **METHODS**

142

143   STUDY SITES. – We conducted field surveys in the Panama Canal Watershed, where vegetation is

144   classified as tropical moist forest (Holdridge & Budowski 1956). The climate is seasonal with a

145   distinct dry season, typically from mid-December until early May, and annual rainfall of 1900 –

146   3600mm (Windsor, 1990; Turner et al. 2015). We selected study sites in the Barro Colorado

147   Nature Monument, Soberania National Park and the adjacent Agua Salud Project (Fig. 1). The

148   Barro Colorado Nature Monument (5,600 ha; 9°9' N, 79°51' W) is comprised of five peninsulas

149   and Barro Colorado Island (BCI), all situated in Lake Gatun, which was formed in 1914 by the

150   flooding of the Panama Canal. The Barro Colorado Nature Monument is a mosaic of PF mixed

151   with SF stands of different ages that were used for cattle pasture or fruit production between the

152   1880s and the establishment of the park in 1979 (Leigh *et al.* 1982). Soberania National Park

153   (22,000 ha; 9°9' N, 79°44' W) was established in 1980 and is a mix of PF and very old SF (Van

154   Bael *et al.* 2013). The Agua Salud Project research site (664 ha; 9°13' N, 79°47' W) was once

155   predominantly cattle pasture or small-scale shifting cultivation but, after establishment in 2008,

156   the landscape is now predominantly SF of relatively young age (Van Breugel *et al.* 2013). The

157   difference in annual rainfall between our northernmost and southernmost sites (separated by a

158   latitudinal distance of 9.8 km) is 159 mm pa (Rompre *et al.* 2007). As this variation is minor

159 compared to a difference of 2100 mm pa across the full rainfall gradient in Central Panama

160 (Rompre *et al.* 2007), we treated the study area as a single climatic band (see Fig. 1).

161

162 SITE SELECTION. – We selected secondary forest sites along a chronosequence of approximately

163 20, 40, 60, 90 and 120 yr since abandonment, with two replicates per forest age. We selected

164 sites within existing research areas having data on long-term vegetation dynamics, tree

165 communities and accurate age estimates compiled from historical records, aerial photographs and

166 interviews with residents; for details see Denslow & Guzman (2000) and van Breugel et al.

167 (2013). The youngest SF in the Barro Colorado Nature Monument is 40-yr-old, while SF in

168 Agua Salud is 10–34 yr old (mean = 19 yr old). For ease of presentation, we refer to Agua Salud

169 sites as 20-yr-old. We selected four PF sites: two in a relatively small patch (c. 800 ha) of

170 isolated PF on Barro Colorado Island (henceforth referred to as isolated PF) and two in an

171 extensive area of mainland PF in Soberania National Park (c. 22,000 ha; henceforth referred to as

172 extensive PF). The PF are at least 500 yr old and there is no indication that they have ever been

173 logged or cultivated (Piperno 1990). There is no ongoing disturbance (such as logging or

174 hunting) in Barro Colorado Nature Monument, whereas in Agua Salud there may be some forest

175 clearance and disturbance in the wider landscape. Across the Barro Colorado Nature Monument

176 chronosequence, average canopy height and structural complexity increases with SF age

177 (DeWalt *et al.* 2003, Mascaro *et al.* 2012). Further details of vegetation structure and

178 composition are available in Dent *et al.* (2013), DeWalt *et al.* (2003), and Mascaro *et al.* (2012).

179   Habitat patch size is an important determinant of species' persistence in fragmented

180 landscapes (Bender *et al.* 1998). However, the importance of patch size relates to the

181 composition of the surrounding matrix. The SF sites in our study are embedded within a mixed-

182　age forest matrix, which buffers the effects of fragment size and limits our ability to accurately

183　calculate areas of single-aged fragments. The three forest areas in which study sites are

184　embedded include Barro Colorado Island (1,560 ha), Gigante peninsulas (2,600 ha), and

185　Soberania National Park and surrounding contiguous forest (22,000 ha; see Fig. 1 for details).

186　The SF and PF sites in this study experience different connectivity. The 20-yr-old Agua Salud SF

187　sites form part of a large forest network connected to extensive PF in Soberania National Park,

188　while both island and peninsula SF sites are smaller, isolated areas of forest surrounded by water.

189　Island SF sites (90–120 yr old) are connected only to isolated PF, and are separated from

190　extensive mainland PF by water. Secondary forest on the Gigante Peninsula is more extensive,

191　and contains older patches (>200 yr old) interspersed with patches of 40–60 yr old SF, but is

192　separated from extensive PF by either water or agriculture. We sampled PF sites on both island

193　and mainland settings to examine the effects of different types and extents of forest isolation, and

194　to provide a baseline for studying the effects of SF age on bird communities. Due to the

195　restrictions of available PF and SF in the study landscape, it was not possible to replicate within

196　categories (e.g., isolation type x isolation extent x forest type), and even where replicates were

197　possible, the sampling design is weakened because some sites are embedded within the same

198　geographical feature (e.g. BCI) and therefore to some extent non-independent. We take these

199　factors into account in our analyses (see below) and emphasise that the study landscape has

200　distinct advantages—not least the comparison across different levels of isolation, and the

201　availability of background data on the history of forest regeneration—which provide a unique

202　opportunity to understand secondary forests in a spatial and temporal context.

203

204 BIRD SURVEY METHODS. - At each of the 14 sites, we established nine point counts with each

205 point separated by a minimum of 100 m from other points, and by at least 50 m from forest of a

206 different age (Van Bael *et al.* 2013, Robinson *et al.* 2000). Two trained observers surveyed one

207 site per morning, with the first count beginning ten mins before sunrise and the last completed by

208 10:30 h. All nine stations at a site were sampled once during a survey visit, with a minimum of

209 three days between surveys; no surveys were conducted on days with heavy rain or strong wind

210 because these limit bird activity and detectability.

211   Point counts were 10 mins in duration, and all birds seen or heard within a 50 m-radius

212 were identified, following previous studies (De Bonilla *et al.* 2012, Martin & Blackburn 2014,

213 O'Dea & Whittaker 2007, Raman & Sukumar 2002). Limiting counts to a 50 m radius can help

214 to reduce the differences in detectability of birds among habitat types due to vegetation structure,

215 and minimises biases and errors in species identification and distance estimates (Petit *et al.*

216 1995). For each bird seen or heard, observers used a laser rangefinder to estimate the Euclidean

217 distance from the centre of the point count to the bird (Buckland *et al.* 2008). Distance estimates

218 to birds detected only by ear are likely to be less consistent than estimates based on visual

219 detections, but in most cases the location of calling birds can be judged reasonably accurately.

220 Birds flying above the canopy were excluded from the survey. Along with the point count data,

221 we kept a list of additional species encountered as we walked between the point count stations

222 during a survey. We conducted surveys over three years: July to October 2014 (wet season),

223 January 2015 and January to March 2016 (dry season). Each site was surveyed a total of ten

224 times over the three years; five times in the wet season and five times in the dry, giving a total of

225 1,260 point counts.

226   Observers had considerable ornithological field experience, including in tropical forest

227   habitats. Two observers were Panamanian, with many years' experience identifying local

228   avifauna. All observers received training before data collection began, including detection tests

229   to check for any bias in identification ability and for consistency in estimations of distance.

230   Recordings of calls and songs were used intensively to improve identification skills and check

231   identifications based on vocalisations.

232

233   DATA ANALYSIS. - Prior to analysis, we removed unidentified birds from the dataset (1.8% of

234   total number of detections). We conducted all analyses both on the remaining bird species

235   (henceforth, all birds), and on a dataset restricted to birds with a higher dependency on forest

236   habitats (henceforth, forest specialists). We defined forest specialists as species characteristic of

237   the interior of undisturbed forest, breeding almost invariably within forests, occurring less often

238   away from forest interior and rarely seen in non-forest habitats, even though they may persist in

239   secondary forest and forest patches if their particular ecological requirements are met (BirdLife

240   International 2018, Buchanan *et al.* 2011). We note that classification of forest dependency in

241   birds is potentially subjective, partly because species vary in their habitat selection

242   geographically. We used the most recent classification of forest specialism (BirdLife

243   International 2018) because it is global in focus, comprehensive and widely accessible. We

244   found results to be very similar when we used alternative, geographically restricted

245   classifications of forest dependency, including published descriptions by Ridgely & Gwynne

246   (1989), habitat codes of Stotz *et al.* (1996), and habitat scores of Tobias *et al.* (2016).

247   We calculated rarefaction curves to compare rates of species accumulation among forest

248   age classes for all birds and forest specialists. When scaled by the number of samples, curves

249   reached or approached the asymptote for all forest ages and species sets, suggesting survey effort

250   was adequate (Fig. S1 and S2). However, curves did not reach asymptotes for some forest ages

251   and species sets when scaled by individuals, suggesting some sites were under-sampled (Fig. S1

252   and S2). To identify species that were missing from the extensive PF dataset, we compared our

253   dataset to the species list reported in a previous survey of the same extensive PF forest (Robinson

254   *et al.* 2000). This long-term study used intensive survey methods to describe the species

255   composition of the extensive PF site and so provides a complete picture of the species present at

256   this locality.

257   We calculated species richness and the percentage of PF species present in SF by

258   combining both the point count data and the additional species encounters. All other analyses

259   used data from point counts only. We conducted analyses using R (Version 3.4.1, R Core Team

260   2017).

261

262   SPECIES RICHNESS, DIVERSITY AND DOMINANCE. - We compared species richness, Shannon-

263   Weiner diversity indices and dominance across forest ages using data from all surveys combined.

264   We calculated dominance as the percentage of individual birds represented by the five most

265   common species in each site.

266

267   BIRD POPULATION DENSITY. - We used the R package 'Distance' (Laake *et al.* 2015) to estimate

268   bird community population density among forest ages pooled over the 1,260 point counts,

269   following methods described in Buckland *et al.* (2015). We pooled visual and audial detections,

270   and stratified analyses by forest age to allow for differences in detectability among habitats.

271   Using the function 'ds' ('Distance' R package; Laake *et al.* (2015), we fitted 36 detection

272   functions with various combinations of covariates (year, season, detection method and observer)

273   per forest age and used AIC model selection to choose the best-fit models (Burnham *et al.* 2011).

274   The detection functions provided an estimation of bird population density (number of individuals

275   per hectare) in each of the forest ages. The function 'ds' requires a minimum of 80 observations

276   within a category to give reliable estimates per species, thus we did not calculate detection

277   functions for individual species, since only 4–9 bird species in each forest age category had more

278   than 80 detections. Our results should be interpreted with caution since pooling community

279   detectability data assumes that each species is equally detectable across each of the 14 sites.

280

281   SPECIES COMPOSITION AND SIMILARITY TO PRIMARY FOREST. – We calculated the percentage of

282   bird species detected in PF that were also detected in SF separately for isolated PF and extensive

283   PF sites by pooling data for each forest age category.

284   We used the Morisita-Horn abundance-based similarity index (S_{MH}) to compare species

285   composition between pairs of assemblages. The S_{MH} is robust to uneven and insufficient

286   sampling and thus suited to determine if reassembly of PF communities occurs in SF in terms of

287   relative abundance (Chao *et al.* 2006). We examined whether species composition of SF

288   converged with either isolated PF or extensive PF over time by comparing the similarity in

289   composition (S_{MH}) of each SF forest site to each of the PF sites. We examined similarity to

290   isolated and extensive PF sites separately because isolation-related extirpations have altered the

291   island bird communities (Robinson 1999). Similarity values were produced using the function

292   'vegdist' ('vegan' R package; Oksanen et al., 2016).

293   To determine if forest age or geographic location explained patterns in species

294   composition across sites, we performed Mantel tests on three matrices of pair-wise distances

295   among sites: Euclidean geographic distance, difference in forest age, and dissimilarity in species

296   composition ($1 - S_{MH}$). We assigned PF sites a nominal age of 500 yr to include these sites in the

297   distance matrix for forest age. Mantel tests were performed using the function 'mantel' ('vegan'

298   R package; Oksanen et al., 2016).

299   We explored qualitative similarities in species composition among sites with non-metric

300   multidimensional scaling (NMDS; Anderson *et al*. 2011). This approach uses rank order, rather

301   than absolute abundances of species, to represent the original position of communities in

302   multidimensional space as accurately as possible using a reduced number of dimensions. We

303   used similarity matrices generated from both the S_{MH} abundance-based and Jaccard incidence-

304   based similarity values (S_J). We included the S_J similarity values to investigate whether PF

305   species were present in SF, even if patterns of relative abundance were different from those in

306   PF. Ordinations were performed using the function 'metaMDS' ('vegan' R package; Oksanen et

307   al., 2016).

308   To assess the significance of observed differences in species composition as related to SF

309   age, isolation level (isolated or connected), forest type (SF or PF) and distance to extensive PF,

310   we conducted a series of permutational MANOVAs, an analysis of variance using distance

311   matrices. This analysis uses pseudo-F values to compare among-group to within-group similarity

312   and assesses significance by permutation. We also investigated the effect of season (wet or dry)

313   on species composition by conducting a permutational MANOVA at survey level. Permutational

314   MANOVAs were produced using the function 'adonis' ('vegan' R package; Oksanen et al.,

315   2016).

316   We calculated the mean number of migratory bird detections in different forest age

317   categories based on count data with no distance corrections. This gives a relative abundance of

318   migratory birds in habitats for those species with similar detection probabilities. We also used

319   the point count data to list the five most abundant species per forest age, and classified these

320   species using diet and habitat information from Ridgely & Gwynne (1989) and Wilman *et al.*

321   (2014).

322

323   **RESULTS**

324

325   Our surveys recorded a total of 183 bird species from 42 families, of which 55 species from 24

326   families were forest specialists (Table S1). We detected 13,894 individual birds in fixed radius

327   point counts, of which 5,256 were forest specialists (BirdLife International 2018).

328

329   PATTERNS OF SPECIES RICHNESS, DIVERSITY, AND DOMINANCE. - No clear relationship was found

330   between species richness and forest age (Table 1). The youngest SF (20-yr-old) had higher

331   species richness than all other sites, and a species richness of forest specialists similar to

332   extensive PF (Table 1). The oldest SF (120-yr-old) had the lowest species richness for all birds

333   and forest specialists. These counter-intuitive patterns of species richness appear to be influenced

334   by differences in connectivity among sites, with higher species richness found in sites that were

335   connected to extensive PF (Fig. 2). Compared with extensive mainland PF sites, the isolated PF

336   sites had lower species richness for both datasets. Species diversity (Shannon-Weiner index)

337   showed similar patterns across sites, while dominance values were highest in isolated sites and

338   lowest in connected sites (Table 1).

339

340 BIRD POPULATION DENSITY. - There was no clear pattern in bird community population density

341 estimates across the different forest ages or levels of isolation. For all birds, the 20-yr-old SF had

342 the greatest density of birds, estimated at 29 individual birds/ha (95% CI: 26, 31; Fig. 3). This

343 compares with the lowest density estimate of 17 individual birds/ha (95% CI: 16, 19) in the 120-

344 yr-old SF. Qualitatively similar patterns were found for forest specialists.

345

346 SIMILARITY TO PRIMARY FOREST. – Focusing on all birds, we found no clear relationship between

347 SF age and the percentage of PF bird species detected in SF sites (as estimated by our surveys),

348 but there was a relationship between isolation and percentage of PF species present in SF.

349 Percentage of PF species present was consistently highest in connected sites, and lower in

350 isolated sites. When comparing SF ages, we found that the highest percentage of PF species

351 occurred in the 20-yr-old connected SF (86% when compared with extensive PF sites as

352 estimated by our surveys; Fig. 4). Surprisingly, the 120-yr-old isolated SF had the lowest

353 percentage of PF species present, with only 72 percent in common with isolated PF and 57% in

354 common with extensive PF. This is likely due to shifts in species richness driven by isolation

355 effects in the island PF, where we detected just 62% of the species that we found in extensive

356 mainland PF.

357   For all birds, compositional similarity to isolated (but not extensive) PF increased with

358 forest age (Fig. 5). The highest similarity in species composition between PF and SF was

359 recorded on BCI where the community composition of the oldest isolated SF (120-yr-old; $n = 2$

360 sites) was very similar to isolated PF ($n = 2$ sites; similarity index [S_{MH}]: 0.87 ± 0.03). By

361 contrast, the lowest similarity was between the 20-yr-old SF and the isolated PF (0.58 ± 0.03);

362 these sites span the widest range in both isolation level (mainland vs. island) and age (20-yr vs.

363   PF). Similarity was higher between extensive PF sites and 20-yr-old SF (0.69 ± 0.03) than

364   between extensive PF sites and the older, isolated 120-yr-old SF (0.61 ± 0.04). Mantel tests

365   indicated that geographic distance among sites ($R^2 = 0.74$, $P = < 0.001$) explained a greater

366   proportion of variation in species composition than forest age ($R^2 = 0.30$, $P = < 0.05$). Similar

367   patterns were found for forest specialist species, except forest age was not a significant predictor

368   of species composition (geographic distance: $R^2 = 0.66$, $P = < 0.01$; forest age: $R^2 = 0.21$, $P =$

369   0.06).

370   The NMDS of abundance-based species composition (S_{MH}) across all bird species

371   showed a separation of sites in relation to both forest age and isolation level (Fig. 6). Sites

372   displayed a clear split along Axis 1 that related to site location (connected or isolated), while the

373   age of forest sites tended to increase along Axis 2. The NMDS comparisons for forest specialists

374   showed very similar patterns as those seen for all birds, as did the NMDS results for both

375   datasets using S_J, although the effect of forest age became less apparent when restricting analyses

376   to species presence/absence data (Fig. 6).

377   The permutational MANOVA using S_{MH} indicated that forest isolation level explained a

378   greater portion of the variation in community composition of all bird species than forest age or

379   forest type (SF vs PF; Table 2). Distance to extensive PF was not a significant predictor of

380   community composition. The permutational MANOVA using S_J for all birds showed very

381   similar results (Table 2). Season had a significant effect on community composition, but it did

382   not change the patterns observed for forest isolation, forest age or forest type, although distance

383   to extensive PF became significant (Table 2). Community composition of forest dependent

384   species (using S_{MH} or S_J) was largely dictated by forest connectivity. The same patterns were

385   found for forest specialists as the all-bird dataset when season was taken in to account (Table 2).

386

COMPOSITIONAL CHANGES. - The composition of the five most abundant bird species differed

across forest ages (Table S2). Only one species, Black-crowned Antshrike (*Thamnophilus*

atrinucha), was consistently abundant across all sites. Southern Bentbill (*Oncostoma olivaceum*)

was among the top five most abundant species in the youngest forest sites (20, 40 and 60-yr-old

SF), while Red-lored Amazon (*Amazona autumnalis*) appeared in the top five for both the

isolated and extensive PF, as well as the 90-yr-old SF. The five most abundant species in the

isolated and extensive PF, and the 90-yr-old SF exhibited a greater diversity of feeding guilds

and foraging strata than those found in the younger SF sites (Table S2).

We detected 15 species in isolated PF that we did not see in extensive PF, including

species such as Crested Guan (*Penelope purpurascens*) that are susceptible to hunting and

therefore extirpated from most mainland localities. By contrast, 44 species were detected in

extensive PF that were not seen in isolated PF. These were predominantly understorey,

insectivorous species, many of which have become extinct on BCI since its isolation (Robinson

1999, Willis 1974).

The number of migratory birds detected per point count was highest in the 20-yr-old SF

(0.533 ± 0.091) and declined with increasing SF age to only 0.078 ± 0.032 migrants detected per

point count in the 120-yr-old SF (Fig. S3). The number of migrants detected in PF sites was

about half the number detected in the 20-yr-old SF (island PF: 0.27 ± 0.07; mainland PF: $0.29 \pm$

0.06).

DISCUSSION

409

410   Our survey data, sampled across tropical SF of varying ages and isolation levels revealed that

411   variation in avian species richness was best explained by connectivity to extensive PF, rather

412   than forest age. We found the highest species richness in the youngest SF sites, which were

413   adjacent to extensive PF. Similarly, connectivity, rather than the forest age, was the strongest

414   predictor of community composition. Finally, the highest bird population density was also found

415   in younger SF, although broader patterns in density did not appear to be driven by either forest

416   age or connectivity.

417

418   SPECIES RICHNESS, DIVERSITY AND DOMINANCE. - High species richness and abundance of birds

419   in SF or successional areas has been documented in many studies (Blake & Loiselle 2001, Johns

420   1991, Karr 1976, Petit & Petit 2003), supporting the hypothesis that intermediate levels of

421   disturbance may lead to high species richness (Connell 1978). In general, species richness in

422   younger SF is boosted by an influx of non-forest, open habitat and generalist species, although it

423   also may contain an important component of forest species (Barlow *et al.* 2007b, Dunn &

424   Romdal 2005). Most studies report that species richness and community structure of tropical

425   secondary forests progressively approaches that of PF over time, and tends to track the

426   increasing structural complexity of secondary forests (Raman 1998, Dent & Wright 2009). In our

427   study, however, species richness and abundance did not increase with forest age, and were

428   instead highest in the youngest SF even when non-forest bird species were removed. We also

429   found that species richness and abundance both increased with greater connectivity to extensive

430   PF, suggesting that high species richness in the 20-yr-old SF is driven by proximity to extensive

431   PF in adjacent Soberania National Park.

432   Proximity to undisturbed habitats has been shown to increase the diversity of bird

433   communities in degraded sites (Johns 1991, Terborgh & Weske 1969, Waltert *et al.* 2004). In La

434   Selva, Costa Rica, PF was the primary habitat and source population for many of the bird species

435   found in SF (Blake & Loiselle 2001). This pattern is supported by our findings, in which a

436   greater number of forest specialists were found in well-connected 20-yr-old SF, than in isolated

437   PF. In a landscape of mixed ages of SF and varying connectivity among forest patches, our

438   findings suggest that the key factor determining avian diversity is connectivity to extensive PF,

439   rather than forest age. Extinction and colonisation dynamics shape the avifaunas of forests within

440   this landscape, with potentially lower colonization rates in isolated forest sites, and greater

441   colonisation rates in regenerating forests that are sufficiently well connected to PF (Robinson

442   1999, Bradfer-Lawrence *et al.* 2018).

443

444   BIRD POPULATION DENSITY. - The density of birds in SF and PF varied across sites, with the

445   highest density estimates in the youngest SF, matching patterns previously reported for the

446   Neotropics (Blake & Loiselle 2001, Johns 1991, Karr 1976, Petit & Petit 2003). Earlier studies in

447   Soberania National Park have reported densities 2–3 times higher than our PF estimates (Van

448   Bael *et al.* 2013, Robinson *et al.* 2000). The disparity in figures may result from differing

449   methodologies, particularly the spot mapping and smaller point count radius used by previous

450   studies. By contrast, previous population density estimates for young SF (5–6-yr-old) from Agua

451   Salud were about 45 percent lower than estimated population densities from our surveys (20-yr-

452   old), but comparable with our estimates from older SF (Van Bael *et al.* 2013). Higher population

453   density in younger forest may in part reflect increased detectability of some species, particularly

454   those associated with the forest canopy, which is harder to survey in PF (Robinson *et al.* 2018).

455   Our results may also reflect the increased resource availability of both fruit and insects often

456   found in younger SF (Blake & Loiselle 1991, Levey 1988, Martin 1985), which may encourage

457   birds from PF to use adjacent SF for foraging.

458

459   SIMILARITY TO PRIMARY FOREST. - Most studies comparing the similarity of avian species

460   composition between SF and PF report increasing similarity to PF with SF age (Borges 2007,

461   Dent & Wright 2009, Raman 1998). All our SF sites had high levels of compositional similarity

462   to PF, and upper figures were within the range of similarity found in extensive PF. In line with

463   our hypothesis, SF community composition became increasingly similar to that of isolated PF

464   across the chronosequence. However, SF community composition did not converge on that of

465   extensive mainland PF sites with increasing SF age. Similarly, there was no relationship between

466   SF age and the percentage of PF species detected: the highest percentage of PF species was

467   found in the youngest SF that, critically, was also the least isolated and most well-connected to

468   extensive PF.

469   Based on our findings, isolation plays a greater role than forest age in determining the

470   reassembly of bird communities in SF. Despite the persistence of high-stature PF forest on BCI,

471   many species have disappeared from the local community since it was isolated by the inundation

472   of Lake Gatun (Robinson 1999, Willis 1974). While habitat size effects and isolation by water

473   have influenced patterns local extinction, they do not appear to drive our results since peninsula

474   sites have similar bird communities to the island PF, with relatively low species richness. By

475   contrast, bird communities in extensive mainland PF sites include forest specialists that have

476   been lost from both BCI and peninsula sites, and are unlikely to recolonise SF unless it is

477   contiguous with PF that harbours these species. In summary, SF avian communities are at least

478   partially dependent on contiguous PF source populations. If connected PF populations have low

479   species richness then SF will likely never develop the bird communities associated with

480   extensive PF forest stands (Ferraz *et al.* 2007, Jones *et al.* 2016, Stouffer *et al.* 2006). However,

481   if SF sites are adjacent to extensive PF, forest specialists may recolonise relatively rapidly. For

482   example, understorey insectivores increased in abundance just 10 yr after SF was abandoned

483   adjacent to PF in Amazonia (Andrade and Rubio-Torgler, 1994). Our findings highlight that

484   connectivity is critical for reassembly of avian communities in regenerating tropical forests

485   (Barlow *et al.* 2006, Lees & Peres 2009).

486

487   COMPOSITIONAL CHANGES. - Despite the key role of connectivity in determining avian

488   composition, forest age may still influence bird community reassembly, as demonstrated by the

489   increasing similarity of communities in older isolated SF to that of isolated PF. However, six

490   forest species present in isolated PF on BCI were missing from the adjacent 120-yr-old SF,

491   including the forest specialists Long-billed Gnatwren (*Ramphocaenus melanurus*), Rufous

492   Mourner (*Rhytipterna holerythra*), Scaly-throated Leaftosser (*Sclerurus guatemalensis*),

493   Semiplumbeous Hawk (*Leucopternis semiplumbeus*), Spot-crowned Antvireo (*Dysithamnus*

494   *puncticeps*), and Wood Thrush (*Hylocichla mustelina*). Conversely there were no forest

495   specialists detected in the 120-yr-old SF that were not also present in the isolated PF. Although

496   several studies report a high representation of PF species present in SF (> 70% of PF species),

497   SF communities often lack rare species, or those with highly specialised dietary or habitat

498   requirements (Chazdon *et al.* 2009, Dent & Wright 2009).

499   The loss of forest species from isolated sites across this landscape is striking, and is

500   especially evident when comparing isolated PF with extensive PF. BCI is a relatively large forest

501   fragment (1560 ha), but it has been isolated for > 100 yr and during this time numerous avian

502   extinctions have been documented (Chapman 1938, Eisenmann 1952, Karr 1990, 1982,

503   Robinson 1999, Willis & Eisenmann 1979); 65 species have been lost from the island, including

504   30 forest species and 35 edge species (Robinson 1999). Many of the forest species missing from

505   the PF sites on BCI are understorey insectivores such as Dusky Antbird (*Cercomacroides*

506   *tyrannina*), Ocellated Antbird (*Phaenostictus mcleannani*) and Black-faced Antthrush

507   (*Formicarius analis*). In addition, we only detected two of the ten species identified by Robinson

508   (1999) as forest birds that are close to extirpation on BCI: Black-tailed Trogon (*Trogon*

509   *melanurus*) and Rufous Piha (*Lipaugus unirufus*). The isolation of BCI within a large waterbody

510   makes recolonization by many forest species unlikely as they are poorly adapted to sustained

511   flight, and unwilling or incapable of dispersing across open water (Moore *et al.* 2008, Tobias *et*

512   *al.* 2013).

513   Species richness and relative abundance of migratory birds was highest in younger SF,

514   with numbers decreasing with increasing SF forest age. Similarly, Van Bael *et al.* (2013) found

515   more migrant species in SF (5–6-yr-old) than PF sites in central Panama (0.5 and 0.2 birds/point

516   count for SF and PF respectively). Migrant birds may occupy degraded and open habitats

517   because they are excluded from optimal habitats by resident species, or because they are better

518   able to adapt to the resources offered by SF (Greenberg *et al.* 1994, Willis 1980, Wunderle &

519   Latta 1996). Our results add to a growing body of evidence confirming that secondary and

520   degraded tropical forests are important habitats for migrant bird species (Van Bael *et al.* 2007,

521   Greenberg *et al.* 1994, 1997, Wunderle & Latta 1996).

522   It is possible that other aspects of community structure, such as functional and

523   phylogenetic composition, may be affected by forest age and connectivity (Bregman *et al.* 2016,

524   Pigot *et al.* 2016). For example, if SF provides a simplified range of structural and dietary

525   resources for roosting and foraging birds then young forests may not be able to support as many

526   closely related or functionally similar species, resulting in functional and phylogenetic over-

527   dispersion (Bregman *et al.* 2016). In addition, isolation may increase functional and phylogenetic

528   clustering as certain groups are selected against due to their inability to cross gaps between forest

529   fragments (Bregman *et al.* 2016). Further studies are needed to clarify how forest successional

530   status and connectivity across the wider landscape interact to shape bird community

531   composition.

532

533   CAVEATS. – Our study design is limited by the historical and geographical features of the study

534   landscape, making it impossible to establish a fully replicated study within the different levels of

535   isolation and forest age (Denslow & Guzman 2000). Thus, some of the patterns detected may be

536   specific to the local context of water barriers associated with the Panama Canal. Nonetheless,

537   while further studies are now required to assess how far our conclusions can be generalised to

538   other tropical landscapes, we argue that the water barriers and detailed history of forest

539   regeneration in central Panama provide a valuable setting for testing the relative effects of

540   isolation and forest age on the conservation value of SF.

541   Effectively surveying birds across differing habitats remains a methodological challenge

542   for studies such as ours (Buckland *et al.* 2008). We standardised survey effort at all sites at the

543   risk of generating spurious differences in bird communities due to variation in detectability

544   (Bregman *et al.* 2016, Robinson *et al.* 2018). For example, it is possible that estimates of species

545   richness and population density in younger SF are inflated because (1) individual birds tend to be

546   more detectable at forest edges and in lower-stature forests (Barlow *et al.* 2007b, Buckland *et al.*

547   2008, Ruiz-Gutiérrez *et al.* 2010) and (2) PF bird species may have been missed by our surveys

548   because they are relatively quiet, inactive, inconspicuous or occur at low population densities

549   (Terborgh *et al.* 1990, Robinson *et al.* 2018). To explore how detectability may have affected our

550   results, we compared our species counts to a dataset from a previous study surveying the same

551   extensive PF site with more intensive survey methods (including mist-netting), over a far longer

552   survey period, and across an expanded set of species (Robinson *et al.* 2000). Overall, Robinson

553   *et al.* (2000) reported an additional 132 species in the community. However, the majority (65%)

554   of these were either unavoidably or deliberately excluded from our study because they fall into

555   one of three categories: 1) nocturnal, vagrant or migratory species which are not core

556   components of the diurnal communities we studied (45%), 2) aerial species (e.g. swifts and

557   raptors) (15%), and 3) birds associated with aquatic landscape features (5%). Because of our

558   study aims, we did not survey species in the second and third categories, and indeed discounted

559   all individual birds detected on waterbodies or in flight passing over the forest. Excluding these

560   species, 46 species from Robinson *et al.* (2000) were not observed, most of which are rare or

561   difficult to detect. While the absence of these 46 species from our censuses may underestimate

562   the importance of PF for conservation in our analysis, we note that this is a relatively minor

563   component of overall biodiversity and represents a small number of individual birds. Moreover,

564   increased surveying and mist-netting of our SF sites would no doubt also increase species

565   richness in SF by an unknown amount, thus we do not believe our main conclusions would be

566   altered by further surveying.

567   A separate issue relates to the breeding status or viability of populations of forest birds in

568   younger SF. It has been hypothesised that populations of many PF bird species in SF may be

569   non-viable, and therefore less important to conservation, because they are largely made up of (1)

570   transient individuals or (2) temporary territories with infrequent breeding and low breeding

571   success (Tobias *et al.* 2013). We cannot rule out this possibility based on our results, and more

572   research is needed to clarify population demography and viability in SF. However, the relatively

573   high population density of primary forest bird species in younger SF suggests that, at a

574   minimum, SF can greatly increase the population carrying capacity of adjacent PF, thus

575   increasing its importance for conservation.

576

577   CONCLUSIONS. - Our results suggest that the link between tropical bird communities and

578   successional trajectories differs between isolated and non-isolated SF sites; in isolated sites, bird

579   communities converge with isolated PF over time, whereas highly-connected SF sites converge

580   rapidly with extensive PF. In addition, we find evidence that SF, even when relatively young,

581   can support dense populations of PF species, so long as forests are connected to extensive PF.

582   Crucially, even if these populations are transitory, SF may theoretically increase the population

583   carrying capacity of PF, reducing the risk of local extinction. The importance of habitat

584   connectivity highlighted by our results is specifically relevant to tropical forests as species at

585   higher latitudes are often better adapted for survival in SFs or dispersal between patches of PF

586   (Stratford & Robinson 2005). These findings emphasise the importance of reforesting and

587   maintaining existing SF at the borders of extensive tropical forest, and highlight the need for

588   improved protection of SF in protected area buffer zones throughout the tropics.

589

590

591   **ACKNOWLEDGEMENTS**

592

603

604

605 **Data Availability:** Data available from the Dryad Digital Repository: https://doi.

606 org/10.5061/dryad.77m6100.

607

608

609 **LITERATURE CITED**

610 ANDERSON, M.J., T.O. CRIST, J. M. CHASE, M. VELLEND, B. D. INOUYE, A. L. FREESTONE, N. J.

611   SANDERS, H.V. CORNELL, L. S. COMITA, K. F. DAVIES, S. P. HARRISON, N. J. B. KRAFT, J. C.

612   STEGEN, N. G. SWENSON. 2011. Navigating the multiple meanings of beta diversity: A

613   roadmap for the practicing ecologist. Ecol. Lett. 14, 19–28.

614 ANDRADE, G. I., and H. RUBIO-TORGLER. 1994. Sustainable use of the tropical rain forest:

615   Evidence from the avifauna in a shifting-culitvation habitat mosaic in the Colombian

616   Amazon. Conserv. Biol. 8: 545–554.

617 VAN BAEL, S. A., P. BICHIER, I. OCHOA, and R. GREENBERG. 2007. Bird diversity in cacao farms

618   and forest fragments of western Panama. Biodivers. Conserv. 16: 2245–2256.

619 VAN BAEL, S. A., R. ZAMBRANO, and J. S. HALL. 2013. Bird communities in forested and human-

620   modified landscapes of Central Panama: a baseline survey for a native species reforestation

621   treatment. Int. J. Biodivers. Sci. Ecosyst. Serv. Manag. 9: 281–289.

622 BARLOW, J. T. A. GARDNER, I. S. ARAUJO, T. C. ÁVILA-PIRES, A. B. BONALDO, J. E. COSTA, M. C.

623   ESPOSITO, L. V. FERREIRA, J. HAWES, M. I. M. HERNANDEZ, M. S. HOOGMOED, R. N. LEITE,

624   N. F. LO-MAN-HUNG, J. R. MALCOLM, M. B. MARTINS, L. A. M. MESTRE, R. MIRANDA-

625   SANTOS, A. L. NUNES-GUTJAHR, W. L. OVERAL, L. PARRY, S. L. PETERS, M. A. RIBEIRO-

626   JUNIOR, M. N. F. DA SILVA, C. DA SILVA MOTTA, and C. A. PERES. 2007a. Quantifying the

627   biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl. Acad.

628   Sci. U. S. A. 104: 18555–60.

629 BARLOW, J., L. A. M. MESTRE, T. A. GARDNER, and C. A. PERES. 2007b. The value of primary,

630   secondary and plantation forests for Amazonian birds. Biol. Conserv. 136: 212–231.

631 BARLOW, J., C. A. PERES, L. M. P. HENRIQUES, P. C. STOUFFER, and J. M. WUNDERLE. 2006. The

632   responses of understorey birds to forest fragmentation, logging and wildfires: An

633   Amazonian synthesis. Biol. Conserv. 128: 182–192.

634 BENDER, D. J., T. A. CONTRERAS and J. FAHRIG. 1998. Habitat loss and population decline: a

635   meta-analysis of the patch size effect. Ecology 79: 517-533

636 BIRDLIFE INTERNATIONAL. 2018. World Bird Database. BirdLife Int. Available at:

637   http://www.birdlife.org [Accessed January 18, 2018].

638 BLAKE, J. G., and B. A. LOISELLE. 1991. Variation in resource abundance affects capture rates of

639   birds in three lowland habitats in Costa Rica. Auk 108: 114–130.

640   BLAKE, J. G., and B. A. LOISELLE. 2001. Bird assemblages in second-growth and old-growth

641   forests, Costa Rica: perspectives from mist nets and point counts. Auk 118: 304–326.

642   DE BONILLA, E. P.-D., J. L. LEÓN-CORTÉS, and J. L. RANGEL-SALAZAR. 2012. Diversity of bird

643   feeding guilds in relation to habitat heterogeneity and land-use cover in a human-modified

644   landscape in southern Mexico. J. Trop. Ecol. 28: 369–376.

645   BORGES, S. H. 2007. Bird assemblages in secondary forests developing after slash-and-burn

646   agriculture in the Brazilian Amazon. J. Trop. Ecol. 23: 469.

647   BOWMAN, D., J. WOINARSKI, D. SANDS, A. WELLS, and V. T. MCSHANE. 1990. Slash-and-burn

648   agriculture in the wet coastal lowlands of Papua New Guinea: response of birds, butterflies

649   and reptiles. J. Biogeogr. 17: 227–239.

650   BRADFER-LAWRENCE, T., N. GARDNER, and D.H. DENT. 2018. Canopy bird assemblages are less

651   influenced by habitat age and isolation than understory bird assemblages in neotropical

652   secondary forest. Ecol. Evol. DOI: 10.1002/ece3.4086.

653   BREGMAN, T. P., A. C. LEES, H. E. A. MACGREGOR, B. DARSKI, N. G. DE MOURA, A. ALEIXO, J.

654   BARLOW, and J. A. TOBIAS. 2016. Using avian functional traits to assess the impact of land-

655   cover change on ecosystem processes linked to resilience in tropical forests. Proc. R. Soc. B

656   Biol. Sci. 283 (1844): 20161289.

657   VAN BREUGEL, M., J. S. HALL, D. CRAVEN, M. BAILON, A. HERNANDEZ, M. ABBENE, and P. VAN

658   BREUGEL. 2013. Succession of ephemeral secondary forests and their limited role for the

659   conservation of floristic diversity in a human-modified tropical landscape. PLoS One. 8:

660   e82433.

661   BUCHANAN, G. M., P. F. DONALD, and S. H. M. BUTCHART. 2011. Identifying priority areas for

662   conservation: A global assessment for forest-dependent birds. PLoS One. 6: e29080

663   BUCKLAND, S. T., S. J. MARSDEN, and R. E. GREEN. 2008. Estimating bird abundance: making

664   methods work. Bird Conserv. Int. 18.

665   BUCKLAND, S. T., E. A. REXSTAD, T. A. MARQUES, and C. S. OEDEKOVEN. 2015. Distance

666   Sampling: Methods and Applications A. P. Robinson, S. T. Buckland, P. Reich, and M.

667   McCarthy (Eds.). Springer, London.

668   BURNHAM, K. P., D. R. ANDERSON, and K. P. HUYVAERT. 2011. AIC model selection and

669   multimodel inference in behavioral ecology: some background, observations, and

670   comparisons. Behav. Ecol. Sociobiol. 65: 23–35.

671   CASAS, G., B. DARSKI, P. M. A. FERREIRA, A. KINDEL, and S. C. MÜLLER. 2016. Habitat Structure

672   Influences the Diversity, Richness and Composition of Bird Assemblages in Successional

673   Atlantic Rain Forests. Trop. Cons. Sci. 9: 503-524.

674   CHAO, A., R. L. CHAZDON, R. K. COLWELL, and T. SHEN. 2006. Abundance-based similarity

675   indices and their estimation when there are unseen species in samples. Biometrics 62: 361–

676   371.

677   CHAPMAN, F. M. 1938. Life in an air castle. Appleton-Century, New York.

678   CHAZDON, R. L., C. A. PERES, D. H. DENT, D. SHEIL, A. E. LUGO, D. LAMB, N. E. STORK, and S.

679   E. MILLER. 2009. The potential for species conservation in tropical secondary forests.

680   Conserv. Biol. 23: 1406–17.

681   CONNEL, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science. 199: 1302–1310.

682   DENSLOW, J., and G. GUZMAN. 2000. Variation in stand structure, light and seedling abundance

683   across a tropical moist forest chronosequence, Panama. J. Veg. Sci. 11: 201–212.

684   DENT, D. H., S. J. DEWALT, and J. S. DENSLOW. 2013. Secondary forests of central Panama

685   increase in similarity to old-growth forest over time in shade tolerance but not species

686   composition. J. Veg. Sci. 24: 530–542.

687 DENT, D. H., and S. J. WRIGHT. 2009. The future of tropical species in secondary forests: A

688   quantitative review. Biol. Conserv. 142: 2833–2843.

689 DEWALT, S. J., S. K. MALIAKAL, and J. S. DENSLOW. 2003. Changes in vegetation structure and

690   composition along a tropical forest chronosequence: implications for wildlife. For. Ecol.

691   Manage. 182: 139–151.

692 DIRZO, R., and P. H. RAVEN. 2003. Global state of biodiversity and loss. Annu. Rev. Environ.

693   Resour. 28: 137–167.

694 DUNN, R. R., and T. S. ROMDAL. 2005. Mean latitudinal range sizes of bird assemblages in six

695   Neotropical forest chronosequences. Glob. Ecol. Biogeogr. 14: 359–366.

696 EISENMANN, E. 1952. Annotated list of birds of Barro Colorado Island, Panama Canal Zone.

697   Smithsonian Institution, Washington, D.C.

698 FAO. 2015. Global Forest Resources Assessment 2015. Rome.

699 FERRAZ, G., J. D. NICHOLS, J. E. HINES, P. C. STOUFFER, R. O. BIERREGAARD JR., and T. E.

700   LOVEJOY. 2007. A large-scale deforestation experiment: effects of patch area and isolation

701   on Amazon birds. Science. 315: 238–241.

702 GIBSON, L., T. M. LEE, L. P. KOH, B. W. BROOK, T. A. GARDNER, J. BARLOW, C. A. PERES, C. J.

703   A. BRADSHAW, W. F. LAURANCE, T. E. LOVEJOY, and N. S. SODHI. 2011. Primary forests are

704   irreplaceable for sustaining tropical biodiversity. Nature 478: 378–81.

705 GREENBERG, R., P. BICHIER, A. C. ANGON, and R. REITSMA. 1997. Bird populations of sun and

706   shade coffee plantations in Central Guatemala. Conserv. Biol. 11: 448–459.

707 GREENBERG, R., J. ORTIZ, and C. CABALLERO. 1994. Aggressive competition for critical

708   resources among migratory birds in the Neotropics. Bird Conserv. Int. 4: 115–127.

709   GUARIGUATA, M.R., and R. OSTERTAG. 2001. Neotropical secondary forest succession: changes

710   in structural and functional characteristics. Forest Ecol. Manage. 148: 185–206.

711   HOLDRIDGE, L. R., and G. BUDOWSKI. 1956. Report on an ecological survey of the Republic of

712   Panama. Caribb. For. 17: 92–110.

713   VAN HOUTAN, K. S., S. L. PIMM, J. M. HALLEY, R. O. BIERREGAARD, and T. E. LOVEJOY. 2007.

714   Dispersal of Amazonian birds in continuous and fragmented forest. Ecol. Lett. 10: 219–229.

715   HUGHES, J. B., G. C. DAILY, P. R. EHRLICH, and E. LETTERS. 2002. Conservation of tropical

716   forest birds in countryside habitats. Ecol. Lett. 5: 121–129.

717   JOHNS, A. D. 1991. Responses of Amazonian rain forest birds to habitat modification. J. Trop.

718   Ecol. 7: 417–437.

719   JONES, I. L., N. BUNNEFELD, A. S. JUMP, C. A. PERES, and D. H. DENT. 2016. Extinction debt on

720   reservoir land-bridge islands. Biol. Conserv. 199: 75–83.

721   KARR, J. 1982. Avian extinction on Barro Colorado island, Panama: a reassessment. Am. Nat.

722   119: 220–239.

723   KARR, J. R. 1976. On the relative abundance of migrants from the north temperate zone in

724   tropical habitats. Wilson Bull. 88: 433–458.

725   KARR, J. R. 1990. Avian survival rates and the extinction process on Barro Colorado Island,

726   Panama. Conserv. Biol. 4: 391–397.

727   LAAKE, J., D. BORCHERS, L. THOMAS, M. DAVID, and J. BISHOP. 2015. mrds: Mark-Recapture

728   Distance Sampling. R package version 2.1.14, http://cran.r-project.org/package=mrds.

729   LEES, A. C., and C. A. PERES. 2006. Rapid avifaunal collapse along the Amazonian deforestation

730   frontier. Biol. Conserv. 133: 198–211.

731   LEES, A. C., and C. A. PERES. 2009. Gap-crossing movements predict species occupancy in

732   Amazonian forest fragments. Oikos 118: 280–290.

733   LEIGH, E. G. J., S. A. RAND, and D. M. WINDSOR eds. 1982. The ecology of a tropical forest:

734   seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, DC,

735   USA.

736   LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird

737   abundance. Ecol. Monogr. 58: 251–269.

738   MACARTHUR, R. H. and J. W. MACARTHUR. 1961. On Bird Species Diversity. Ecology 42: 594–

739   598.

740   MARTIN, T. E. 1985. Selection of second-growth woodlands by frugivorous migrating birds in

741   Panama: an effect of fruit size and plant density? J. Trop. Ecol. 1: 157–170.

742   MARTIN, T. E., and G. A. BLACKBURN. 2014. Conservation value of secondary forest habitats for

743   endemic birds, a perspective from two widely separated tropical ecosystems. Ecography

744   (Cop.). 37: 250–260.

745   MASCARO, J., G. P. ASNER, D. H. DENT, S. J. DEWALT, and J. S. DENSLOW. 2012. Scale-

746   dependence of aboveground carbon accumulation in secondary forests of Panama: A test of

747   the intermediate peak hypothesis. For. Ecol. Manage. 276: 62–70.

748   MOORE, R. P., W. D. ROBINSON, I. J. LOVETTE, and T. R. ROBINSON. 2008. Experimental

749   evidence for extreme dispersal limitation in tropical forest birds. Ecol. Lett. 11: 960–968.

750   O'DEA, N., and R. J. WHITTAKER. 2007. How resilient are Andean montane forest bird

751   communities to habitat degradation? Biodivers. Conserv. 16: 1131–1159.

752   OKSANEN, J., F. G. BLANCHET, R. KINDT, P. LEGENDRE, P. R. MINCHIN, R. B. O'HARA, G. L.

753   SIMPSON, P. SOLYMOS, M. H. H. STEVENS, and H. WAGNER. 2016. vegan: Community

754   Ecology Package. R package version 2.3-5, http://cran.r-project.org/package=vegan.

755   PEÑA-CLAROS, M. 2003. Changes in forest structure and species composition during secondary

756   forest succession in the Bolivian Amazon. Biotropica 35: 450–461.

757   PETIT, D. R., L. J. PETIT, V. A. SAAB, and T. E. MARTIN. 1995. Fixed-radius point counts in

758   forests: factors influencing effectiveness and efficiency. Washington (DC): United States

759   Forest Service.

760   PETIT, L. J., and D. R. PETIT. 2003. Evaluating the importance of human-modified lands for

761   Neotropical bird conservation. Conserv. Biol. 17: 687–694.

762   PIPERNO, D. R. 1990. Fitolitos, arquelogía y cambios prehistóricos de la vegetación en un lote de

763   cincuenta hectáreas de la Isla de Barro Colorado. *In* E. G. Leigh, A. S. Rand, and D. M.

764   Windsor (Eds.) Ecología de un bosque tropical: Ciclo estacionales y cambios de largo

765   plazo. pp. 153–156, Smithsonian Tropical Research Institute, Balboa, Panama.

766   PIGOT, A. L., C. H. TRISOS, and J. A. TOBIAS. 2016. Functional traits reveal the expansion and

767   packing of ecological niche space underlying an elevational diversity gradient in passerine

768   birds. Proc. R. Soc. Biol. Sci. 283: 20152013.

769   R CORE TEAM. 2017. R: A language and environment for statistical computing. R Foundation for

770   Statistical Computing, Vienna, Austria.

771   RAMAN, T. R. S. 1998. Recovery of tropical rainforest avifauna in relation to vegetation

772   succession following shifting cultivation in Mizoram, north-east India. J. Appl. Ecol. 35:

773   214–231.

774   RAMAN, T. R. S., and R. SUKUMAR. 2002. Responses of tropical rainforest birds to abandoned

775   plantations, edges and logged forest in the Western Ghats, India. Anim. Conserv. 5: 201–

776   216.

777   RIDGELY, R. S., and J. A. GWYNNE. 1989. A guide to the birds of Panama. Princeton University

778   Press, Chichester, West Sussex, U.K.

779   ROBINSON, W. D. 1999. Long-Term Changes in the Avifauna of Barro Colorado Island, Panama,

780   a Tropical Forest Isolate. Conserv. Biol. 13: 85–97.

781   ROBINSON, W. D., J. D. BRAWN, and S. K. ROBINSON. 2000. Forest Bird Community Structure in

782   Central Panama: Influence of Spatial Scale and Biogeography. Ecol. Monogr. 70: 209–235.

783   ROBINSON, W. D., A.C. LEES, and J.G. BLAKE. 2018. Surveying tropical birds is much harder

784   than you think: a primer of best practices. Biotropica. DOI: 10.1111/btp.12608

785   ROMPRE, G., W. D. ROBINSON, A. DESROCHERS, and G. ANGEHR. 2007. Environmental correlates

786   of avian diversity in lowland Panama rain forests. J. Biogeogr. 11: 674–675.

787   RUIZ-GUTIÉRREZ, V., E. F. ZIPKIN, and A. A. DHONDT. 2010. Occupancy dynamics in a tropical

788   bird community: Unexpectedly high forest use by birds classified as non-forest species. J.

789   Appl. Ecol. 47: 621–630.

790   SCHULZE, C., and M. WALTERT. 2004. Biodiversity indicator groups of tropical land-use systems:

791   comparing plants, birds, and insects. Ecol. Appl. 14: 1321–1333.

792   SEKERCIOGLU, C. 2006. Increasing awareness of avian ecological function. Trends Ecol. Evol.

793   21: 464–471.

794   STOTZ, D. F., J. W. FITPATRICK, T. A. PARKER III, and D. K. MOSKOVITS. 1996. Neotropical

795   birds: ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

796   STOUFFER, P. C., R. O. BIERREGAARD, C. STRONG, and T. E. LOVEJOY. 2006. Long-term

797   landscape change and bird abundance in Amazonian rainforest fragments. Conserv. Biol.

798   20: 1212–1223.

799   STRATFORD, J. A. and W. D. ROBINSON. 2005. Gulliver travels to the fragmented tropics:

800   geographic variation in mechanisms of avian extinction. Front. Ecol. Environ. 3: 85-92.

801 TERBORGH, J., S. K. ROBINSON, T. A. PARKER III, C. A. MUNN, and N. PIERPONT. 1990. Structure

802   and organization of an Amazonian forest bird community. Ecol. Monogr. 60: 213–238.

803 TERBORGH, J., and J. S. WESKE. 1969. Colonisation of secondary habitats by Peruvian birds.

804   Ecology 50: 765–782.

805 TOBIAS, J.A., C. SHEARD., SEDDON, N., MEADE, A., COTTON., A.J. and S. NAKAGAWA. 2016.

806   Territoriality, social bonds, and the evolution of communal signaling in birds. Frontiers in

807   Ecology & Evolution 4: 74.

808 TOBIAS, J. A., Ç. H. ŞEKERCIOĞLU, and F. H. VARGAS. 2013. Bird conservation in tropical

809   ecosystems: challenges and opportunities. *In* D. MacDonald and K. Willis (Eds.) Key

810   Topics in Conservation Biology Volume 2. pp. 258–276, John Wiley & Sons, London.

811 TURNER, B. L., J.B. YAVITT, K.E. HARMS, M.N. GARCIA and S. J. WRIGHT. 2015. Seasonal

812   changes in soil organic matter after a decade of nutrient addition in a lowland tropical

813   forest. Biogeochem. 123, 221–235

814 TVARDÍKOVÁ, K. 2010. Bird abundances in primary and secondary growths in Papua New

815   Guinea: a preliminary assessment. Trop. Conserv. Sci. 3: 373–388.

816 WALTERT, M., A. MARDIASTUTI, and M. MUHLENBERG. 2004. Effects of land use on bird species

817   richness in Sulawesi, Indonesia. Conserv. Biol. 18: 1339–1346.

818 WHELAN, C. J., D. G. WENNY, and R. J. MARQUISE. 2008. Ecosystem services provided by birds.

819   Ann. N. Y. Acad. Sci. 1134: 25–60.

820 WILLIS, E. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama.

821   Ecol. Monogr. 44: 153–169.

822 WILLIS, E., and E. EISENMANN. 1979. A revised list of birds of Barro Colorado Island, Panama.

823   Smithson. Contrib. to Zool.

824 WILLIS, E. O. 1980. Ecological role of migratory and resident birds on Barro Colorado Island,

825   Panama. *In* A. Keast and E. S. Morton (Eds.) Migrant birds in the Neotropics. Ecology,

826   behavior, distribution and conservation. pp. 205–225, Smithsonian Institution Press,

827   Washington, D.C.

828 WILMAN, H., J. BELMAKER, J. SIMPSON, C. DE LA ROSA, M. M. RIVADENEIRA, and W. JETZ. 2014.

829   EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals.

830   Ecology 95: 2027.

831 WINDSOR, D. M. 1990. Climate and moisture availability in a tropical forest, long term record for

832   Barro Colorado Island, Panama. Smithson. Contrib. Earth Sci. 29: 1–145.

833 WOLFE, J. D., P. C. STOUFFER, K. MOKROSS, L. L. POWELL, and M. M. ANCIAES. 2015. Island vs.

834   countryside biogeography: An examination of how Amazonian birds respond to forest

835   clearing and fragmentation. Ecosphere 6: 1–14.

836 WRIGHT, S. J. 2005. Tropical forests in a changing environment. Trends Ecol. Evol. 20: 553–60.

837 WRIGHT, S. J., and H. MULLER-LANDAU. 2006. The uncertain future of tropical forest species.

838   Biotropica 38: 443–445.

839 WUNDERLE, J. M., and C. S. LATTA. 1996. Avian abundance in sun and shade coffee plantations

840   and remnant pine forest in the Cordillera Central, Dominican Republic. Ornitol. Neotrop. 7:

841   19–34.

842 ZAHAWI, R. A., J. P. DANDOIS, K. D. HOLL, D. NADWODNY, J. L. REID, and E. C. ELLIS. 2015.

843   Using lightweight unmanned aerial vehicles to monitor tropical forest recovery. Biol.

844   Conserv. 186: 287–295.

845

TABLES

847

848   TABLE 1. Approximate forest age, level of isolation, species richness, Shannon-Weiner

849   diversity index and dominance statistics for bird communities of ten secondary forest and four

850   primary forest sites in central Panama, for both forest specialists and all bird species.

Site	Age (yr)	Level of Isolation	All Birds			Forest Specialists [a]		
			Species richness	Shannon–Wiener index	Dominance (%)	Species richness	Shannon–Wiener index	Dominance (%)
1	20	Connected	117	3.97	29.86	40	3.07	46.19
2	20	Connected	113	4.03	27.65	37	3.01	49.22
3	40	Isolated	84	3.63	36.75	26	2.72	54.55
4	40	Isolated	90	3.73	38.01	25	2.75	53.67
5	60	Isolated	76	3.61	37.16	25	2.83	50.00
6	60	Isolated	89	3.73	34.35	30	2.93	45.21
7	90	Connected	95	4.04	22.32	34	3.19	40.05
8	90	Isolated	83	3.77	32.12	26	2.77	54.25
9	120	Isolated	63	3.27	48.37	22	2.45	66.57
10	120	Isolated	62	3.37	46.42	23	2.49	63.84
11	Primary	Isolated	74	3.63	36.89	27	2.78	54.77
12	Primary	Isolated	75	3.64	35.94	28	2.79	54.17

13	Primary	Extensive	99	4.11	21.02	39	3.41	28.74
14	Primary	Extensive	96	3.95	25.13	38	3.20	39.87

851

852 [a] Forest Specialists: species that are scored as having high forest-dependence (BirdLife

853 International 2018).

854

855 TABLE 2. Permutational MANOVA results assessing species composition using community

856 similarity matrices generated with both Morisita-Horn abundance-based similarity index (S_{MH})

857 and Jaccard incidence-based similarity index (S_J). We tested observed differences between forest

858 age, isolation level (isolated or connected), forest type (SF or PF) and geographic distance to

859 extensive mainland PF. We also investigated the effect of season (wet or dry) on species

860 composition by conducting a perMANOVA at survey level.

		All Birds				Forest Specialists [a]			
		R^2	F	df	P	R^2	F	df	P
S_{MH}	Forest isolation	0.15	9.12	1	< 0.01	0.18	6.28	1	< 0.05
	Forest age	0.13	7.80	1	< 0.01	0.02	0.84	1	ns
	Forest type (SF vs PF)	0.08	5.10	1	< 0.01	0.01	0.51	1	ns
	Distance to extensive PF	0.02	1.35	1	ns	0.04	1.31	1	ns
S_J	Forest isolation	0.10	2.19	1	< 0.05	0.11	2.18	1	< 0.05
	Forest age	0.11	2.42	1	< 0.05	0.07	1.37	1	ns
	Forest type (SF vs PF)	0.09	1.93	1	< 0.05	0.06	1.14	1	ns
	Distance to extensive PF	0.06	1.29	1	ns	0.06	1.17	1	ns
S_{MH} [b]	Season (wet v. dry)	0.05	11.69	1	< 0.01	0.04	8.84	1	< 0.01
	Forest isolation	0.03	7.45	1	< 0.01	0.05	9.38	1	< 0.01
	Forest age	0.05	10.29	1	< 0.01	0.04	7.15	1	< 0.01
	Forest type (SF vs PF)	0.03	6.30	1	< 0.01	0.02	5.35	1	< 0.01
	Distance to extensive PF	0.03	5.69	1	< 0.01	0.02	3.56	1	< 0.05

861 [a] Forest Specialists: species that are scored as having high forest-dependence (BirdLife

862 International 2018).

863　[b] Data analysed at survey level, with season included.

FIGURE LEGENDS

865

866 FIGURE 1. Map of the 14 study sites in central Panama. Sites are colour-coded by forest age (PF

867 = primary forest; SF = secondary forest). This area of central Panama is composed of a mosaic of

868 contiguous forest stands of different age interspersed among a matrix of water and agricultural

869 land. The main areas in which forest stands are embedded among other patches of forest (and

870 therefore difficult to discretely identify) are the Barro Colorado National Monument (BCNM),

871 including Barro Colorado Island (1,560 ha) and Gigante peninsulas (2,600 ha), Soberania

872 National Park (SNP) and surrounding contiguous forest (22,000 ha), including the Agua Salud

873 Project (ASP).

874

875 FIGURE 2. Bird species richness by forest age, forest type, and degree of isolation from

876 extensive PF. "Forest Specialists" are species that are scored as having high forest-dependence

877 (BirdLife International 2018).

878

879 FIGURE 3. Population density estimates and 95% confidence intervals for all bird species

880 (number of birds per hectare) using distance corrections. Species data has been pooled for the

881 two sites in each of seven forest age categories.

882

883 FIGURE 4. Percentage of bird species detected in primary forest (PF) that were also detected in

884 secondary forest (SF) in five SF age categories for isolated PF sites and extensive PF sites.

885 Species data has been pooled for the two sites in each of seven forest age categories.

886

887   FIGURE 5. Similarity (Morisita-Horn) between secondary forest sites (SF) and both isolated and

888   extensive primary forest (PF). Each bar represents the mean similarity index (±1 SE) between the

889   two SF sites in each age category (20, 40, 60, 90 and 120 yr old) and the PF sites. Calculated

890   using the all bird dataset.

891

892   FIGURE 6. Non-metric multidimensional scaling (NMDS) plots of bird communities in two

893   forest sites in each of five secondary forest (SF) age categories (20, 40, 60, 90, 120-yr-old), and

894   isolated primary forest (PF) and extensive PF. NMDS were generated using the Morisita-Horn

895   index (all birds stress = 0.07; forest specialists stress = 0.08) and Jaccard index (all birds stress =

896   0.07; forest specialists stress = 0.06). Isolation levels are represented by different symbols.

897   "Forest Specialists" are species that are scored as having high forest-dependence (BirdLife

898   International 2018).

899

900   FIGURE S1: Species accumulation curves scaled by (A) sample and (B) by number of individual

901   birds detected for bird communities in each of five secondary forest (SF) age categories: 20, 40,

902   60, 90, 120-yr-old, and isolated primary forest (PF) and extensive PF for all birds.

903

904   FIGURE S2: Species accumulation curves scaled by (A) sample and (B) by number of individual

905   birds detected for bird communities in each of five secondary forest (SF) age categories: 20, 40,

906   60, 90, 120-yr-old, and isolated primary forest (PF) and extensive PF for forest specialists.

907   "Forest Specialists" are species that are scored as having high forest-dependence (BirdLife

908   International 2018).

909

910   FIGURE S3. Mean number of migratory birds detected per point count (±1 SE), from 126

911   locations.

912   **FIGURES**
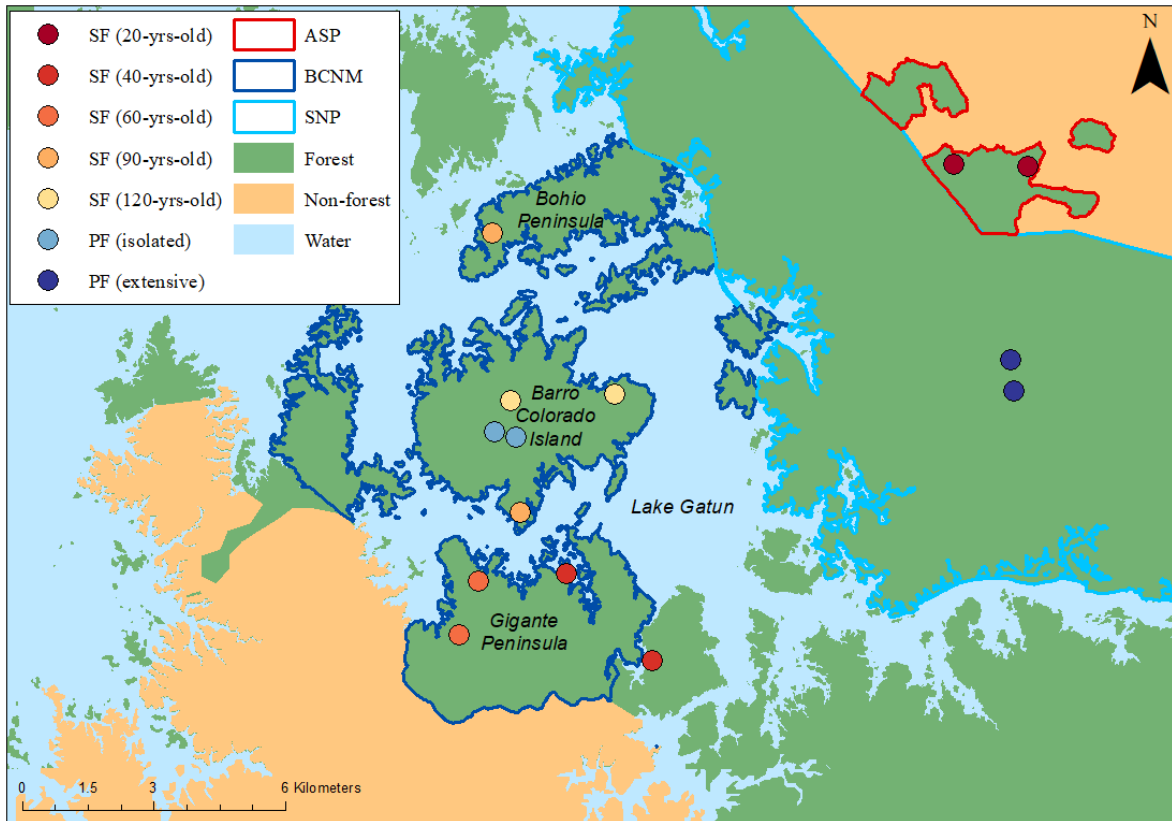
913

914   FIGURE 1.

915
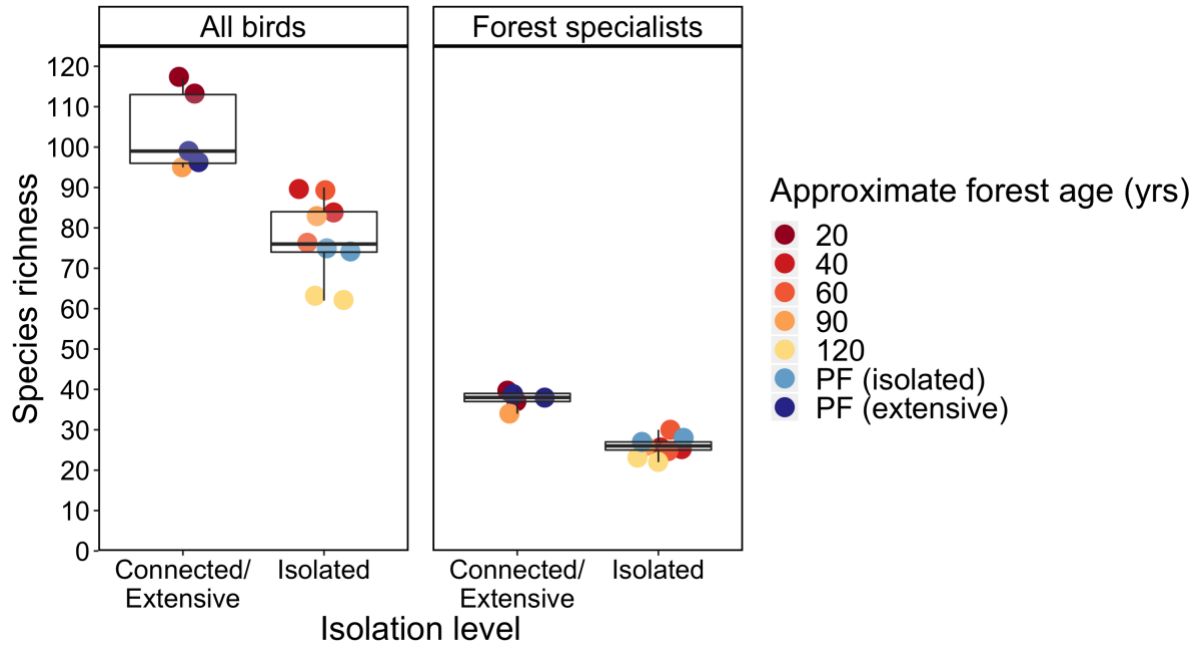
916

917 FIGURE 2.

918
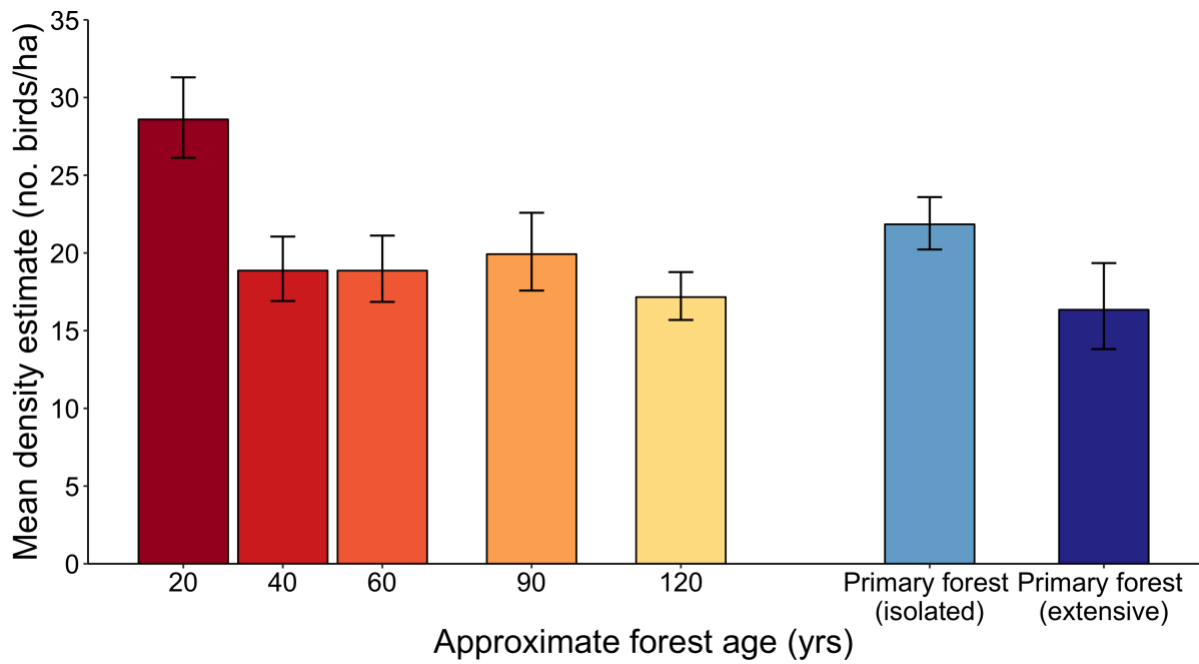
919

920 FIGURE 3.

921

922
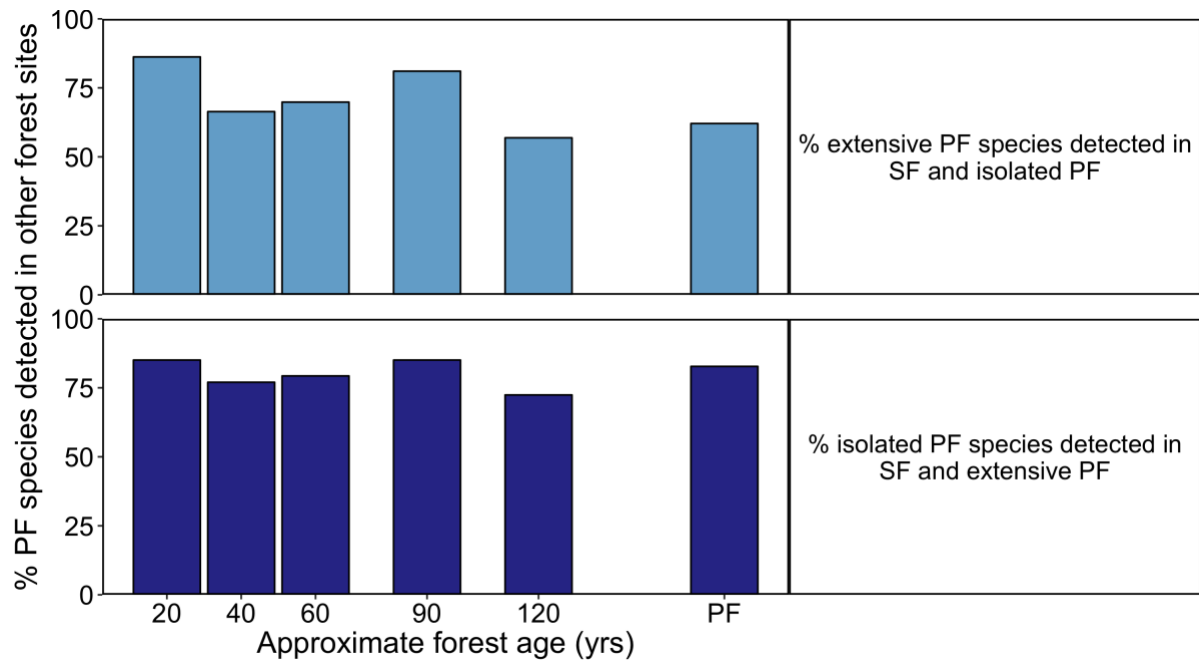
923

924   FIGURE 4.

925
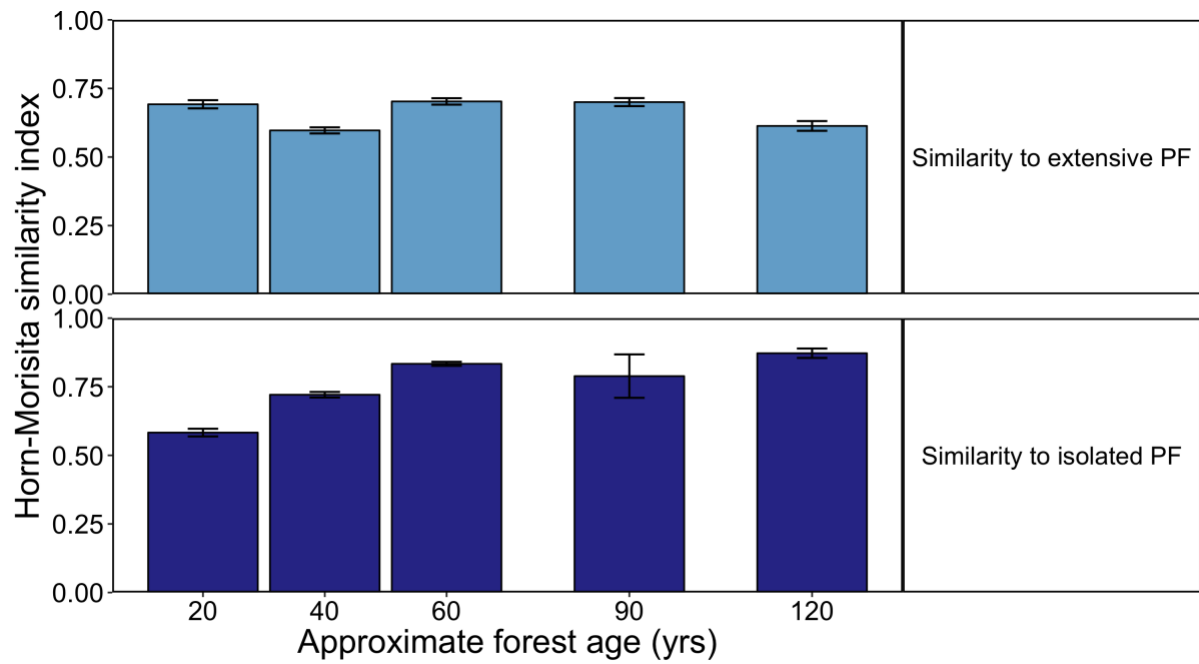
926

927   FIGURE 5.

928

929

930
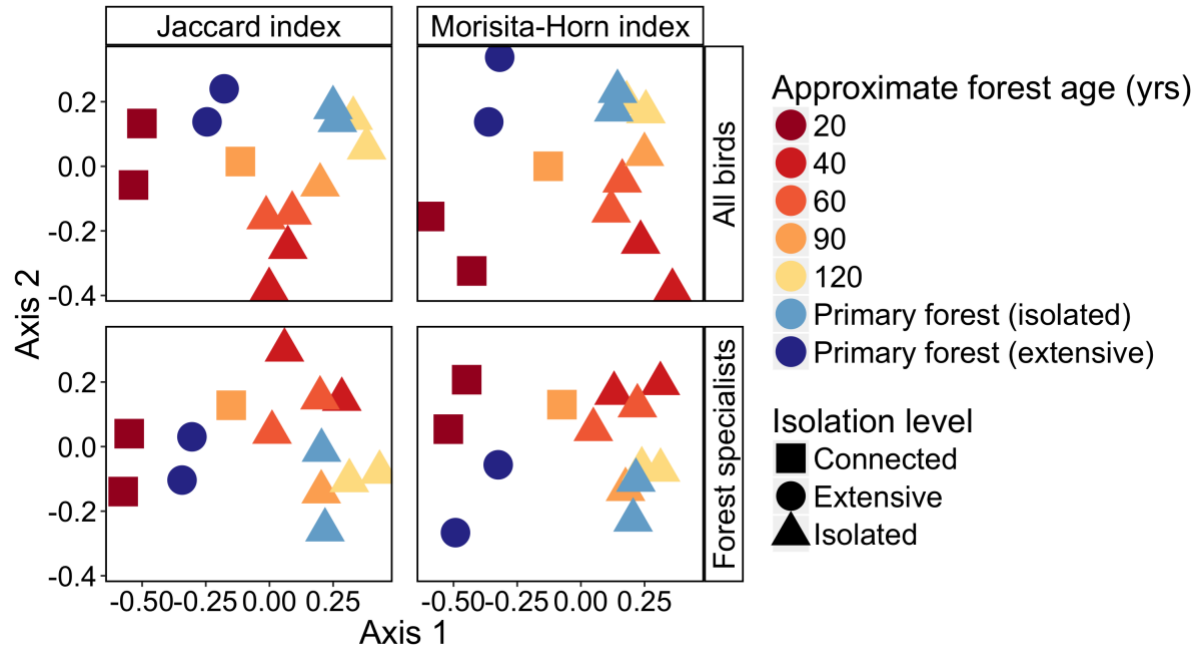
931   FIGURE 6.

SUPPLEMENTARY INFORMATION

933

934 TABLE S1: Bird species list from our surveys in central Panama, with ecological classifications

935 used in analyses and species presence/absence in sites.

Scientific Name	Migrant Species	Forest Specialist [b]	Site [c]													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
Tinamus major	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Crypturellus soui	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Penelope purpurascens	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0
Ortalis cinereiceps	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0
Odontophorus gujanensis [a]	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Patagioenas speciosa	0	0	1	1	1	0	0	1	0	1	0	0	1	0	1	0
Patagioenas cayennensis	0	0	1	0	1	1	1	1	1	1	0	0	1	1	1	1
Patagioenas nigrirostris	0	0	1	1	1	1	0	0	1	0	0	1	1	1	1	1
Geotrygon montana	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Leptotila verreauxi	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Leptotila cassinii	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Columbina talpacoti	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Claravis pretiosa	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Nyctibius griseus [a]	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Chordeiles minor [a]	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Species																
Nyctidromus albicollis	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Antrostomus rufus	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Florisuga mellivora	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0
Phaethornis striigularis	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1
Phaethornis longirostris	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Heliothryx barroti	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Thalurania colombica	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0
Amazilia tzacatl	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Amazilia amabilis	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lepidopyga coeruleogularis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Juliamyia julie	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dromococcyx phasianellus	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Piaya cayana	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Aramides cajaneus	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
Pulsatrix perspicillata	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Leptodon cayanensis	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Elanoides forficatus	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Harpagus bidentatus	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
Buteogallus anthracinus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Buteogallus urubitinga	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pseudastur albicollis	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Leucopternis semiplumbeus	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0
Buteo nitidus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

Species																
Buteo platypterus	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Buteo albonotatus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Trogon massena	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Trogon melanurus	0	0	1	0	1	1	1	1	1	1	0	0	0	0	1	0
Trogon chionurus	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0
Trogon caligatus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Trogon rufus	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Momotus subrufescens	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
Baryphthengus martii	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Electron platyrhynchum	0	1	1	1	0	1	0	1	1	0	0	0	0	0	1	1
Notharchus hyperrhynchus	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0
Notharchus pectoralis	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
Malacoptila panamensis	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1
Ramphastos ambiguus	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ramphastos sulfuratus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pteroglossus torquatus	0	1	0	0	1	1	1	1	1	0	1	0	1	0	1	0
Campephilus melanoleucos	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Celeus loricatus	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	1
Hylatomus lineatus	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1
Melanerpes pucherani	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Melanerpes rubricapillus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Micrastur mirandollei	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Micrastur semitorquatus	0	0	1	0	1	0	0	1	1	1	1	1	1	1	0	1

Species																
Falco rufigularis	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1
Brotogeris jugularis	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	1
Pyrilia haematotis	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1
Pionus menstruus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amazona autumnalis	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amazona farinosa	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Microrhopias quixensis	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Epinecrophylla fulviventris	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Myrmotherula ignota	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Myrmotherula axillaris	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Dysithamnus puncticeps	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1
Cymbilaimus lineatus	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1
Taraba major	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Thamnophilus atrinucha	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cercomacroides tyrannina	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1	1
Phaenostictus mcleannani	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	1
Gymnopithys bicolor	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
Hylophylax naevioides	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Poliocrania exsul	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Myrmeciza longipes	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Hylopezus perspicillatus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Formicarius analis	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1
Sclerurus mexicanus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Species																
Sclerurus guatemalensis	0	1	1	1	0	1	0	1	1	0	0	0	1	1	1	1
Deconychura typica	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Sittasomus griseus	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0
Dendrocincla fuliginosa	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Glyphorynchus spirurus	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1
Dendrocolaptes sanctithomae	0	0	1	0	0	1	1	0	1	0	1	1	1	1	0	1
Xiphorhynchus susurrans	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Xiphorhynchus lachrymosus	0	0	1	1	0	0	0	0	0	0	1	1	1	1	1	1
Lepidocolaptes souleyetii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Xenops genibarbis	0	1	1	1	0	1	0	1	1	0	1	1	1	1	1	1
Automolus ochrolaemus	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Manacus vitellinus	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Ceratopipra mentalis	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lepidothrix coronata	0	1	1	1	0	0	1	1	1	0	0	0	0	0	1	1
Querula purpurata	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Lipaugus unirufus	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0
Onychorhynchus coronatus	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Terenotriccus erythrurus	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Tityra semifasciata	0	0	0	1	1	0	1	1	1	1	0	1	1	1	1	1
Pachyramphus polychopterus [a]	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Schiffornis veraepacis	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Platyrinchus coronatus	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Mionectes oleagineus	0	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1

Species																
Cnipodectes subbrunneus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Rhynchocyclus aequinoctialis	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1
Tolmomyias sulphurescens	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Tolmomyias assimilis	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Myiornis atricapillus	0	0	1	0	0	0	0	1	1	1	0	1	1	1	1	1
Oncostoma olivaceum	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Todirostrum nigriceps	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Zimmerius vilissimus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ornithion brunneicapillus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Camptostoma obsoletum	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0
Tyrannulus elatus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Myiopagis gaimardii	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0
Myiopagis viridicata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Attila spadiceus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Legatus leucophaius	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Pitangus sulphuratus	0	0	1	0	1	1	0	1	1	1	0	0	0	0	0	0
Megarynchus pitangua	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Myiodynastes maculatus	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	0
Myiozetetes cayanensis	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0
Myiozetetes similis	0	0	1	0	1	1	1	0	1	1	0	0	0	1	0	0
Tyrannus melancholicus	0	0	0	0	1	1	0	0	1	1	1	0	0	0	0	0
Rhytipterna holerythra	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0
Myiarchus tuberculifer	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Species																
Myiarchus crinitus	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1
Empidonax virescens	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1
Contopus cooperi	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Contopus virens	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Vireolanius pulchellus	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	1
Tunchiornis ochraceiceps	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Pachysylvia decurtata	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pachysylvia aurantiifrons	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Vireo olivaceus	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Microbates cinereiventris	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Ramphocaenus melanurus	0	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1
Polioptila plumbea	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Microcerculus marginatus	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Pheugopedius fasciatoventris	0	0	1	1	1	0	0	1	1	0	0	0	0	0	1	1
Thryophilus rufalbus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Cantorchilus leucotis [a]	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cantorchilus nigricapillus	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Henicorhina leucosticta	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1	1
Cyphorhinus phaeocephalus	0	1	1	1	1	1	0	0	1	1	0	0	0	0	1	1
Hylocichla mustelina	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Turdus grayi	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Euphonia luteicapilla	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Euphonia laniirostris	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0

Species																
Euphonia fulvicrissa	0	0	0	1	0	0	1	0	1	0	0	0	0	1	1	1
Euphonia minuta	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhodinocichla rosea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Arremonops conirostris	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Arremon aurantiirostris	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amblycercus holosericeus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Psarocolius wagleri	0	0	1	1	0	1	0	1	1	1	1	0	0	0	1	1
Cacicus microrhynchus	0	0	1	1	1	0	1	1	1	0	0	0	0	0	1	1
Cacicus cela	0	0	0	0	1	1	1	1	1	1	0	0	0	1	1	0
Icterus chrysater	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	0
Parkesia noveboracensis	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Mniotilta varia	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Leiothlypis peregrina	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
Setophaga ruticilla	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Setophaga castanea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Setophaga pensylvanica	1	0	1	1	0	0	0	0	0	1	1	1	0	0	0	1
Cyanoloxia cyanoides	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1
Habia fuscicauda	0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	1
Habia carmioli [a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Piranga rubra	1	0	0	1	1	1	0	0	0	1	0	0	0	1	1	0
Chlorophanes spiza	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	1
Cyanerpes cyaneus	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0
Cyanerpes lucidus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Species																
Dacnis cayana	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Saltator grossus	0	0	1	1	0	1	1	1	1	0	0	0	0	0	1	1
Eucometis penicillata	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Islerothraupis luctuosa	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Chrysocorypha delatrii	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Tangara palmarum	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Tangara inornata	0	0	0	1	0	1	0	1	0	1	1	0	1	1	0	0

936

937 [a] Species detected only in encounters, and not in fixed radius point counts.

938 [b] Forest Specialists: species that are scored as having high forest-dependence (BirdLife

939 International 2018).

940 [c] Site details: 1 and 2 = mainland 20-yr-old SF; 3 and 4 = peninsula 40-yr-old SF; 5 and 6 =

941 peninsula 60-yr-old SF; 7 = mainland 90-yr-old SF; 8 = island 90-yr-old SF; 9 and 10 = island

942 120-yr-old SF; 11 and 12 = island PF; 13 and 14 = mainland PF.

943   TABLE S2. Most abundant bird species in each forest age category in Central Panama and their

944   primary foraging substrate, feeding guild and forest specialist status.

Forest age	Scientific name	No. individuals	% of all observations	Foraging Height [a]	Feeding Guild [b]	Forest Specialist [c]
20 (n = 2640 individuals)	*Oncostoma olivaceum*	155	5.9	L	I	0
	Thamnophilus atrinucha	154	5.8	L	I	0
	Cercomacroides tyrannina	140	5.3	L	I	0
	Ramphocaenus melanurus	104	3.9	L	I	1
	Poliocrania exsul	99	3.8	L	I	1
40 (n = 2239 individuals)	*Thamnophilus atrinucha*	248	11.1	L	I	0
	Pachysylvia decurtata	183	8.2	M/U	I	0
	Xiphorhynchus susurrans	121	5.4	L	I	0
	Oncostoma olivaceum	115	5.1	L	I	0
	Tyrannulus elatus	107	4.8	L/M	I	0
60 (n = 2223 individuals)	*Thamnophilus atrinucha*	264	11.9	L	I	0
	Pachysylvia decurtata	169	7.6	M/U	I	0
	Xiphorhynchus susurrans	108	4.9	L	I	0
	Poliocrania exsul	101	4.5	L	I	1
	Oncostoma olivaceum	93	4.2	L	I	0
90	*Pachysylvia decurtata*	161	6.4	M/U	I	0

(n = 2534	*Poliocrania exsul*	151	6	L	I	1
individuals)	*Amazona autumnalis*	133	5.2	U	F	0
	Thamnophilus atrinucha	115	4.5	L	I	0
	Xiphorhynchus susurrans	100	3.9	L	I	0
	Thamnophilus atrinucha	299	13.9	L	I	0
120	*Poliocrania exsul*	203	9.4	L	I	1
(n = 2149	*Pachysylvia decurtata*	162	7.5	M/U	I	0
individuals)	*Xiphorhynchus susurrans*	149	6.9	L	I	0
	Hylophylax naevioides	134	6.2	L	I	1
	Amazona autumnalis	272	9.3	U	F	0
PF (isolated)	*Thamnophilus atrinucha*	243	8.3	L	I	0
(n = 2922	*Poliocrania exsul*	237	8.1	L	I	1
individuals)	*Pachysylvia decurtata*	221	7.6	M/U	I	0
	Hylophylax naevioides	135	4.6	L	I	1
	Amazona autumnalis	159	6.6	U	F	0
PF (extensive)	*Thamnophilus atrinucha*	129	5.4	L	I	0
(n = 2391	*Pachysylvia decurtata*	119	5	M/U	I	0
individuals)	*Microrhopias quixensis*	91	3.8	L/M	I	1
	Zimmerius vilissimus	72	3	C	O	0

945 [a] Foraging height, classified using information in Ridgely & Gwynne (1989): L = "lower levels"

946 (from ground to about 10 feet above the ground); M = "middle levels" (from about 10 to 30 feet

947 above the ground); U = "upper levels" (everything above 30 feet including the canopy); C =

948   "only canopy" (the very top layer of the forest, within about 10ft of the upper level of leaves

949   only).

950   [b] Feeding Guild, classified using information in Wilman *et al.* (2014): F = frugivore; I =

951   insectivore; O = omnivore.

952   [c] Forest Specialist: species that are scored as having high forest-dependence (BirdLife
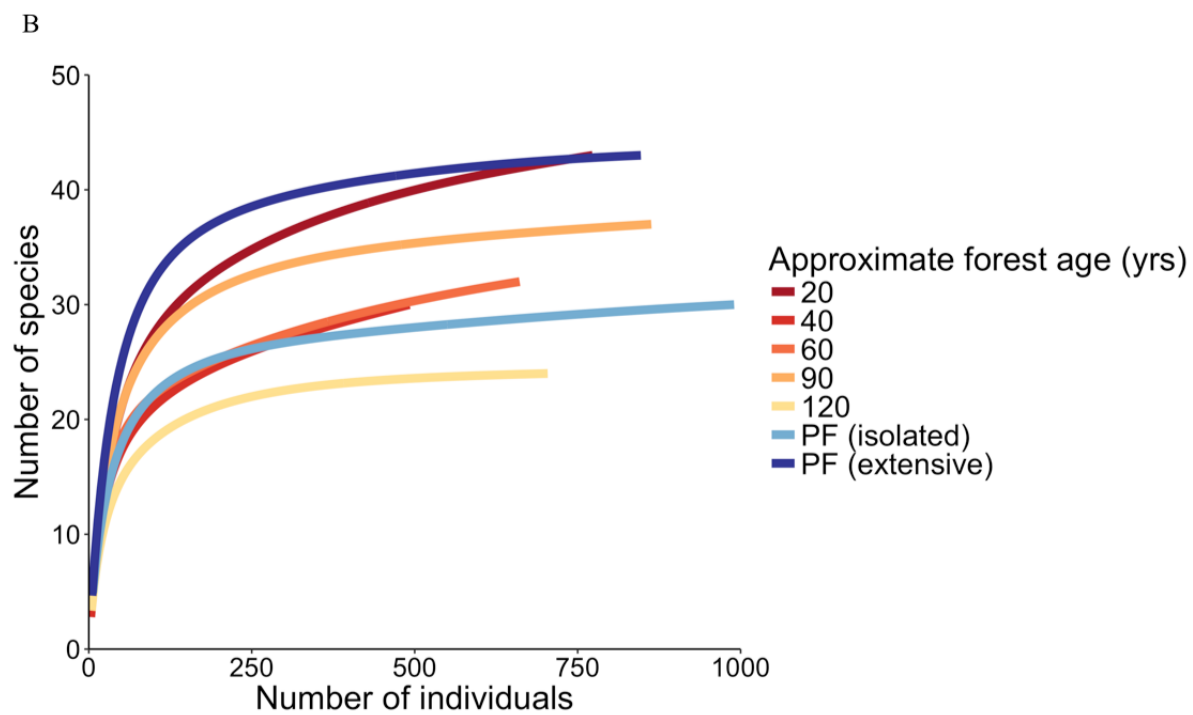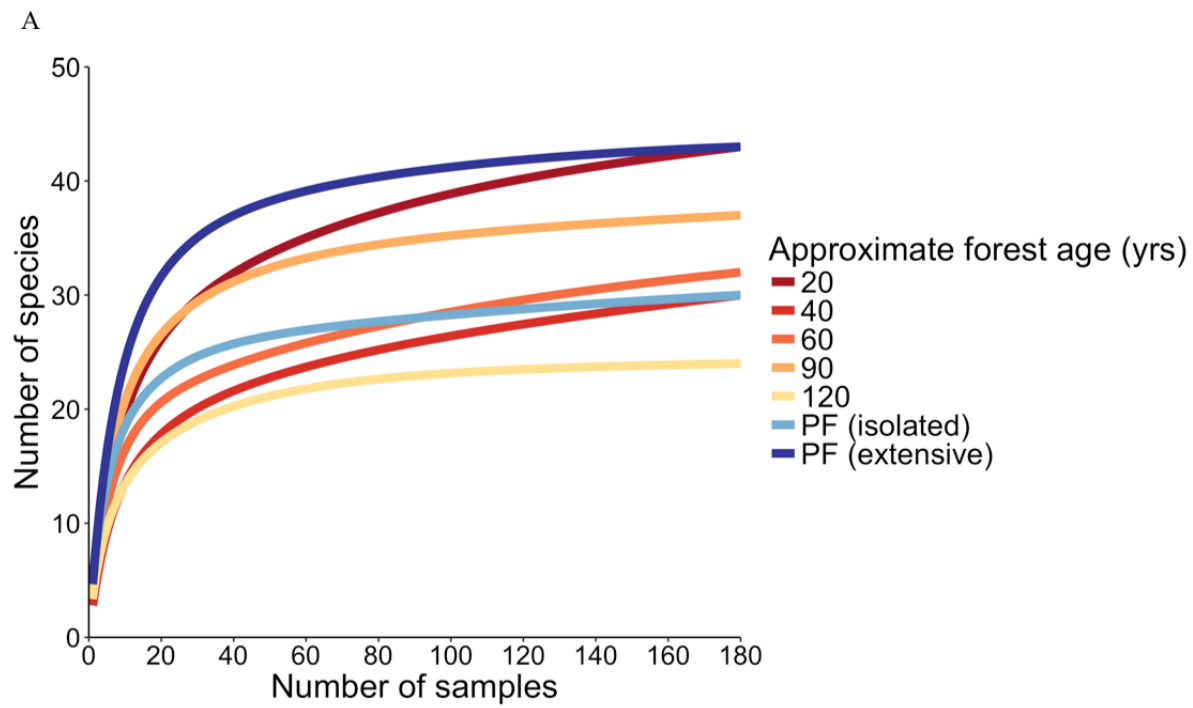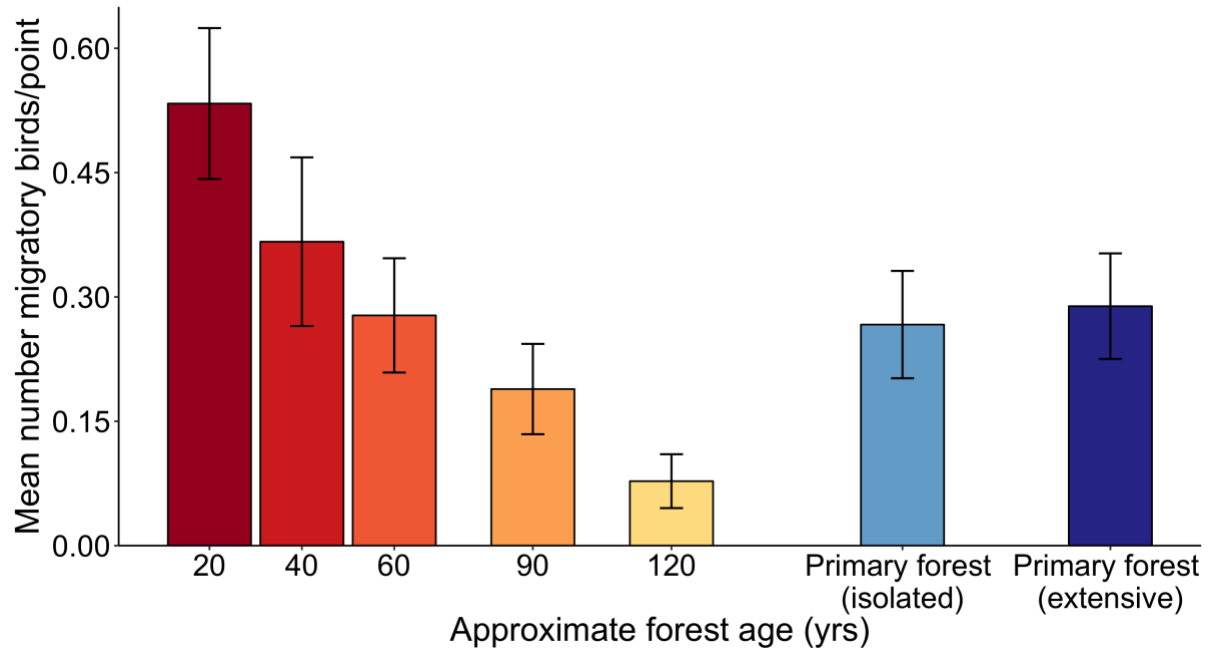
953   International 2018).

954

955
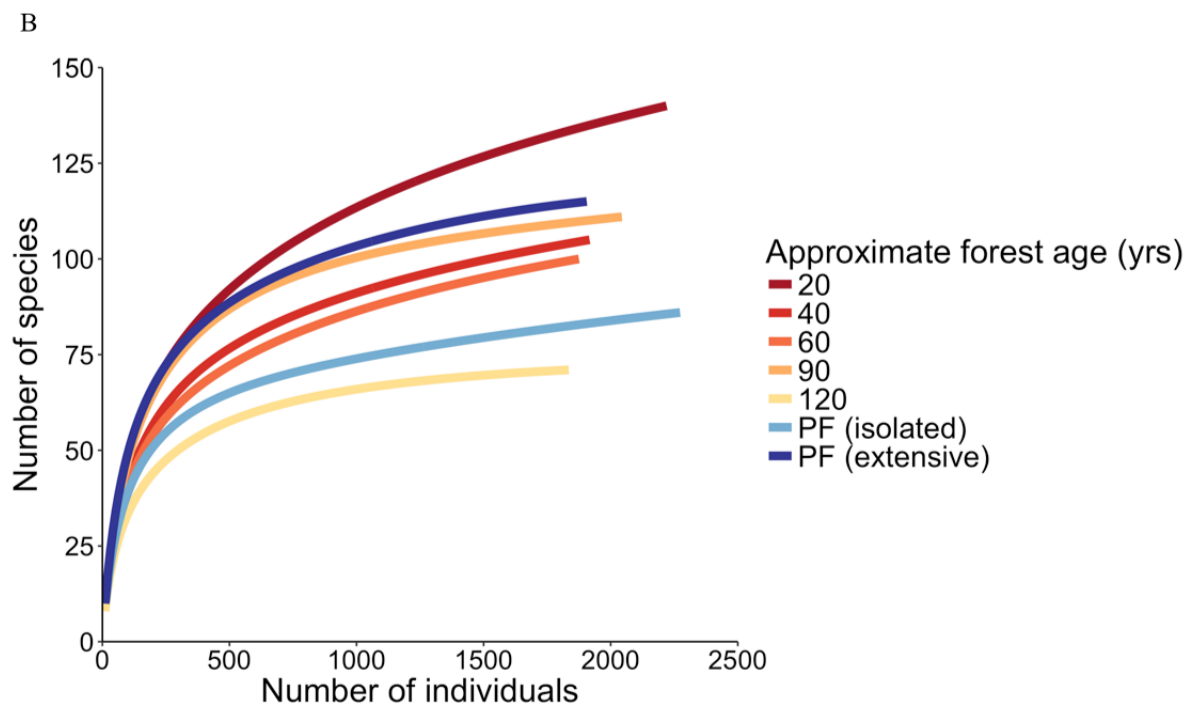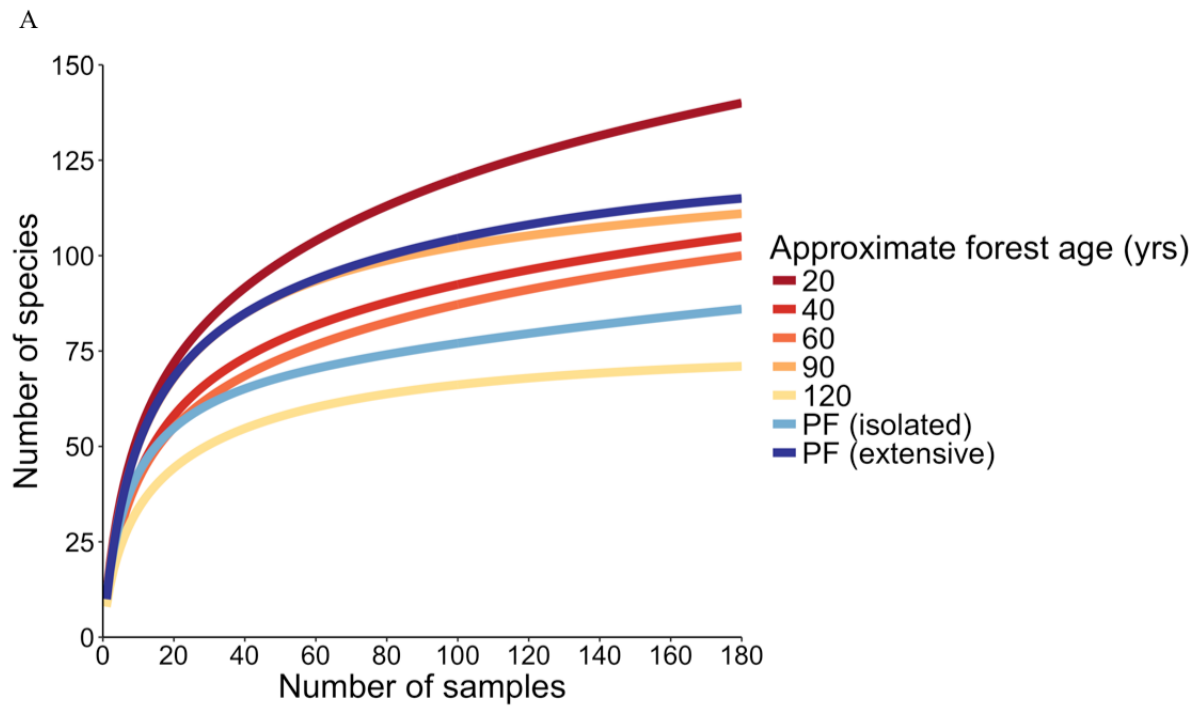
956

957 FIGURE S1

958

959   FIGURE S2

960

63

961

962

963   FIGURE S3.

964