

Article (refereed) - postprint

Sayer, C.A.; Bullock, J.M.; Martin, P.A.. 2017. **Dynamics of avian species and functional diversity in secondary tropical forests.** *Biological Conservation*, 211 (A). 1-9. <https://doi.org/10.1016/j.biocon.2017.05.004>

© 2017 Elsevier Ltd

This manuscript version is made available under the CC-BY-NC-ND 4.0 license <http://creativecommons.org/licenses/by-nc-nd/4.0/>



This version available <http://nora.nerc.ac.uk/id/eprint/517760/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

NOTICE: this is the author's version of a work that was accepted for publication in *Biological Conservation*. Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in *Biological Conservation*, 211 (A). 1-9. <https://doi.org/10.1016/j.biocon.2017.05.004>

www.elsevier.com/

Contact CEH NORA team at
noraceh@ceh.ac.uk

1 **Dynamics of avian species and functional diversity in secondary tropical forests**

2
3 C.A. Sayer^{a,b}, J.M. Bullock^b and P.A. Martin^{b,c}

4 ^aImperial College London, Silwood Park, Buckhurst Road, Ascot, Berkshire, SL5 7QN, UK.

5 ^bNERC Centre for Ecology and Hydrology, Benson Lane, Wallingford, Oxfordshire, OX10 8BB,
6 UK.

7 ^cCentre for Conservation Ecology and Environmental Science, School of Applied Sciences,
8 Bournemouth University, Poole, BH12 5BB, UK.

9
10 Corresponding author (C.A. Sayer) email address: catherinesayer28@gmail.com

11 Corresponding author (C.A. Sayer) telephone number: +44(0)7963 417046

12 Corresponding author (C.A. Sayer) postal address: 11 Lancaster Drive, St Ives, Cambridgeshire,
13 PE27 3YE, UK.

14
15 J.M Bullock email address: jmbul@ceh.ac.uk

16 P.A. Martin email address: phil.martin.research@gmail.com

17
18 **Abstract**

19 Deforestation for agriculture in the tropics, followed by abandonment, has resulted in large areas
20 of secondary forest. Some authors have suggested that this secondary regrowth could help
21 prevent mass extinction in the tropics by providing habitat for forest species. However, there is
22 little generalised understanding of the biodiversity value of secondary forest. To address this
23 knowledge gap, we conducted an analysis of avian responses to secondary forest succession,
24 comparing data from 44 tropical secondary forest sites with nearby primary forest sites and
25 investigating both species and functional diversity based metrics. Total species richness in
26 secondary forests was 12% lower than in primary forests and was not related to secondary forest
27 age. In contrast, forest specialist species richness increased with time since disturbance, reaching
28 99% of primary forest values after 100 years. In terms of functional diversity, functional
29 dispersion (FDis) and functional divergence (FDiv) were similar in primary and secondary
30 forests. However, functional evenness (FEve) was 5% higher in secondary than in primary
31 forests. The standardized effect size of functional diversity (sesFD) was higher in young
32 secondary forests than primary forests and declined with time since disturbance. Overall, these
33 results suggest that secondary tropical forests can support provision of ecosystem services but
34 that these services may be less stable in young forests. Therefore, secondary tropical forests,
35 particularly older regrowth, have biodiversity value and can support important ecosystem
36 functions. These secondary forests should be protected from further disturbance but preserving
37 primary forest is vital for supporting overall and forest specialist species richness.

38
39 **Key words:** forest recovery; birds; functional diversity; ecosystem functioning; avian
40 biodiversity

43 **Introduction**

44 Agricultural expansion in the tropics has led to large-scale deforestation (Gibbs et al., 2010),
45 causing loss of forest species. Traditionally, protected areas have been seen as the best way to
46 reduce deforestation and limit the resulting loss of biodiversity. These protected areas generally
47 consist of natural or near-natural ecosystems, such as primary forest (Dudley, 2008). In the
48 tropics such primary forests are generally considered to be irreplaceable for their biodiversity
49 value (Gibson et al., 2011), as well as providing numerous ecosystem services. However,
50 biodiversity declines continue in many tropical forest protected areas (Curran, 2004; Laurance et
51 al., 2012). Additionally, it is not always feasible to designate sufficient land to adequately
52 represent the range of communities found in specific biomes (Cox and Underwood, 2011) or
53 support viable populations of all species (Struhsaker et al., 2005). Thus, it is clear that we cannot
54 rely solely on protected areas of primary forest to conserve tropical forest biodiversity.

55 Forests that have been altered as a result of unsustainable use or natural disasters are
56 considered degraded, and this includes secondary forests, which have undergone forest clearance
57 (ITTO, 2002). While degraded tropical forests may be of lower biodiversity value than primary
58 forests, given that over half of all tropical forests are now considered to be degraded (ITTO,
59 2002), they may provide a valuable opportunity for conservation. Wright and Muller-Landau
60 (2006) suggested that expansion of secondary forests could play an important role in preventing
61 extinctions by providing alternative habitat for forest species. Previous reviews suggest that
62 secondary forests may provide habitat for forest specialists, but also that these forests differ in
63 their conservation value depending on connectivity, disturbance history and, in particular, site
64 age (Bowen et al., 2007; Chazdon et al., 2009; Gardner et al., 2007). Recently, the increasing
65 recognition of the importance of degraded forests has led to ambitious restoration targets such as
66 the Aichi Targets and the New York Declaration on Forests, which aim to restore more than 15%
67 of degraded forests (Convention on Biological Diversity, 2010) and 200 million hectares of
68 degraded forests (United Nations, 2014) worldwide, respectively. However, although there are
69 numerous site and landscape level studies, there are a lack of syntheses on the benefits of
70 secondary forests for biodiversity and ecosystem services, and those published are largely
71 limited to impacts on plant communities and carbon storage (Derroire et al., 2016; Martin et al.,
72 2013) or to a limited number of biodiversity metrics, such as species richness (Dent and Wright,
73 2009; Dunn, 2004a).

74 Measures of the conservation value of an ecosystem commonly use species-based metrics
75 (Myers et al., 2000), with the value of an area measured by the community species richness or
76 the presence of particular species of interest. A complementary approach to species-based
77 metrics is to assess changes in functional diversity, which describes the range of functional roles
78 played by species within a community (Petchey and Gaston, 2006). Ecosystem functioning in
79 general tends to be correlated with both species richness and functional diversity, with indices
80 based on traits (e.g. feeding behaviour) performing better than those based solely on species
81 richness and abundance (Griffin et al., 2009; Petchey and Gaston, 2006). Both the identity and
82 distribution of functional traits have been shown to be important in predicting function (Gagic et
83 al., 2015).

84 In this study we focus on birds as they provide key functions, such as pollination, seed
85 predation and dispersal, removal of carrion, and predation of other animals, in tropical forests,
86 and as the roles of individual species can be characterized in terms of their feeding behaviour
87 (Sekercioglu et al., 2004). We conducted a systematic review and analysis to assess: i) how avian
88 species richness and species richness of forest specialists in secondary tropical forests compares

89 with that of primary tropical forests; ii) the functional diversity of avian communities in
90 secondary tropical forests compared with that of primary tropical forests; and iii) how both
91 metrics change, and possibly recover, with secondary forest age.

92

93 **Materials and Methods**

94 ***Data collation***

95 Using a standard methodology (Pullin and Stewart, 2006), a systematic review of the literature
96 was conducted in May 2013 by searching Thomson Reuters Web of Knowledge with the terms
97 bird* AND (secondary or disturb*) AND forest AND tropic*. Additional studies were found in
98 the reviews by Barlow et al. (2007), Bowen et al. (2007), Gardner et al. (2007), Dent and Wright
99 (2009) and Chazdon et al. (2009). Gilroy et al. (2014) and the PREDICTS database (Hudson et
100 al., 2017), were searched for additional relevant data.

101 Studies were selected if they included details of avian community composition in at least
102 one secondary forest site and a reference undisturbed primary forest site. A primary forest was
103 defined as a naturally forested area where there was no evidence of previous deforestation or
104 degradation. A secondary forest was defined as a previously forested area undergoing secondary
105 succession following total or near-total removal of trees (Corlett, 1994). This definition allowed
106 inclusion of forests that had previously been clear-cut or cleared for agriculture or villages, but
107 not those undergoing succession after fires. Additionally, forests that had been selectively logged
108 were excluded as these recover differently (Corlett, 1994; Dunn, 2004b). Only studies from the
109 tropics and sub-tropics between the latitudes of 40°N and 40°S were included.

110 Data on the abundances of bird species present in forest sites were extracted from the
111 articles. Additionally, for each secondary forest site, the age, land use history and whether the
112 site was continuous or discontinuous with primary forest were noted. Article authors were
113 contacted to request these data when articles suggested that they had been collected but were not
114 presented. The median age of the secondary forest was recorded when a range of values was
115 given. Methodologies used to sample bird communities, including sampling effort, were
116 consistent within studies, but differed among studies. Methodologies used were recorded for use
117 in statistical analyses to control for differences among studies. Data were recorded from only one
118 study when multiple studies used the same dataset.

119 Data on the traits of bird species were obtained from Wilman *et al.* (2014), the Handbook
120 of the Birds of the World (del Hoyo et al., 2016) and BirdLife International (BirdLife
121 International, 2013). For this study we selected traits with importance for ecological functions:
122 (i) foraging strata (ground, understory, mid-high levels in trees, canopy, or well above
123 vegetation); (ii) diet (invertebrates, mammals/birds, reptiles/amphibians, fish, scavenger, fruit,
124 nectar, seeds, or other plant material); (iii) body mass in grams; (iv) body length in cm; and (v)
125 movement pattern (migrant/not migrant). We selected these traits because they can be directly
126 linked to ecosystem processes such as seed dispersal and pollination. Where no match was found
127 for the Latin binomial name of a species in the trait database of Wilman *et al.* (2014) a web
128 search was carried out to find synonymous names and the correct trait values assigned using
129 these (10 species). Forest dependency data for all bird species were provided by BirdLife
130 International, with each species categorised as having high, medium or low forest dependency, or
131 being a non-forest species (BirdLife International, 2013). Species with high forest dependency
132 were then classed as forest specialists and forest specialist species richness was calculated for
133 each site.

134 We then calculated total species richness and six functional diversity metrics: functional
135 diversity (FD), the standardized effect size of FD (sesFD), functional richness (FRic), functional
136 evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) for each of our
137 secondary and primary forest sites (see Table 1 for a description of the functional diversity
138 metrics used). Species richness was calculated by summing the number of species found at each
139 site. Using the R package fundiv we calculated FD (Petchey and Gaston, 2006). Since FD is
140 known to be correlated with species richness, following this we calculated sesFD, a metric which
141 adjusts FD for species richness. To calculate sesFD we used the r package picante (Kembel et al.,
142 2010) to compare observed FD to 999 iterations in which the number of species is constant but
143 the identity of species is randomly drawn from the community, following previous studies
144 (Edwards et al., 2013; Prescott et al., 2016). We calculated the remaining functional diversity
145 metrics (FRic, FEve, FDiv and FDis; Table 1) using the R package FD (Laliberté and Legendre,
146 2010).

147 148 **Statistical analyses**

149 This work aimed to compare changes in different metrics of species and functional diversity in
150 avian communities in secondary tropical forests. However, functional diversity metrics are often
151 highly correlated with species richness. Prior to analysis the log response ratio (Hedges et al.,
152 1999) for species richness and all functional diversity metrics, apart from sesFD, in secondary
153 forests relative to primary forests was calculated for all paired sites. The log response ratio
154 represents a standardized effect size which can range from $-\infty$ to ∞ , where negative values
155 indicate lower values in secondary forests, positive values represent higher values in secondary
156 forests, and 0 indicates no difference. The log response ratio is commonly used in ecological
157 syntheses because it conforms to statistical assumptions and is intuitive (Hedges et al., 1999).
158 Since values of sesFD can be negative or positive, calculation of the log response ratio for this
159 metric would be problematic. As a result, we calculated the raw difference between secondary
160 and primary forests sesFD. Before analysis, data exploration was carried out following the
161 protocol of Zuur *et al.* (2010). As a result we identified that a small number of older sites
162 strongly influenced coefficient values. To reduce the effect of these outliers we log transformed
163 the variable forest age as recommended by Zuur *et al.* (2010).

164 Linear mixed-effects models were constructed for all response variables using the R
165 package lme4 (Bates et al., 2015). Models tested included additive models containing all
166 combinations of variables describing secondary forest age and land-use history, as well as a null
167 intercept only model. Models including a variable describing proximity of forests to undisturbed
168 forests were not possible as not all studies contained data on this. Study identity was included as
169 a random effect to avoid pseudoreplication as some studies compared multiple secondary forest
170 sites with a single primary forest site. Models were run using maximum likelihood methods and
171 model selection was based on Akaike information criterion adjusted for small sample size
172 (AICc). The models with lowest AICc were considered to be the most well supported. The
173 goodness of fit of the most parsimonious models was estimated by calculating R^2_{GLMM} using the
174 package MuMIn (Barton, 2015) following Nakagawa and Schielzeth (2013).

175 Prior to model selection the impact of different sampling methods on results was tested
176 by fitting models with methods (point count, transect, mist-netting) included as random effects
177 with the model with lowest AICc selected. On no occasion did a model including sampling
178 methods outperform one which solely contained a random effect for each individual study (Table
179 S1). Phylogenetic correction was not used as we assessed functional trait changes in terms of

180 their putative impact on ecosystem function and not to explain changes in the avian community.
181 All statistical analyses were performed using R version 3.3.0 (R Core Team, 2016).

182

183 **Results**

184 A total of 24 studies that aimed to sample the entire avian community with data on 44 paired
185 secondary and primary forest sites were found through the systematic review (Table 2). These
186 studies documented 29,023 observations of 1,673 bird species. Sites were widely distributed
187 across the tropics but most were found in the Americas or Asia (Table 2, Figure 1). Secondary
188 forest sites had regenerated for between one and 100 years but nearly half of the sites had been
189 disturbed within 10 years prior to the studies taking place (Table 2). Only five sites had been
190 recovering for at least 40 years since disturbance.

191

192 ***Total and forest specialist species richness***

193 The most well supported model describing differences in species richness in secondary and
194 primary forests was a null model (Table S2). Species richness in secondary forests was on
195 average 12% lower than in primary forests (intercept=-0.13, SE=0.06, p=0.03, Figure 3).

196 The species richness of forest specialists was best described by a model including only
197 secondary forest age as a predictor (Table S2). Forest specialist species richness increased with
198 time since disturbance (slope=0.21, SE=0.07, p=0.01), but was not predicted to reach
199 equivalence with primary forests within 100 years (Figure 2a). After one year since disturbance
200 forest specialist species richness in secondary forests was predicted to be 63% lower than
201 primary forests, and after 100 years this had risen to 1% lower than primary forests. This model
202 showed a reasonable explanatory power ($R^2_{\text{GLMM}}=0.14$, Table S2).

203

204 ***Functional diversity metrics***

205 FD and FRic were found to be highly correlated both with each other (correlation coefficient of
206 0.9) and with species richness (correlation coefficient of 0.9 with FD and 0.8 with FRic). As a
207 result, these two metrics were removed from this analysis. A null, intercept only model was the
208 most well supported for FDis, FDiv and FEve (Table S2, Figure 3). FDis and FDiv did not differ
209 significantly between primary and secondary forests. However, FEve was 5% higher in
210 secondary forests than in primary forests (intercept=0.06, SE=0.03, p=0.03).

211 sesFD declined with time since last disturbance (slope=-1.17, SE=0.24, Figure 2b) and
212 was higher in younger forests than in primary forests (Table S2). sesFD was predicted to reach
213 equivalence with primary forest values after approximately 22 years (Figure 2b). This model
214 showed relatively high explanatory power ($R^2_{\text{GLMM}}=0.35$, Table S2).

215

216 **Discussion**

217 Our study represents the largest quantitative synthesis of avian responses to secondary tropical
218 forest succession to date. Our results indicate that avian species richness is lower in secondary
219 forests than in primary forests. Forest specialist species richness increases with secondary forest
220 age and is likely to take over 100 years to recover. Regarding functional diversity, two metrics
221 (FDis and FDiv) were similar in secondary and primary forests, whereas FEve was higher in
222 secondary forests. Once differences in species richness were accounted for, sesFD showed a
223 marked decline with increasing age of secondary forests, suggesting increasing functional
224 redundancy in avian communities during succession.

225

226 ***Species Richness***

227 Our results show that avian species richness is lower in secondary forests than in primary forests,
228 in agreement with previous reviews (Barlow et al., 2007; Bowen et al., 2007), and also that
229 species richness does not respond to secondary forest age. The latter result is in contrast to Dunn
230 (2004a) who found that avian species richness in secondary forests increased with time since
231 disturbance and reached equivalence with primary forests after 20 years. However, Dunn (2004a)
232 considered a more limited number of sites than our analysis and only one of these sites had been
233 recovering for more than 40 years. It is possible that in younger secondary forests time since
234 disturbance has an important role in determining avian community composition, but for older
235 secondary forests other factors, such as patch size, have a greater influence on the successional
236 state.

237 Although our analysis found species richness of forest specialists failed to recover within
238 100 years, this metric was predicted to be only 1% lower in secondary forests after 100 years of
239 recovery than in primary forests. This mirrors the observation that avian community composition
240 of secondary forests approaches equivalence with that of primary forests after around 100 years
241 (Dent and Wright, 2009). The rate of change in forest specialist species richness is perhaps
242 unsurprising given that although secondary forests attain much of the structure and plant
243 diversity of primary forests within 50 years, tree community composition, and therefore the
244 structural complexity of forests, is likely to take much longer (Derroire et al., 2016; Martin et al.,
245 2013; Poorter et al., 2016). Thus, the results of our study reinforce the view that, although
246 conservation value is accumulated relatively rapidly in secondary forests, primary forests (and
247 potentially mature secondary forests) are vital to prevent extinctions of forest specialists (Gibson
248 et al., 2011).

249 Although some guilds are particularly sensitive to disturbance (e.g. understory
250 insectivores; see Powell et al., 2016, 2015), our results indicate that some forest specialist species
251 are found in young secondary forests. After one year of succession forest specialist species
252 richness in secondary forests was 63% lower than in primary forests. This raises the question of
253 why are there any forest specialist species at all in such young secondary forests. Part of the
254 answer to this relates to how forests are cleared prior to agricultural use. Many secondary forests
255 in the tropics are the result of abandonment of subsistence agriculture during which some large
256 trees are often retained during forest clearance (Guevara et al., 1986; Harvey and Haber, 1998).
257 Harvey and Haber (1998) found that agricultural fields in Costa Rica contained an average of 25
258 trees per hectare, and that a third of these trees were primary forest specialist species. As a result,
259 large trees located in the agricultural matrix may be used by forest species to feed or roost
260 (Harvey and Haber, 1998), increasing the species richness of avian forest specialists in young
261 secondary forests.

262
263 ***Functional diversity***

264 FDis, a unified metric for functional diversity (Laliberté and Legendre, 2010), was found to be
265 equivalent between primary and secondary forests. FDiv in secondary forests was also similar to
266 primary forest levels, suggesting that the degree to which abundant species had the most extreme
267 trait values was similar in secondary and primary forests. These results both suggest similar
268 levels of ecosystem functioning between the two forest types. Only one other study has
269 investigated the effects of forest degradation or conversion on FDis, finding that it was higher in
270 pastures and oil palm plantations than in forest remnants (Prescott et al., 2016). Together with
271 our results, this study hints that degradation through conversion of forests to other habitat types

272 may lead to increased FDis and a reduction in ecosystem function (Prescott et al., 2016),
273 although more work is needed to relate FDis to specific ecosystem functions.

274 FEve was 5% higher in secondary forests than primary forests, suggesting a more equal
275 abundance of species in trait space in secondary forests. Assuming that resources are evenly
276 distributed, this means in theory that resources within secondary forests are being used more
277 efficiently than in primary forests (Mason et al., 2005), which would be an unexpected result.
278 However alternatively, a high FEve value could also suggest that the habitat is not very
279 structurally complex, meaning that there are a smaller number of evenly occupied niches with
280 few interactions between species (García-Morales et al., 2016; Schleuter et al., 2010). As
281 primary forests have greater structural complexity than secondary forests (Derroire et al., 2016),
282 this could explain the difference in FEve between these two forest types in our analysis.

283 At present, there is no clear picture on the relationship between FEve of avian
284 communities and forest degradation in the literature. Prescott et al. (2016) found FEve to be
285 lower in pasture than in forest remnants but equivalent in forest remnants and oil palm
286 plantations. In contrast, Edwards et al. (2013) found that FEve was lower in oil palm plantations
287 (and in twice-logged forests) than in unlogged (and once-logged) forests. Thirdly, Ibarra and
288 Martin (2015) found no relationship between the degree of deforestation and FEve. Given these
289 conflicting results, we suggest this is an area requiring further research.

290 The most pronounced relationship with forest age was seen in the standardized effect size
291 of FD (sesFD). As secondary forest age increased sesFD declined, reaching equivalence with
292 primary forests after approximately 22 years. This metric adjusts FD by accounting for species
293 richness at sites, with negative values indicating lower FD than expected given site level
294 richness. Thus, the reduction in relative sesFD with forest age that we observed suggests
295 increasing functional redundancy in older secondary forests (Pavoine and Bonsall, 2011).
296 Previous studies have found that sesFD for bird communities can increase (Edwards et al., 2013)
297 or decrease across a gradient of degradation (Prescott et al., 2016). However, our observation of
298 an increase in functional redundancy suggests that the resilience of ecosystem processes may
299 increase with secondary forest age due to buffering of the negative impacts of species extinction.
300 Equally this suggests that even where functional diversity in young secondary tropical forests is
301 similar to that found in primary forests, these communities and the ecosystem services they
302 supply may be less stable over time.

303 304 *Caveats*

305 Our study represents the most comprehensive synthesis of avian functional diversity in
306 secondary forests to date but, like all syntheses, it was affected by the quality and
307 representativeness of the data we used (Gonzalez et al., 2016). As a result there are two
308 important caveats that relate to our analysis. Firstly, our study highlights the importance of the
309 age of secondary forests as a determinant of the biodiversity it plays host to, but there are many
310 other important variables that we could not account for in this study. For example, the duration
311 and intensity of previous land use affect the initial conditions of secondary forests following
312 abandonment (Jakovac et al., 2015). Following abandonment, the connectivity, proximity to
313 primary forest, and patch size can all play important roles in determining the rate at which forest
314 species colonise degraded forests (Banks-Leite et al., 2010; Maldonado-Coelho and Marini,
315 2000; Prugh et al., 2008). Secondly, the primary forest sites used in our study may have varied in
316 quality as statistical controls since definitions of primary forest probably differed between
317 studies. In both of these cases it was not possible to account for this potential variation amongst

318 studies and addressing how these factors interact with age of secondary forests is a key research
319 gap.

320 Regarding representativeness, the sites used in our study are likely to be broadly
321 representative of secondary forests throughout the tropics. Few sites had been intensively farmed
322 and the majority of sites were under 40 years old, reflecting secondary tropical forests generally
323 (Asner et al., 2009; Smith et al., 2003).

324

325 ***Conclusion***

326 The conservation value of secondary tropical forests will vary depending upon the aims of
327 conservation strategies. If the aims are to support overall or forest specialist species richness at
328 primary forest levels then our results suggest that preservation of primary forests is vital, in
329 agreement with previous reviews (Barlow et al., 2007; Bowen et al., 2007), although the richness
330 of forest specialist species, and hence the conservation value of regrowth, does increase with
331 secondary forest age. If strategies are related to the levels of ecosystem functioning of the forests
332 then, although there were some differences between secondary and primary tropical forests for
333 functional diversity metrics, our results suggest that secondary forests can support provision of
334 ecosystem functions, including pollination and seed dispersal (but see Markl et al., 2012). Our
335 results also suggest that secondary forest age influences conservation value in terms of
336 ecosystem functioning, with older secondary forests having increased functional redundancy.

337 The conservation value of secondary forests will never be maximised if regrowth is
338 deforested. However, mid-age stands are often converted to agriculture in South America (Smith
339 et al., 2003) and degraded forests are regularly converted to oil palm or rubber plantations in
340 Southeast Asia (Abood et al., 2015; Koh and Wilcove, 2008), resulting in loss of avian species
341 and functional diversity (Edwards et al., 2013; Prescott et al., 2016; Tscharntke et al., 2008).
342 Therefore, to maximise the biodiversity value of tropical landscapes, secondary forests should be
343 protected, particularly in landscapes where little pristine habitat remains. Protecting older
344 secondary forests provides high conservation value now, whereas protecting young regrowth
345 promises future returns. Restoration of young secondary forests could also play a role.
346 Enrichment planting can be used to enhance biodiversity by adding tree species that are unlikely
347 to colonise unassisted, for example late-successional species or those lacking dispersers
348 (Griscom and Ashton, 2011; Lamb et al., 2005). Assisting vegetative recovery to a late-
349 successional species composition could improve habitat suitability for forest specialists and
350 hence, accelerate their recovery. Secondary forests have a role to play in the conservation of
351 forest species and provision of ecosystem services and this should be recognised in tropical
352 conservation strategies.

353

354 **Conflict of Interest:** The authors declare that they have no conflict of interest.
355

356 **Acknowledgements**

357 Thank you to the authors of all of the studies considered, in particular S.H. Borges, C. Banks-
358 Leite, R.F. de Lima, D. Becker, R.K. Mulwa, E.L. Neuschulz, B. Maas, G. Ferraz, D. Edwards
359 and J. Gilroy, to A. Symes and to BirdLife International for providing data.
360

361 **Funding**

362 P.A. Martin was funded by a NERC PhD studentship and by NERC via the Biodiversity &
363 Ecosystem Service Sustainability (BESS) programme (Project ref. NE/K01322X/1).
364

365 **References**

- 366 Abood, S.A., Lee, J.S.H., Burivalova, Z., Garcia-Ulloa, J., Koh, L.P., 2015. Relative
367 contributions of the logging, fiber, oil palm, and mining industries to forest loss in
368 Indonesia. *Conserv. Lett.* 8, 58–67. doi:10.1111/conl.12103
- 369 Andrade, G.I., Rubio-Torgler, H., 1994. Sustainable use of the tropical rain forest: Evidence
370 from the avifauna in a shifting-cultivation habitat mosaic in the Colombian Amazon.
371 *Conserv. Biol.* 8, 545–554. doi:10.1046/j.1523-1739.1994.08020545.x
- 372 Asner, G.P., Rudel, T.K., Aide, T.M., Defries, R., Emerson, R., 2009. A contemporary
373 assessment of change in humid tropical forests. *Conserv. Biol.* 23, 1386–1395.
374 doi:10.1111/j.1523-1739.2009.01333.x
- 375 Banks-Leite, C., Ewers, R.M., Metzger, J.P., 2012. Unraveling the drivers of community
376 dissimilarity and species extinction in fragmented landscapes. *Ecology* 93, 2560–2569.
- 377 Banks-Leite, C., Ewers, R.M., Metzger, J.-P., 2010. Edge effects as the principal cause of area
378 effects on birds in fragmented secondary forest. *Oikos* 119, 918–926. doi:10.1111/j.1600-
379 0706.2009.18061.x
- 380 Barlow, J., Mestre, L.A., Gardner, T.A., Peres, C., 2007. The value of primary, secondary and
381 plantation forests for Amazonian birds. *Biol. Conserv.* 136, 212 – 231.
382 doi:http://dx.doi.org/10.1016/j.biocon.2006.11.021
- 383 Barton, K., 2015. MuMIn: Multi-Model Inference.
- 384 Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using
385 lme4. *J. Stat. Softw.* 67, 1–48. doi:10.18637/jss.v067.i01
- 386 Becker, C.D., Agreda, A., 2005. Bird community differences in mature and second growth Garua
387 forest in Machalilla National Park, Ecuador. *Ornitol. Neotropical* 16, 297–319.
- 388 Becker, C.D., Loughin, T.M., Santander, T., 2008. Identifying forest-obligate birds in tropical
389 moist cloud forest of Andean Ecuador. *J. Field Ornithol.* 79, 229–244.
390 doi:10.1111/j.1557-9263.2008.00184.x
- 391 BirdLife International, 2013. IUCN Red List for birds [WWW Document]. URL
392 http://www.birdlife.org (accessed 6.1.13).
- 393 Blake, J.G., Loiselle, B.A., 2001. Bird assemblages in second-growth and old-growth forests,
394 Costa Rica: Perspectives from mist nets and point counts. *The Auk* 118, 304–326.
395 doi:10.1642/0004-8038(2001)118[0304:BAISGA]2.0.CO;2
- 396 Borges, S.H., 2007. Bird assemblages in secondary forests developing after slash-and-burn
397 agriculture in the Brazilian Amazon. *J. Trop. Ecol.* 23, 469–477.
398 doi:10.1017/S0266467407004105

399 Bowen, M.E., McAlpine, C.A., House, A.P.N., Smith, G.C., 2007. Regrowth forests on
400 abandoned agricultural land: A review of their habitat values for recovering forest fauna.
401 *Biol. Conserv.* 140, 273 – 296. doi:http://dx.doi.org/10.1016/j.biocon.2007.08.012

402 Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E., Miller, S.E.,
403 2009. The potential for species conservation in tropical secondary forests. *Conserv. Biol.*
404 *J. Soc. Conserv. Biol.* 23, 1406–1417. doi:10.1111/j.1523-1739.2009.01338.x

405 Convention on Biological Diversity, 2010. Decision adopted by the conference of the parties to
406 the convention on biological diversity at its tenth meeting - The Strategic Plan for
407 Biodiversity 2011-2020 and the Aichi Biodiversity Targets.

408 Corlett, R.T., 1994. What is secondary forest? *J. Trop. Ecol.* 10, 445–447. doi:10.2307/2560329

409 Cox, R.L., Underwood, E.C., 2011. The importance of conserving biodiversity outside of
410 protected areas in Mediterranean ecosystems. *PLoS ONE* 6, e14508.
411 doi:10.1371/journal.pone.0014508

412 Curran, L.M., 2004. Lowland Forest Loss in Protected Areas of Indonesian Borneo. *Science* 303,
413 1000–1003. doi:10.1126/science.1091714

414 Dawson, J., Turner, C., Pileng, O., Farmer, A., McGary, C., Walsh, C., Tamblyn, A., Yosi, C.,
415 2011. Bird communities of the lower Waria Valley, Morobe Province, Papua New
416 Guinea: a comparison between habitat types. *Trop. Conserv. Sci.* 4, 317–348.

417 Del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E., 2016. Handbook of the Birds
418 of the World Alive. Lynx Edicions, Barcelona [WWW Document]. URL (accessed
419 10.21.16).

420 Dent, D.H., Wright, S.J., 2009. The future of tropical species in secondary forests: A quantitative
421 review. *Biol. Conserv.* 142, 2833 – 2843.
422 doi:http://dx.doi.org/10.1016/j.biocon.2009.05.035

423 Derroire, G., Balvanera, P., Castellanos-Castro, C., Decocq, G., Kennard, D.K., Lebrija-Trejos,
424 E., Leiva, J.A., Odén, P.-C., Powers, J.S., Rico-Gray, V., Tigabu, M., Healey, J.R., 2016.
425 Resilience of tropical dry forests – a meta-analysis of changes in species diversity and
426 composition during secondary succession. *Oikos* 125, 1386–1397. doi:10.1111/oik.03229

427 Dudley, N., 2008. Guidelines for applying protected area management categories. IUCN, Gland,
428 Switzerland.

429 Dunn, R.R., 2004a. Recovery of faunal communities during tropical forest regeneration.
430 *Conserv. Biol.* 18, 302–309. doi:10.1111/j.1523-1739.2004.00151.x

431 Dunn, R.R., 2004b. Managing the tropical landscape: a comparison of the effects of logging and
432 forest conversion to agriculture on ants, birds, and lepidoptera. *For. Ecol. Manag.* 191,
433 215–224. doi:10.1016/j.foreco.2003.12.008

434 Edwards, F.A., Edwards, D.P., Hamer, K.C., Davies, R.G., 2013. Impacts of logging and
435 conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. *Ibis*
436 155, 313–326. doi:10.1111/ibi.12027

437 Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-
438 Dewenter, I., Emmerson, M., Potts, S.G., Tschamtker, T., Weisser, W., Bommarco, R.,
439 2015. Functional identity and diversity of animals predict ecosystem functioning better
440 than species-based indices. *Proc. R. Soc. B Biol. Sci.* 282, 20142620–20142620.
441 doi:10.1098/rspb.2014.2620

442 García-Morales, R., Moreno, C.E., Badano, E.I., Zuria, I., Galindo-González, J., Rojas-Martínez,
443 A.E., Ávila-Gómez, E.S., 2016. Deforestation Impacts on Bat Functional Diversity in
444 Tropical Landscapes. *PLOS ONE* 11, e0166765. doi:10.1371/journal.pone.0166765

- 445 Gardner, T.A., Barlow, J., Parry, L.W., Peres, C.A., 2007. Predicting the uncertain future of
446 tropical forest species in a data vacuum. *Biotropica* 39, 25–30. doi:10.1111/j.1744-
447 7429.2006.00228.x
- 448 Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., Foley,
449 J.A., 2010. Tropical forests were the primary sources of new agricultural land in the
450 1980s and 1990s. *Proc. Natl. Acad. Sci.* 107, 16732–16737.
451 doi:10.1073/pnas.0910275107
- 452 Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A.,
453 Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are
454 irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–381.
455 doi:10.1038/nature10425
- 456 Gilroy, J.J., Woodcock, P., Edwards, F.A., Wheeler, C., Baptiste, B.L.G., Medina Uribe, C.A.,
457 Haugaasen, T., Edwards, D.P., 2014. Cheap carbon and biodiversity co-benefits from
458 forest regeneration in a hotspot of endemism. *Nat. Clim. Change* 4, 503–507.
459 doi:10.1038/nclimate2200
- 460 Gonzalez, A., Cardinale, B.J., Allington, G.R.H., Byrnes, J., Arthur Endsley, K., Brown, D.G.,
461 Hooper, D.U., Isbell, F., O'Connor, M.I., Loreau, M., 2016. Estimating local biodiversity
462 change: a critique of papers claiming no net loss of local diversity. *Ecology* 97, 1949–
463 1960. doi:10.1890/15-1759.1
- 464 Griffin, J.N., Méndez, V., Johnson, A.F., Jenkins, S.R., Foggo, A., 2009. Functional diversity
465 predicts overyielding effect of species combination on primary productivity. *Oikos* 118,
466 37–44. doi:10.1111/j.1600-0706.2008.16960.x
- 467 Griscom, H.P., Ashton, M.S., 2011. Restoration of dry tropical forests in Central America: A
468 review of pattern and process. *For. Ecol. Manag.* 261, 1564–1579.
469 doi:10.1016/j.foreco.2010.08.027
- 470 Guevara, S., Purata, S.E., Van der Maarel, E., 1986. The role of remnant forest trees in tropical
471 secondary succession. *Vegetatio* 66, 77–84. doi:10.1007/BF00045497
- 472 Harvey, C.A., Haber, W.A., 1998. Remnant trees and the conservation of biodiversity in Costa
473 Rican pastures. *Agrofor. Syst.* 44, 37–68. doi:10.1023/A:1006122211692
- 474 Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in
475 experimental ecology. *Ecology* 80, 1150–1156. doi:10.2307/177062
- 476 Hudson, L.N., Newbold, T., Contu, S., Hill, S.L.L., Lysenko, I., De Palma, A., Phillips, H.R.P.,
477 Alhusseini, T.I., Bedford, F.E., Bennett, D.J., Booth, H., Burton, V.J., Chng, C.W.T.,
478 Choimes, A., Correia, D.L.P., Day, J., Echeverría-Londoño, S., Emerson, S.R., Gao, D.,
479 Garon, M., Harrison, M.L.K., Ingram, D.J., Jung, M., Kemp, V., Kirkpatrick, L., Martin,
480 C.D., Pan, Y., Pask-Hale, G.D., Pynegar, E.L., Robinson, A.N., Sanchez-Ortiz, K.,
481 Senior, R.A., Simmons, B.I., White, H.J., Zhang, H., Aben, J., Abrahamczyk, S., Adum,
482 G.B., Aguilar-Barquero, V., Aizen, M.A., Albertos, B., Alcalá, E.L., del Mar Alguacil,
483 M., Alignier, A., Ancrenaz, M., Andersen, A.N., Arbeláez-Cortés, E., Armbrrecht, I.,
484 Arroyo-Rodríguez, V., Aumann, T., Axmacher, J.C., Azhar, B., Azpiroz, A.B., Baeten,
485 L., Bakayoko, A., Báldi, A., Banks, J.E., Baral, S.K., Barlow, J., Barratt, B.I.P., Barrico,
486 L., Bartolommei, P., Barton, D.M., Basset, Y., Batáry, P., Bates, A.J., Baur, B., Bayne,
487 E.M., Beja, P., Benedick, S., Berg, Å., Bernard, H., Berry, N.J., Bhatt, D., Bicknell, J.E.,
488 Bihn, J.H., Blake, R.J., Bobo, K.S., Bóçon, R., Boekhout, T., Böhning-Gaese, K.,
489 Bonham, K.J., Borges, P.A.V., Borges, S.H., Boutin, C., Bouyer, J., Bragagnolo, C.,
490 Brandt, J.S., Brearley, F.Q., Brito, I., Bros, V., Brunet, J., Buczkowski, G., Buddle, C.M.,

491 Bugter, R., Buscardo, E., Buse, J., Cabra-García, J., Cáceres, N.C., Cagle, N.L., Calviño-
 492 Cancela, M., Cameron, S.A., Cancellato, E.M., Caparrós, R., Cardoso, P., Carpenter, D.,
 493 Carrijo, T.F., Carvalho, A.L., Cassano, C.R., Castro, H., Castro-Luna, A.A., Rolando,
 494 C.B., Cerezo, A., Chapman, K.A., Chauvat, M., Christensen, M., Clarke, F.M., Cleary,
 495 D.F.R., Colombo, G., Connop, S.P., Craig, M.D., Cruz-López, L., Cunningham, S.A.,
 496 D’Aniello, B., D’Cruze, N., da Silva, P.G., Dallimer, M., Danquah, E., Darvill, B.,
 497 Dauber, J., Davis, A.L.V., Dawson, J., de Sassi, C., de Thoisy, B., Deheuvels, O., Dejean,
 498 A., Devineau, J.-L., Diekötter, T., Dolia, J.V., Domínguez, E., Dominguez-Haydar, Y.,
 499 Dorn, S., Draper, I., Dreber, N., Dumont, B., Dures, S.G., Dynesius, M., Edenius, L.,
 500 Eggleton, P., Eigenbrod, F., Elek, Z., Entling, M.H., Esler, K.J., de Lima, R.F., Faruk, A.,
 501 Farwig, N., Fayle, T.M., Felicioli, A., Felton, A.M., Fensham, R.J., Fernandez, I.C.,
 502 Ferreira, C.C., Ficetola, G.F., Fiera, C., Filgueiras, B.K.C., Firincioglu, H.K., Flaspohler,
 503 D., Floren, A., Fonte, S.J., Fournier, A., Fowler, R.E., Franzén, M., Fraser, L.H.,
 504 Fredriksson, G.M., Freire, G.B., Frizzo, T.L.M., Fukuda, D., Furlani, D., Gaigher, R.,
 505 Ganzhorn, J.U., García, K.P., Garcia-R, J.C., Garden, J.G., Garilleti, R., Ge, B.-M.,
 506 Gendreau-Berthiaume, B., Gerard, P.J., Gheler-Costa, C., Gilbert, B., Giordani, P.,
 507 Giordano, S., Golodets, C., Gomes, L.G.L., Gould, R.K., Goulson, D., Gove, A.D.,
 508 Granjon, L., Grass, I., Gray, C.L., Grogan, J., Gu, W., Guardiola, M., Gunawardene,
 509 N.R., Gutierrez, A.G., Gutiérrez-Lamus, D.L., Haarmeyer, D.H., Hanley, M.E., Hanson,
 510 T., Hashim, N.R., Hassan, S.N., Hatfield, R.G., Hawes, J.E., Hayward, M.W., Hébert, C.,
 511 Helden, A.J., Henden, J.-A., Henschel, P., Hernández, L., Herrera, J.P., Herrmann, F.,
 512 Herzog, F., Higuera-Diaz, D., Hilje, B., Höfer, H., Hoffmann, A., Horgan, F.G.,
 513 Hornung, E., Horváth, R., Hylander, K., Isaacs-Cubides, P., Ishida, H., Ishitani, M.,
 514 Jacobs, C.T., Jaramillo, V.J., Jauker, B., Hernández, F.J., Johnson, M.F., Jolli, V.,
 515 Jonsell, M., Juliani, S.N., Jung, T.S., Kapoor, V., Kappes, H., Kati, V., Katovai, E.,
 516 Kellner, K., Kessler, M., Kirby, K.R., Kittle, A.M., Knight, M.E., Knop, E., Kohler, F.,
 517 Koivula, M., Kolb, A., Kone, M., Kőrösi, Á., Krauss, J., Kumar, A., Kumar, R., Kurz,
 518 D.J., Kutt, A.S., Lachat, T., Lantschner, V., Lara, F., Lasky, J.R., Latta, S.C., Laurance,
 519 W.F., Lavelle, P., Le Féon, V., LeBuhn, G., Légaré, J.-P., Lehouck, V., Lencinas, M.V.,
 520 Lentini, P.E., Letcher, S.G., Li, Q., Litchwark, S.A., Littlewood, N.A., Liu, Y., Lo-Man-
 521 Hung, N., López-Quintero, C.A., Louhaichi, M., Lövei, G.L., Lucas-Borja, M.E., Luja,
 522 V.H., Luskin, M.S., MacSwiney G, M.C., Maeto, K., Magura, T., Mallari, N.A., Malone,
 523 L.A., Malonza, P.K., Malumbres-Olarte, J., Mandujano, S., Måren, I.E., Marin-Spiotta,
 524 E., Marsh, C.J., Marshall, E.J.P., Martínez, E., Martínez Pastur, G., Moreno Mateos, D.,
 525 Mayfield, M.M., Mazimpaka, V., McCarthy, J.L., McCarthy, K.P., McFrederick, Q.S.,
 526 McNamara, S., Medina, N.G., Medina, R., Mena, J.L., Mico, E., Mikusinski, G., Milder,
 527 J.C., Miller, J.R., Miranda-Esquivel, D.R., Moir, M.L., Morales, C.L., Muchane, M.N.,
 528 Muchane, M., Mudri-Stojnic, S., Munira, A.N., Muñoz-Alonso, A., Munyekenye, B.F.,
 529 Naidoo, R., Naithani, A., Nakagawa, M., Nakamura, A., Nakashima, Y., Naoe, S., Nates-
 530 Parra, G., Navarrete Gutierrez, D.A., Navarro-Iriarte, L., Ndang’ang’a, P.K., Neuschulz,
 531 E.L., Ngai, J.T., Nicolas, V., Nilsson, S.G., Noreika, N., Norfolk, O., Noriega, J.A.,
 532 Norton, D.A., Nöske, N.M., Nowakowski, A.J., Numa, C., O’Dea, N., O’Farrell, P.J.,
 533 Oduro, W., Oertli, S., Ofori-Boateng, C., Oke, C.O., Oostra, V., Osgathorpe, L.M.,
 534 Otavo, S.E., Page, N.V., Paritsis, J., Parra-H, A., Parry, L., Pe’er, G., Pearman, P.B.,
 535 Pelegrin, N., Péliissier, R., Peres, C.A., Peri, P.L., Persson, A.S., Petanidou, T., Peters,
 536 M.K., Pethiyagoda, R.S., Phalan, B., Philips, T.K., Pillsbury, F.C., Pincheira-Ulbrich, J.,

537 Pineda, E., Pino, J., Pizarro-Araya, J., Plumptre, A.J., Poggio, S.L., Politi, N., Pons, P.,
 538 Poveda, K., Power, E.F., Presley, S.J., Proença, V., Quaranta, M., Quintero, C., Rader,
 539 R., Ramesh, B.R., Ramirez-Pinilla, M.P., Ranganathan, J., Rasmussen, C., Redpath-
 540 Downing, N.A., Reid, J.L., Reis, Y.T., Rey Benayas, J.M., Rey-Velasco, J.C., Reynolds,
 541 C., Ribeiro, D.B., Richards, M.H., Richardson, B.A., Richardson, M.J., Ríos, R.M.,
 542 Robinson, R., Robles, C.A., Römbke, J., Romero-Duque, L.P., Rös, M., Rosselli, L.,
 543 Rossiter, S.J., Roth, D.S., Roulston, T.H., Rousseau, L., Rubio, A.V., Ruel, J.-C., Sadler,
 544 J.P., Sáfián, S., Saldaña-Vázquez, R.A., Sam, K., Samnegård, U., Santana, J., Santos, X.,
 545 Savage, J., Schellhorn, N.A., Schilthuizen, M., Schmiedel, U., Schmitt, C.B., Schon,
 546 N.L., Schüepp, C., Schumann, K., Schweiger, O., Scott, D.M., Scott, K.A., Sedlock, J.L.,
 547 Seefeldt, S.S., Shahabuddin, G., Shannon, G., Sheil, D., Sheldon, F.H., Shochat, E.,
 548 Siebert, S.J., Silva, F.A.B., Simonetti, J.A., Slade, E.M., Smith, J., Smith-Pardo, A.H.,
 549 Sodhi, N.S., Somarriba, E.J., Sosa, R.A., Soto Quiroga, G., St-Laurent, M.-H.,
 550 Starzomski, B.M., Stefanescu, C., Steffan-Dewenter, I., Stouffer, P.C., Stout, J.C.,
 551 Strauch, A.M., Struebig, M.J., Su, Z., Suarez-Rubio, M., Sugiura, S., Summerville, K.S.,
 552 Sung, Y.-H., Sutrisno, H., Svenning, J.-C., Teder, T., Threlfall, C.G., Tiitsaar, A., Todd,
 553 J.H., Tonietto, R.K., Torre, I., Tóthmérész, B., Tschardtke, T., Turner, E.C., Tylianakis,
 554 J.M., Uehara-Prado, M., Urbina-Cardona, N., Vallan, D., Vanbergen, A.J., Vasconcelos,
 555 H.L., Vassilev, K., Verboven, H.A.F., Verdasca, M.J., Verdú, J.R., Vergara, C.H.,
 556 Vergara, P.M., Verhulst, J., Virgilio, M., Vu, L.V., Waite, E.M., Walker, T.R., Wang, H.-
 557 F., Wang, Y., Watling, J.I., Weller, B., Wells, K., Westphal, C., Wiafe, E.D., Williams,
 558 C.D., Willig, M.R., Woinarski, J.C.Z., Wolf, J.H.D., Wolters, V., Woodcock, B.A., Wu,
 559 J., Wunderle, J.M., Yamaura, Y., Yoshikura, S., Yu, D.W., Zaitsev, A.S., Zeidler, J., Zou,
 560 F., Collen, B., Ewers, R.M., Mace, G.M., Purves, D.W., Scharlemann, J.P.W., Purvis, A.,
 561 2017. The database of the PREDICTS (Projecting Responses of Ecological Diversity In
 562 Changing Terrestrial Systems) project. *Ecol. Evol.* 7, 145–188. doi:10.1002/ece3.2579
 563 Hutto, R.L., 1989. The effect of habitat alteration on migratory land birds in a west Mexican
 564 tropical deciduous forest: a conservation perspective. *Conserv. Biol.* 3, 138–148.
 565 doi:10.1111/j.1523-1739.1989.tb00066.x
 566 Ibarra, J.T., Martin, K., 2015. Biotic homogenization: Loss of avian functional richness and
 567 habitat specialists in disturbed Andean temperate forests. *Biol. Conserv.* 192, 418–427.
 568 doi:10.1016/j.biocon.2015.11.008
 569 ITTO, 2002. ITTO guidelines for the restoration, management and rehabilitation of degraded and
 570 secondary tropical forests.
 571 Jakovac, C.C., Peña-Claros, M., Kuyper, T.W., Bongers, F., 2015. Loss of secondary-forest
 572 resilience by land-use intensification in the Amazon. *J. Ecol.* 103, 67–77.
 573 doi:10.1111/1365-2745.12298
 574 Johns, A.D., 1991. Responses of Amazonian rain forest birds to habitat modification. *J. Trop.*
 575 *Ecol.* 7, 417–437. doi:10.1017/S0266467400005812
 576 Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D.,
 577 Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and
 578 ecology. *Bioinformatics* 26, 1463–1464. doi:10.1093/bioinformatics/btq166
 579 Koh, L.P., Wilcove, D.S., 2008. Is oil palm agriculture really destroying tropical biodiversity?:
 580 Oil palm agriculture and tropical biodiversity. *Conserv. Lett.* 1, 60–64.
 581 doi:10.1111/j.1755-263X.2008.00011.x

- 582 Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity
583 from multiple traits. *Ecology* 91, 299–305.
- 584 Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes.
585 *Science* 310, 1628–1632. doi:10.1126/science.1111773
- 586 Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., Sloan, S.P.,
587 Laurance, S.G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V.,
588 Ashton, P., Benítez-Malvido, J., Blom, A., Bobo, K.S., Cannon, C.H., Cao, M., Carroll,
589 R., Chapman, C., Coates, R., Cords, M., Danielsen, F., De Dijn, B., Dinerstein, E.,
590 Donnelly, M.A., Edwards, D., Edwards, F., Farwig, N., Fashing, P., Forget, P.-M.,
591 Foster, M., Gale, G., Harris, D., Harrison, R., Hart, J., Karpanty, S., John Kress, W.,
592 Krishnaswamy, J., Logsdon, W., Lovett, J., Magnusson, W., Maisels, F., Marshall, A.R.,
593 McClearn, D., Mudappa, D., Nielsen, M.R., Pearson, R., Pitman, N., van der Ploeg, J.,
594 Plumptre, A., Poulsen, J., Quesada, M., Rainey, H., Robinson, D., Roetgers, C., Rovero,
595 F., Scatena, F., Schulze, C., Sheil, D., Struhsaker, T., Terborgh, J., Thomas, D., Timm,
596 R., Nicolas Urbina-Cardona, J., Vasudevan, K., Joseph Wright, S., Carlos Arias-G., J.,
597 Arroyo, L., Ashton, M., Auzel, P., Babaasa, D., Babweteera, F., Baker, P., Banki, O.,
598 Bass, M., Bila-Isia, I., Blake, S., Brockelman, W., Brokaw, N., Brühl, C.A.,
599 Bunyavechewin, S., Chao, J.-T., Chave, J., Chellam, R., Clark, C.J., Clavijo, J.,
600 Congdon, R., Corlett, R., Dattaraja, H.S., Dave, C., Davies, G., de Mello Beisiegel, B., de
601 Nazaré Paes da Silva, R., Di Fiore, A., Diesmos, A., Dirzo, R., Doran-Sheehy, D., Eaton,
602 M., Emmons, L., Estrada, A., Ewango, C., Fedigan, L., Feer, F., Fruth, B., Giacalone
603 Willis, J., Goodale, U., Goodman, S., Guix, J.C., Guthiga, P., Haber, W., Hamer, K.,
604 Herbinger, I., Hill, J., Huang, Z., Fang Sun, I., Ickes, K., Itoh, A., Ivanauskas, N., Jackes,
605 B., Janovec, J., Janzen, D., Jiangming, M., Jin, C., Jones, T., Justiniano, H., Kalko, E.,
606 Kasangaki, A., Killeen, T., King, H., Klop, E., Knott, C., Koné, I., Kudavidanage, E.,
607 Lahoz da Silva Ribeiro, J., Lattke, J., Laval, R., Lawton, R., Leal, M., Leighton, M.,
608 Lentino, M., Leonel, C., Lindsell, J., Ling-Ling, L., Eduard Linsenmair, K., Losos, E.,
609 Lugo, A., Lwanga, J., Mack, A.L., Martins, M., Scott McGraw, W., McNab, R., Montag,
610 L., Myers Thompson, J., Nabe-Nielsen, J., Nakagawa, M., Nepal, S., Norconk, M.,
611 Novotny, V., O'Donnell, S., Opiang, M., Ouboter, P., Parker, K., Parthasarathy, N.,
612 Pisciotta, K., Prawiradilaga, D., Pringle, C., Rajathurai, S., Reichard, U., Reinartz, G.,
613 Renton, K., Reynolds, G., Reynolds, V., Riley, E., Rödel, M.-O., Rothman, J., Round, P.,
614 Sakai, S., Sanaiotti, T., Savini, T., Schaab, G., Seidensticker, J., Siaka, A., Silman, M.R.,
615 Smith, T.B., de Almeida, S.S., Sodhi, N., Stanford, C., Stewart, K., Stokes, E., Stoner,
616 K.E., Sukumar, R., Surbeck, M., Tobler, M., Tschardtke, T., Turkalo, A., Umapathy, G.,
617 van Weerd, M., Vega Rivera, J., Venkataraman, M., Venn, L., Vereá, C., Volkmer de
618 Castilho, C., Waltert, M., Wang, B., Watts, D., Weber, W., West, P., Whitacre, D.,
619 Whitney, K., Wilkie, D., Williams, S., Wright, D.D., Wright, P., Xiankai, L., Yonzon, P.,
620 Zamzani, F., 2012. Averting biodiversity collapse in tropical forest protected areas.
621 *Nature* 489, 290–294. doi:10.1038/nature11318
- 622 Maas, B., Putra, D.D., Waltert, M., Clough, Y., Tschardtke, T., Schulze, C.H., 2009. Six years of
623 habitat modification in a tropical rainforest margin of Indonesia do not affect bird
624 diversity but endemic forest species. *Biol. Conserv.* 142, 2665–2671.
625 doi:10.1016/j.biocon.2009.06.018

- 626 Maldonado-Coelho, M., Marini, M.Â., 2000. Effects of forest fragment size and successional
627 stage on mixed-species bird flocks in southeastern Brazil. *The Condor* 102, 585–594.
628 doi:10.2307/1369789
- 629 Mallari, N.A.D., Collar, N.J., Lee, D.C., McGowan, P.J.K., Wilkinson, R., Marsden, S.J., 2011.
630 Population densities of understorey birds across a habitat gradient in Palawan,
631 Philippines: implications for conservation. *Oryx* 45, 234–242.
632 doi:10.1017/S0030605310001031
- 633 Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J.,
634 Böhning-Gaese, K., 2012. Meta-Analysis of the effects of human disturbance on seed
635 dispersal by animals. *Conserv. Biol.* 26, 1072–1081. doi:10.1111/j.1523-
636 1739.2012.01927.x
- 637 Marsden, S.J., Symes, C.T., Mack, A.L., 2006. The response of a New Guinean avifauna to
638 conversion of forest to small-scale agriculture. *Ibis* 148, 629–640. doi:10.1111/j.1474-
639 919X.2006.00577.x
- 640 Martin, P.A., Newton, A.C., Bullock, J.M., 2013. Carbon pools recover more quickly than plant
641 biodiversity in tropical secondary forests. *Proc. R. Soc. B Biol. Sci.* 280.
642 doi:10.1098/rspb.2013.2236
- 643 Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional
644 evenness and functional divergence: the primary components of functional diversity.
645 *Oikos* 111, 112–118. doi:10.1111/j.0030-1299.2005.13886.x
- 646 Mulwa, R.K., Böhning-Gaese, K., Schleuning, M., 2012. High bird species diversity in
647 structurally heterogeneous farmland in western Kenya. *Biotropica* 44, 801–809.
648 doi:10.1111/j.1744-7429.2012.00877.x
- 649 Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000.
650 Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
651 doi:10.1038/35002501
- 652 Naidoo, R., 2004. Species richness and community composition of songbirds in a tropical forest-
653 agricultural landscape. *Anim. Conserv.* 7, 93–105. doi:10.1017/S1367943003001185
- 654 Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from
655 generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142.
656 doi:10.1111/j.2041-210x.2012.00261.x
- 657 O’Dea, N., Whittaker, R., 2007. How resilient are Andean montane forest bird communities to
658 habitat degradation? *Biodivers. Conserv.* 16, 1131–1159. doi:10.1007/s10531-006-9095-
659 9
- 660 Pavoine, S., Bonsall, M.B., 2011. Measuring biodiversity to explain community assembly: a
661 unified approach. *Biol. Rev.* 86, 792–812. doi:10.1111/j.1469-185X.2010.00171.x
- 662 Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward.
663 *Ecol. Lett.* 9, 741–758. doi:10.1111/j.1461-0248.2006.00924.x
- 664 Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M.,
665 Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., de
666 Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B.H.J., Denslow, J.S., Dent, D.H.,
667 DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César,
668 R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D.,
669 Letcher, S.G., Licona, J.-C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M.,
670 Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes,
671 Y.R.F., Ochoa-Gaona, S., de Oliveira, A.A., Orihuela-Belmonte, E., Peña-Claros, M.,

672 Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez,
673 I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K.,
674 Swenson, N.G., Toledo, M., Uriarte, M., van Breugel, M., van der Wal, H., Veloso,
675 M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Bentos, T.V., Williamson, G.B.,
676 Rozendaal, D.M.A., 2016. Biomass resilience of Neotropical secondary forests. *Nature*
677 530, 211–214.

678 Powell, L.L., Wolfe, J.D., Johnson, E.I., Hines, J.E., Nichols, J.D., Stouffer, P.C., 2015.
679 Heterogeneous movement of insectivorous Amazonian birds through primary and
680 secondary forest: A case study using multistate models with radiotelemetry data. *Spec.*
681 *Issue Ecol. Conserv. Avian Insectivores Rainfor. Understory Pan-Trop. Perspect.* 188,
682 100–108. doi:10.1016/j.biocon.2015.01.028

683 Powell, L.L., Wolfe, J.D., Johnson, E.I., Stouffer, P.C., 2016. Forest recovery in post-pasture
684 Amazonia: Testing a conceptual model of space use by insectivorous understory birds.
685 *Biol. Conserv.* 194, 22–30. doi:10.1016/j.biocon.2015.11.025

686 Prescott, G.W., Gilroy, J.J., Haugeaasen, T., Medina Uribe, C.A., Foster, W.A., Edwards, D.P.,
687 2016. Reducing the impacts of Neotropical oil palm development on functional diversity.
688 *Biol. Conserv.* 197, 139–145. doi:10.1016/j.biocon.2016.02.013

689 Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., Brashares, J.S., 2008. Effect of habitat area and
690 isolation on fragmented animal populations. *Proc. Natl. Acad. Sci. U. S. A.* 105, 20770–
691 20775. doi:10.1073/pnas.0806080105

692 Pullin, A.S., Stewart, G.B., 2006. Guidelines for systematic review in conservation and
693 environmental management. *Conserv. Biol.* 20, 1647–1656. doi:10.1111/j.1523-
694 1739.2006.00485.x

695 Raman, T.R.S., Rawat, G.S., Johnsingh, A.J.T., 1998. Recovery of tropical rainforest avifauna in
696 relation to vegetation succession following shifting cultivation in Mizoram, north-east
697 India. *J. Appl. Ecol.* 35, 214–231. doi:10.1046/j.1365-2664.1998.00297.x

698 R Core Team, 2016. R 3.3.0. R: A language and environment for statistical computing. R
699 Foundation for Statistical Computing, Vienna, Austria.

700 Reid, J.L., Harris, J.B.C., Zahawi, R.A., 2012. Avian habitat preference in tropical forest
701 restoration in southern Costa Rica. *Biotropica* 44, 350–359. doi:10.1111/j.1744-
702 7429.2011.00814.x

703 Renner, S., Waltert, M., Mühlenberg, M., 2006. Comparison of bird communities in primary vs.
704 young secondary tropical montane cloud forest in Guatemala. *Biodivers. Conserv.* 15,
705 1545–1575. doi:10.1007/s10531-005-2930-6

706 Schleuter, D., Daufresne, M., Massol, F., Argillier, C., 2010. A user’s guide to functional
707 diversity indices. *Ecol. Monogr.* 80, 469–484. doi:10.1890/08-2225.1

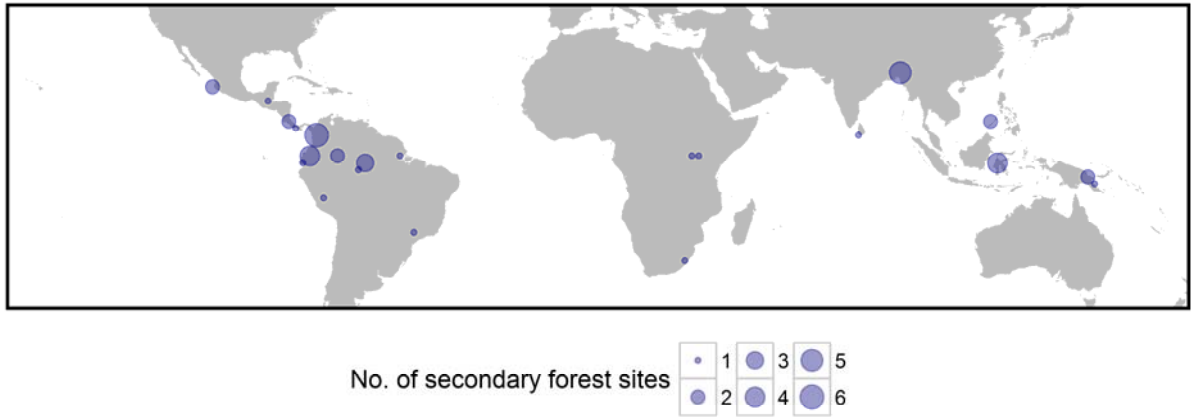
708 Sekercioglu, C.H., Daily, G.C., Ehrlich, P.R., 2004. Ecosystem consequences of bird declines.
709 *Proc. Natl. Acad. Sci.* 101, 18042–18047. doi:10.1073/pnas.0408049101

710 Smith, J., Ferreira, S., van de Kop, P., Palheta Ferreira, C., Sabogal, C., 2003. The persistence of
711 secondary forests on colonist farms in the Brazilian Amazon. *Agrofor. Syst.* 58, 125–135.
712 doi:10.1023/A:1026049507421

713 Sodhi, N.S., Koh, L.P., Prawiradilaga, D.M., Darjono, Tinulele, I., Putra, D.D., Tong Tan, T.H.,
714 2005. Land use and conservation value for forest birds in Central Sulawesi (Indonesia).
715 *Biol. Conserv.* 122, 547–558. doi:10.1016/j.biocon.2004.07.023

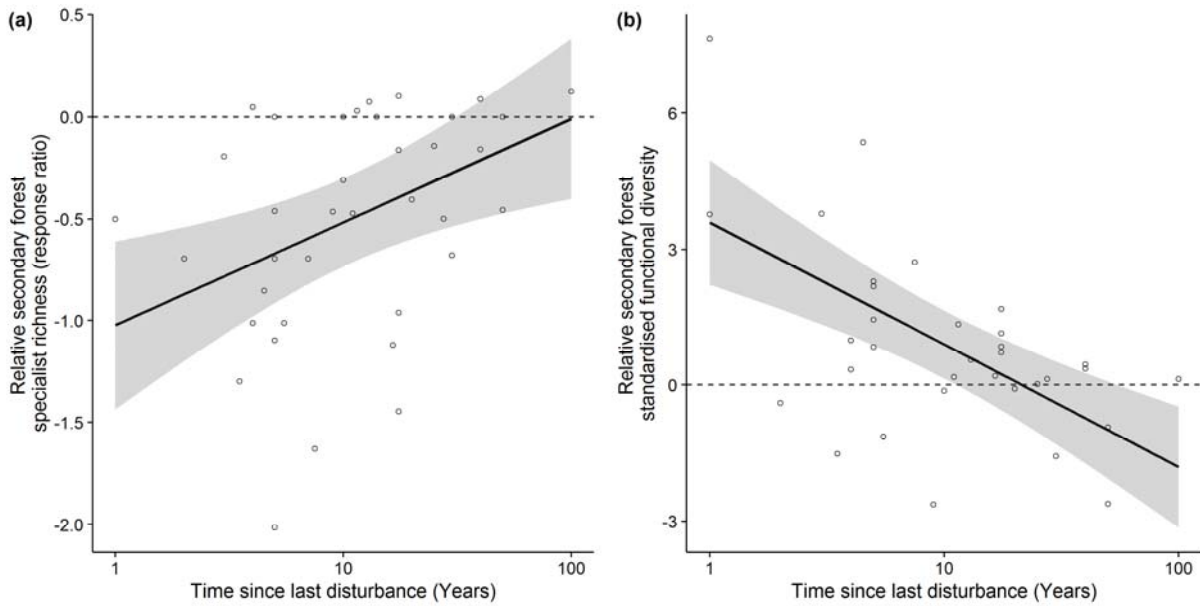
716 Struhsaker, T.T., Struhsaker, P.J., Siex, K.S., 2005. Conserving Africa's rain forests: problems in
717 protected areas and possible solutions. *Biol. Conserv.* 123, 45 – 54.
718 doi:<http://dx.doi.org/10.1016/j.biocon.2004.10.007>
719 Terborgh, J., Weske, J.S., 1969. Colonization of secondary habitats by Peruvian birds. *Ecology*
720 50, 765–782. doi:10.2307/1933691
721 Tscharrntke, T., Sekercioglu, C.H., Dietsch, T.V., Sodhi, N.S., Hoehn, P., Tylianakis, J.M., 2008.
722 Landscape constraints on functional diversity of birds and insects in tropical
723 agroecosystems. *Ecology* 89, 944–951. doi:10.1890/07-0455.1
724 Tvardikova, K., 2010. Bird abundances in primary and secondary growths in Papua New Guinea:
725 a preliminary assessment. *Trop. Conserv. Sci.* 3, 373–388.
726 United Nations, 2014. New York Declaration on Forests [WWW Document]. URL
727 [http://www.un.org/climatechange/summit/wp-content/uploads/sites/2/2014/07/New-](http://www.un.org/climatechange/summit/wp-content/uploads/sites/2/2014/07/New-York-Declaration-on-Forests_19May2014.pdf)
728 [York-Declaration-on-Forests_19May2014.pdf](http://www.un.org/climatechange/summit/wp-content/uploads/sites/2/2014/07/New-York-Declaration-on-Forests_19May2014.pdf) (accessed 11.27.16).
729 Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity
730 indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301.
731 doi:10.1890/07-1206.1
732 Wijesinghe, M.R., Brooke, M. de L., 2005. Impact of habitat disturbance on the distribution of
733 endemic species of small mammals and birds in a tropical rain forest in Sri Lanka. *J.*
734 *Trop. Ecol.* 21, 661–668. doi:10.1017/S0266467405002695
735 Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., Jetz, W., 2014.
736 EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals.
737 *Ecology* 95, 2027–2027. doi:10.1890/13-1917.1
738 Wright, S.J., Muller-Landau, H.C., 2006. The future of tropical forest species. *Biotropica* 38,
739 287–301. doi:10.1111/j.1744-7429.2006.00154.x
740 Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common
741 statistical problems. *Methods Ecol. Evol.* 1, 3–14. doi:10.1111/j.2041-
742 210X.2009.00001.x
743
744

745 **Figures**
746



747 **Figure 1** Geographic distribution of the study sites used in this analysis.
748
749

750



751

752

753

754

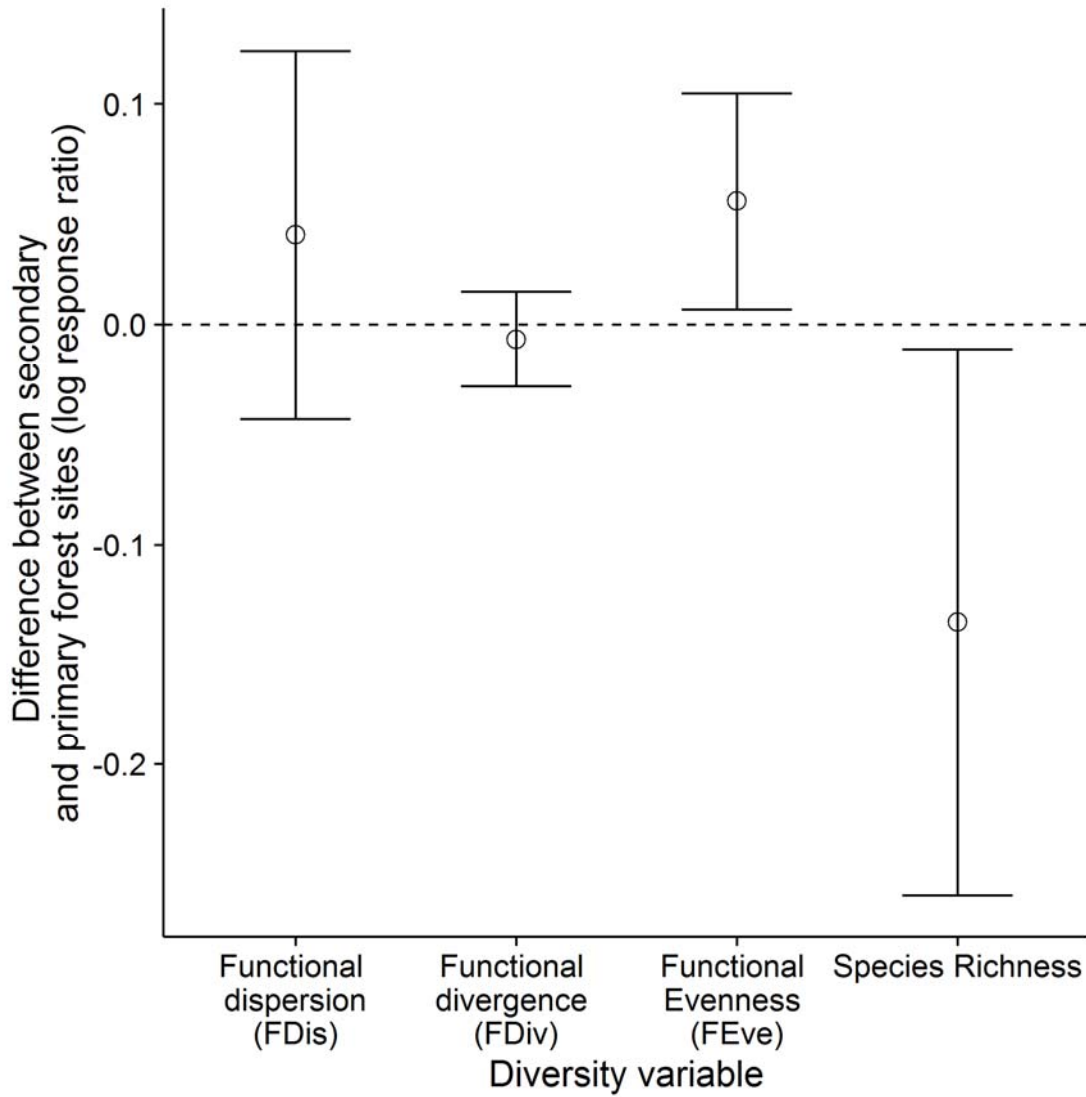
755

756

757

758

Figure 2 The relationship between secondary forest age and (a) forest specialist species richness and (b) standardized functional diversity (sesFD) in secondary tropical forests relative to primary tropical forests. The dotted black line represents the point at which metrics are equal in secondary and primary forest sites. Solid lines represent predictions from models with the lowest AICc and grey shaded areas represent the 95% confidence intervals for these predictions.



760

761

762 **Figure 3** Difference between secondary and primary tropical forest site diversity for variables
 763 where the null model was considered most parsimonious. Dots represent mean differences
 764 between secondary and primary sites and error bars represent 95% confidence intervals. The
 765 dotted black line represents the point at which metrics are equal in secondary and primary forest
 766 sites.

767

768 **Tables**

769

770 **Table 1** Descriptions of functional diversity metrics used in this study

Metric name	Abbreviation used in this study	Metric description	Relevant references
Functional Diversity	FD	A distance based metric of functional diversity that is not influenced by species abundances.	Petchey and Gaston, 2006
Functional Richness	FRic	The volume multidimensional trait space occupied by a community. High FRic indicates that many traits are present within a community.	Laliberté and Legendre, 2010; Villéger et al., 2008
Functional Evenness	FEve	The evenness of species abundances in multidimensional trait space. High FEve values suggest a relatively equal abundance of species in trait space, and in theory this means that resources within an ecosystem are being used in an efficient manner (Prescott et al., 2016)	Laliberté and Legendre, 2010; Villéger et al., 2008
Functional Divergence	FDiv	The distribution of species abundance along multidimensional trait axes. FDiv is low when abundant species have trait values that are close to the centre of functional trait space, but high when abundant species have extreme trait values (Villéger et al., 2008). This can be seen as a measure of the niche differentiation within a community, such that if FDiv is high, then there are high levels of niche differentiation (Prescott et al., 2016).	Laliberté and Legendre, 2010; Villéger et al., 2008
Functional Dispersion	FDis	The distance from the centroid of multidimensional trait space, weighted by species abundances. This metric has been suggested as a unified metric for functional diversity (Laliberté and Legendre, 2010).	Laliberté and Legendre, 2010; Villéger et al., 2008

771

772 **Table 2** Studies from which avian community composition data were extracted, with location
773 recorded at a country level and the age of secondary forest sites (measured as the number of
774 years since disturbance) in each study

Reference	Location of forest sites	Age of secondary forest site(s) (years)
Andrade and Rubio-Torgler, 1994	Colombia	3, 11.5
Banks-Leite et al., 2012	Brazil	50
Barlow et al., 2007	Brazil	16.5
Becker and Agreda, 2005	Ecuador	17.5
Becker et al., 2008	Ecuador	17.5, 17.5, 40
Blake and Loiselle, 2001	Costa Rica	5, 27.5
Borges, 2007	Brazil	4.5, 11, 27.5
Dawson et al., 2011	Papua New Guinea	20
Gilroy et al., 2014	Colombia	3, 8, 8, 20, 20, 35
Hutto, 1989	Mexico	2, 5
Johns, 1991	Brazil	1
Maas et al., 2009	Indonesia	3.5, 4, 5.5
Mallari et al., 2011	Philippines	10, 30
Marsden et al., 2006	Papua New Guinea	5, 14
Mulwa et al., 2012	Kenya	50
Naidoo, 2004	Uganda	13
O’Dea and Whittaker, 2007	Ecuador	17.5
Raman et al., 1998	India	1, 5, 10, 25, 100
Reid et al., 2012	Costa Rica	9
Renner et al., 2006	Guatemala	4
Sodhi et al., 2005	Indonesia	40
Terborgh and Weske, 1969	Peru	7.5
Tvardikova, 2010	Papua New Guinea	7

Wijesinghe and Brooke, 2005	Sri Lanka	5
-----------------------------	-----------	---

775

776

777 **Supplementary materials**

778

779 **Table S1** Model selection table showing test of different random effects structures for different
780 variables investigated.

Variable	Random_effects	AICc	Model Rank
Species Richness	Study	33.76	1
	Mist_nets+Transect+Study	36.45	2
	Mist_nets+Study	36.45	3
	Mist nets+ Transect+Vocal+Study	39.31	4
	Mist nets+Transect+Vocal+Study	42.38	5
	Point obs+Mist nets+Transect+Vocal+Study	45.66	6
Forest Specialist Species Richness	Study	70.59	1
	Mist_nets+Transect+Study	73.15	2
	Mist_nets+Study	73.15	3
	Mist nets+ Transect+Vocal+Study	75.87	4
	Mist nets+Transect+Vocal+Study	78.73	5
	Point observation+Mist nets+Transect+Vocal+Study	81.77	6
Functional Diversity (FD)	Study	20.16	1
	Mist_nets+Study	22.81	2
	Mist_nets+Transect+Study	22.84	3
	Mist nets+ Transect+Vocal+Study	25.71	4
	Mist nets+Transect+Vocal+Study	28.77	5
	Point obs+Mist nets+Transect+Vocal+Study	32.05	6
Functional Richness (FRic)	Study	171.03	1
	Mist_nets+Transect+Study	173.72	2
	Mist_nets+Study	173.72	3
	Mist nets+ Transect+Vocal+Study	176.58	4
	Mist nets+Transect+Vocal+Study	179.64	5
	Point obs+Mist nets+Transect+Vocal+Study	182.92	6
Functional Evenness (FEve)	Study	-44.77	1
	Mist_nets+Study	-42.09	2
	Mist_nets+Transect+Study	-42.09	3
	Mist nets+ Transect+Vocal+Study	-40.07	4
	Mist nets+Transect+Vocal+Study	-37.01	5
	Point obs+Mist nets+Transect+Vocal+Study	-33.73	6
Functional Divergence (FDiv)	Study	-77.38	1
	Mist_nets+Transect+Study	-74.69	2
	Mist_nets+Study	-74.69	3
	Mist nets+ Transect+Vocal+Study	-73.27	4

	Mist nets+Transect+Vocal+Study	-70.22	5
	Point obs+Mist nets+Transect+Vocal+Study	-66.93	6
Functional Dispersion (FDis)	Study	-9.47	1
	Mist_nets+Transect+Study	-6.82	2
	Mist_nets+Study	-6.80	3
	Mist nets+ Transect+Vocal+Study	-4.42	4
	Mist nets+Transect+Vocal+Study	-1.36	5
	Point obs+Mist nets+Transect+Vocal+Study	1.92	6

781

782 **Table S2** Model selection table for all models considered in this study.

Variable	Model	AICc	ΔAICc	Conditional R²
Species Richness	Null model	24.93	0.00	0.00
	Age	25.68	0.76	0.04
	Disturbance type	28.83	3.90	0.22
Forest Specialist Species Richness	Null model	65.41	1.78	0
	Age	63.63	0	0.14
	Disturbance type	70.50	6.87	0.25
Functional Diversity (FD)	Null model	8.78	0.00	0.00
	Age	11.29	2.51	0.00
	Disturbance type	14.80	6.02	0.17
Functional Richness (FRic)	Null model	168.37	0.00	0.00
	Age	170.74	2.36	0.00
	Disturbance type	174.16	5.79	0.16
Functional Evenness (FEve)	Null model	-58.52	0.00	0.00
	Age	-57.24	1.28	0.02
	Disturbance type	-50.65	7.87	0.12
Functional Divergence (FDiv)	Null model	-93.68	0.00	0.00
	Age	-92.15	1.54	0.03
	Disturbance type	-84.39	9.30	0.05
Functional Dispersion (FDis)	Null model	-21.34	0.00	0.00
	Age	-19.92	1.42	0.01
	Disturbance type	-16.47	4.87	0.24
Standardised Effect Size of FD (sesFD)	Null model	148.74	12.59	0
	Age	136.15	0	0.35
	Disturbance type	145.09	8.94	0.19

783