1 **Carbon pools recover more quickly than plant biodiversity in tropical**

2 **secondary forests**

3

4 **Philip A Martin[1,2], Adrian C.Newton[2] and James M. Bullock[1]**

5

6 [1]Centre for Ecology and Hydrology, Benson Lane, Wallingford, Oxfordshire. OX10 8BB. UK.

7 [2] Centre for Conservation Ecology and Environmental Science, School of Applied Sciences,

8 Bournemouth University, Poole, BH12 5BB, UK.

9

10 **Summary**

11 Although increasing efforts are being made to restore tropical forests, little information is available

12 regarding the timescales required for carbon and plant biodiversity to recover to the values associated

13 with undisturbed forests. To address this knowledge gap, we carried out a meta-analysis comparing

14 data from >600 secondary tropical forest sites with nearby undisturbed reference forests. Above-

15 ground biomass approached equivalence to reference values within 80 years since last disturbance,

16 whereas below-ground biomass took longer to recover. Soil carbon content showed little relationship

17 with time since disturbance. Tree species richness recovered after about 50 years. In contrast, epiphyte

18 richness did not reach equivalence to undisturbed forests. The proportion of undisturbed forest tree

19 and epiphyte species found in secondary forests was low and changed little over time. Our results

20 indicate that carbon pools and biodiversity show different recovery rates under passive, secondary

21 succession, and that colonisation by undisturbed forest plant species is slow. Initiatives such as the

22 Convention on Biological Diversity and REDD+ should therefore encourage active management to

23 help achieve their aims of restoring both carbon and biodiversity in tropical forests.

24

25 Key words: secondary forest, forest restoration, biomass, carbon, plant biodiversity, meta-analysis

26

27 **1. Introduction**

28 Tropical forests contain between half and two thirds of terrestrial global biodiversity [1] and

29 approximately 37% of the global terrestrial carbon pool [2]. These forests also provide vital

30 ecosystem services at local, regional and global scales [3, 4]. Despite these benefits, tropical forests

31 are undergoing widespread loss, largely as a result of agricultural expansion [5]. These losses have led

32 to increased carbon emissions, species extinctions and structural alteration of the majority of tropical

33 forests worldwide [3, 4].

34   To combat these on-going losses, many projects have been implemented in different countries

35 over the past two decades with the aim of restoring millions of hectares of tropical forest [6, 7]. The

36 need for tropical forest restoration is recognised in international policy through the Convention on

37 Biological Diversity (CBD) and REDD+ initiatives [8, 9]. The 2020 targets of the CBD aim to

38 enhance biodiversity and carbon stocks, by restoring 15% of the world's degraded ecosystems [9]. In

39 addition, REDD+ aims to enhance carbon stocks partly through forest restoration, using funding from

40 carbon credits [8]. However, despite the perceived importance of restoring tropical forests for both

41 carbon storage and biodiversity, information is lacking on their patterns and rates of recovery

42 following disturbance.

43   To determine the relative value of recovering forests as carbon pools and for biodiversity

44 conservation, comparison with a reference forest is required, such as a site that is relatively free of

45 human disturbance. Previous studies of carbon accumulation in tropical secondary forests [e.g. 10, 11]

46 have not undertaken comparisons against such reference systems. As such, these syntheses provide

47 limited information about the recovery of carbon pools in tropical forests, but rather examine the

48 factors explaining differences in biomass and soil carbon among tropical secondary forest sites, with

49 climate emerging as a major driver [11-13].

50   As biomass recovers following disturbance, it is to be expected that forest ecosystems should

51 accumulate carbon pools with time [10, 14]. In the case of secondary tropical forests, little

52 information is available regarding the time period required for recovery of these carbon pools to the

53 values of undisturbed forests. The most studied of these pools is that associated with aboveground

54 biomass, for which recovery appears to become asymptotic over time [15-18]. However, the time

55 required for this pool to recover completely has been hypothesised to be anywhere between 50 and

56 200 years [15, 17]. Below-ground biomass has been studied less frequently, but may require similar

57 periods for complete recovery, with Saldarriaga [16] suggesting an interval of over 80 years.

58   Changes in soil carbon in secondary forests are less well documented than biomass recovery.

59 A transition from agricultural use to secondary forest generally results in an increase in soil carbon

60 content [19], but the evidence for soil carbon accumulation during secondary succession is

61 conflicting. Recovery of soil carbon in secondary tropical forests to values similar to those in

62 undisturbed forest can take 20-100 years [20, 21], but some secondary forests have higher soil carbon

63 than undisturbed forest [22].

64   In contrast to studies of carbon pools, there have been a number of syntheses of biodiversity

65 recovery in secondary tropical forests. These suggest that faunal species richness recovers relatively

66 quickly during succession [23], but more than 150 years may be required for community composition

67 to reach equivalence to undisturbed forests [24]. However, relatively little is known about changes in

68 plant communities during secondary succession in tropical forests. The only previous synthesis –

69 albeit of only eight locations across Central and South America – of plant biodiversity in secondary

70 forests suggests that they may take longer to become equivalent to undisturbed forest than faunal

71 communities, with only 40% of undisturbed forest species having colonised secondary forests after 80

72 years of recovery [25].

73   No integrated meta-analysis of the recovery of both carbon pools and plant biodiversity in

74 tropical forests has been undertaken previously. Such information is urgently required to inform

75 policy and management practice. To address this knowledge gap, we address the following questions

76 by conducting a meta-analysis based on systematic review:

77   (a) At what age following forest clearance do carbon pools in secondary tropical forests reach

78 equivalent values to those of undisturbed forest?

79   (b) At what age following forest clearance do plant species richness and the proportion of

80 undisturbed forest species in secondary tropical forests reach equivalent values to those of undisturbed

81 forest?

82   (c) How do the rates of recovery of biodiversity and carbon pools compare, and what are the

83 consequences for tropical forest restoration policy?

84

2. Methods

86

(a) Systematic review

We defined tropical secondary forest as a previously forested area undergoing secondary succession following total or near total removal of trees [26], located between the latitudes 40° N and 40° S [27]. To collate relevant studies a systematic review was carried out using standard methodologies [28], outlined in Appendix S1. Studies were retained if they included: (i) at least one measurement of either above-ground biomass, below-ground biomass, soil carbon content, plant species richness and / or plant species community composition in both a secondary tropical forest and a reference undisturbed forest [following 29]; (ii) the time since last disturbance for secondary forests; and (iii) definition of the type of disturbance prior to secondary succession, which included conversion to pasture, cropland or small-scale shifting agriculture. In addition, we extracted data on forest type determined by Holdridge life zone [30] (hereafter referred to as forest type), and geographic location. Although methodologies differed amongst studies, measurements in secondary and undisturbed forests within a study were carried out using the same methods and using the same plot sizes.

Almost all of data we collated came from chronosequence studies where secondary forest stands of different ages were used to infer successional dynamics. One of the assumptions of chronosequences is that all sites have been subject to the same environmental conditions, though in practice this condition is rarely met [31]. For the purposes of our study we also assumed that undisturbed forests had stable carbon pools and species composition. This assumption is again unlikely to be met since many undisturbed forests are known to be increasing in biomass [32] and undergoing changes in biodiversity, but we consider these changes to be less dramatic than those caused by secondary succession. As such our study is reflective of the wider secondary forest literature which tends to make similar assumptions about chronosequences.

110

(b) Statistical analysis

112   We calculated secondary forest carbon pool and species richness recovery using the equation:

$$logit \frac{\left(\frac{\bar{X}_{Sec} - \bar{X}_{Ref}}{\bar{X}_{Ref}}\right) + 1}{2}$$

114   where $\bar{X}_{Sec}$ is the mean of a measurement in a secondary forest and $\bar{X}_{Ref}$ is the mean of the same

115   measurement in the corresponding undisturbed reference site. This is a logit transformation of the

116   proportional difference between secondary and undisturbed forests that conforms to the assumptions

117   of linear models. Following model fitting, predicted values were converted to proportions relative to

118   reference forests by calculating the inverse logit and multiplying by two.

119   Since most studies did not provide estimates of variation along with measurements of carbon

120   pools or species richness, an unweighted analysis was used. Although this technique gives equal

121   weight to studies that may differ in quality and accuracy, it has been used frequently in the ecological

122   literature [33-35], where data reporting standards are very variable. A linear mixed model was

123   constructed for each variable of interest using time since last disturbance, disturbance type and forest

124   type as explanatory variables. We included quadratic or log relationships with time since disturbance

125   where our hypotheses suggested there may be non-linear changes during succession. A random factor

126   was included to group secondary forests which shared a undisturbed forest reference site eliminating

127   the problems of pseudoreplication at the study scale [36]. In addition, random variables were included

128   to account for differences in study methods, such as in measurement depth for soil carbon and

129   whether allometric equations for calculation of biomass were locally derived or represented general

130   multi-species allometries [e.g. 37]. Random variables accounting for the difference in minimum

131   diameter at breast height (DBH) of trees included in assessments of species richness were also

132   considered, but were found to add little explanatory value and thus were excluded from models (see

133   Table S 15 for details of different minimum DBH used in studies). The proportion of the undisturbed

134   forest plant species found in secondary forests was used as a metric of changes in community

135   composition [see 25, 38] and was analysed using a binomial generalised linear mixed model with logit

136   link. While there are techniques which are better suited to determining whether species are

137   undisturbed forest specialists [e.g. 39], they require detailed data for each study to which we did not

138   have access.

139   All possible additive models were computed using restricted maximum likelihood methods.

140   Model comparison was based on AICc, excluding all models with $\Delta AIC_C \geq 7$ [40]. We estimated the

141   goodness of fit of each model by calculating the marginal R^2 using the equations developed by

142   Nakagawa and Schielzeth [41]. Coefficients were derived from the weighted mean of all models with

143    $\Delta AIC_C \leq 7$. The importance of variables in explaining recovery of carbon pools and plant biodiversity

144   was assessed by summing the weight of all models that included the variable [40]. Analyses were

145   performed in R 2.15.3 [42], with model averaging using the MuMIn package[43], and all graphs

146   produced using the ggplot2 package [44].

147

148   **Results**

149   The systematic review yielded data for 607 secondary forest sites from 74 studies describing

150   aboveground biomass, belowground biomass, soil carbon, plant species richness or plant species

151   composition, with comparable data for a reference undisturbed forest (further details in Table S1). The

152   majority of these sites were relatively young, with mean ages of between 20 and 30 years for each

153   variable of interest (Figure S1). Thus biomass and carbon recovery was measured for forests up to 85

154   years old. Biodiversity data was available for forests up to a little over 150 years old, although

155   virtually all sites were under 100 years old. Most sites were in Central or South America (Figure S2),

156   with few sites in Africa or Asia.

157   Model selection suggested that the best model describing aboveground biomass recovery in

158   secondary forests included only a log relationship with time since disturbance. This model predicted

159   recovery of aboveground biomass to slow over time and to be about 83% of that of undisturbed

160   forests after 85 years (Figure 1). This model had an AICc weight of 0.57 and a marginal R^2 of 0.56

161   (Table S1). The relationship between relative biomass recovery and age was much more important

162   than those of forest type and prior land use (Table S14).

163   Below-ground biomass increased more slowly than above-ground biomass as a function of

164   forest age. As with aboveground biomass there was a log relationship with time since disturbance;

165   after 80 years stocks in sites previously subject to shifting agriculture were still only about 50% of

166   those in reference forests (Figure 1). Forests established on pastures appeared to recover below-

167   ground biomass more rapidly than those following shifting agriculture, with recovery to 76% of

168   reference levels in approximately 80 years. Forest type was not important in explaining differences

169   between undisturbed and secondary forests (Importance value=0, Table S14). Models with $\Delta AIC_C \leq 7$

170   had marginal R^2 values of 0.60-0.64 (Table S3).

171   Soil carbon stocks showed very weak relationships with all variables; an intercept only model

172   had the most support (AICc weight=0.43, Table S3). However, models predicting slight increases in

173   soil carbon with time since disturbance were also supported, although these had extremely small

174   marginal R^2 of ≤ 0.01 (Table S4).

175   Plant species richness increased with time since last disturbance – again following log

176   relationships – with epiphyte richness showing slower recovery than tree richness (Figure 2). Tree

177   species richness was predicted to recover after approximately 50 years, while epiphyte richness was

178   predicted to take longer than 100 years. Model fits of tree species richness were also much better than

179   those for epiphytes, with marginal R^2 of 0.24-0.26 and 0-0.08 respectively (Tables S5 and S6). In

180   contrast, a relationship between time since last disturbance and proportion of species associated with

181   undisturbed forest was relatively poorly supported (Importance value=0.35). The proportion of

182   species associated with undisturbed forest was generally low, with a mean of 26% of species also

183   being found in secondary forest (Upper CI=67%, Lower CI=6%; Figure 3; Tables S7 and S13).

184

185   **Discussion**

186   This study is the first to assess the recovery of both carbon pools and plant biodiversity across a large

187   number of secondary tropical forest sites. Our results indicate that the various carbon pools and

188   measures of biodiversity recover at different rates. Above-ground biomass approaches recovery 85

189   years after the last disturbance. Below-ground biomass also increases over time, with former pastures

190   recovering 75% of belowground biomass after about 80 years, while areas affected by shifting

191   agriculture take longer to recover. Soil carbon remained largely unchanged over time. In terms of

192   biodiversity, tree species richness reached equivalence to reference forests after approximately 50

193 years and epiphyte richness only approached recovery after 100 years while the recovery of

194 undisturbed forest species in secondary forests was limited and showed little relationship with time.

195 (a) **Recovery of carbon pools**

196   Although previous work has suggested that rates of biomass accumulation differ between dry,

197 moist and wet tropical forests [45] as well as among disturbance types [10], our study indicates that

198 these factors are largely unimportant in determining the rate of recovery towards the state of

199 undisturbed forests. Our estimated time required for above-ground biomass to reach approximately

200 85% of undisturbed forest levels is similar to suggested rates for basal area recovery in the neotropics

201 [46]. While our results and previous observations [46] suggest that forest biomass approaches that of

202 undisturbed forest within a century, full recovery may take substantially longer. This is because many

203 secondary forests are often composed of relatively small stemmed trees and lack the very large trees

204 characteristic of old-growth forest, which can have very high biomass [47]. However, without more

205 data from older secondary forests it is difficult to determine how long full recovery takes. One

206 important caveat regarding aboveground biomass recovery is that allometric equations used for its

207 estimation are usually derived from undisturbed forest plots [48]. As a result of this measurements in

208 secondary forests, which are often dominated by trees with low DBH, may overestimate their biomass

209 [48] possibly because of differences in secondary forest height:diameter relationships [49]. This is a

210 potential bias in all the individual studies we used and we suggest that further research should aim to

211 develop and test allometries designed for use in secondary forests to characterise recovery more

212 accurately.

213   Belowground biomass represents an average of 19% of total biomass in tropical forests [50],

214 although root:stem ratios tend to be higher in younger forests [51, 52]. Thus, we would expect

215 belowground biomass to recover more rapidly than those of aboveground biomass and it is surprising

216 that we found the opposite pattern. However this effect may be an artefact because those sites for

217 which we had belowground biomass data had lower aboveground biomass than other forests of

218 similar age (Figures S3 and S4).

219   We found that secondary tropical forests have soil carbon contents similar to undisturbed

220 forests, contradicting a recent meta-analysis [53], which suggested lower soil carbon in secondary

221 forests. The differences between our study and that of Don et al. [53] result from differing definitions

222 of secondary forest, which they considered to be forests affected by any human disturbance. That

223 definition conflates different types of disturbance and covers human-impacted forests and plantations

224 as well as those undergoing secondary succession. As such we believe that our study more accurately

225 represents soil carbon content in secondary forests as more usually defined – those that are

226 recovering from near total removal of tree cover [26]. Our findings do however support those of

227 Marín-Spiotta et al. [11], who also found similar soil carbon pools in secondary and undisturbed

228 tropical forests. These results indicate either that soil carbon in tropical forests is resilient to moderate,

229 short term land use change or that carbon is accumulated rapidly following abandonment of farmland.

230 However, as with belowground biomass, further research is required to explain the drivers of

231 differences in soil carbon between sites. Given that the world's soils contain two to three times the

232 carbon stored in aboveground biomass [54] such research should be considered a priority.

233   Former land use had an inconsistent effect on recovery of carbon pools in our study: there was

234 no effect on above-ground biomass or soil carbon, but below-ground biomass recovered faster in

235 former pastures than following shifting agriculture. The intensity and length of time under previous

236 land-use influence factors such as soil nutrient content and undoubtedly play important roles in

237 biomass recovery [55]. For example, research has suggested that above-ground biomass is lower in

238 secondary tropical forests that have experienced multiple cycles of conversion for shifting agriculture

239 [56, 57]. However, such detailed data were not collected for the majority of studies we analysed, and

240 future studies should do so to aid our understanding of the factors that control carbon stocks in

241 secondary forests.

242   Overall, these findings suggest that when attempting to restore carbon pools on tropical forest

243 sites cleared for agriculture, the greatest gains are likely to be made in plant biomass as soil carbon

244 appears to be relatively insensitive to moderate land use change. Independent of forest type, carbon

245 pools in secondary forest sites could be expected to be 77-81% of those of undisturbed forests

246 approximately 80 years after disturbance, given that aboveground biomass has been estimated as 5

247 times that of belowground biomass in tropical forests [50].

248

249   (b) **Recovery of species richness and community composition**

250   We found that tree species richness recovered within 50 years compared to >100 years for

251 epiphyte richness. We have less confidence in the prediction of a continuing increase after 50 years,

252 which is likely to be an artefact of the steep increase in younger forest and the relatively few data for

253 older forests meaning that the shape of the log-relationship was constrained. Indeed, the data suggest

254 relatively little increase after 50 years and our model tends to over-predict tree richness in older

255 forests. In addition to differing recovery rates, our model of tree species richness change also showed

256 a much better fit than that of epiphyte richness. These differences in recovery and our ability to

257 explain changes in richness are likely to be driven by contrasting dispersal traits and requirements for

258 establishment. Secondary tropical forest tree communities are initially dominated by short lived

259 pioneer tree species and these are sequentially replaced by longer lived species [46]. Some secondary

260 forests may be isolated from seed sources leading to an impeded recovery of richness, but our results,

261 and the observations of others [46], suggest that this is relatively rare. In contrast, epiphyte dispersal is

262 largely local and propagation is often restricted to individual trees [58]. In addition, epiphytes seem to

263 occur more commonly on large trees [59]. These factors may lead to relatively poor recovery of

264 epiphyte species since many secondary forests are fragmented and tend to consist of smaller stemmed

265 trees [46]. An important caveat of our analysis is that few estimates of species richness were rarefied

266 by either number of individuals or area sampled. It is possible that since secondary forests almost

267 always have higher stem densities that our analysis overestimates species richness recovery. However,

268 from a conservation perspective, given that plot size was equal for the secondary and undisturbed

269 plots in all pairwise comparisons, our estimation of species per unit area remains valid.

270   Although tree species richness recovers relatively well in secondary forests, there was little or

271 no accumulation of species associated with the reference undisturbed forests. This contrasts with the

272 more rapid colonisation rates of animal species, communities of which may attain similarity to those

273 of undisturbed forests within 150 years [24]. The poor recovery plant community composition is

274 likely to be the result of a number of interacting mechanisms. Firstly, small secondary forest patches

275 are likely to be subject to greater edge effects than larger undisturbed patches, making them less likely

276 to be colonised by species adapted to old-growth forest conditions [60]. Secondly, patches of

277 secondary forest can be distant from undisturbed forests [61] and thus receive few seeds from them.

278 Finally, the extent of degradation of the landscape surrounding secondary forests will also influence

279 seed dispersal processes, such as the behaviour of frugivorous birds [55].

280   In addition to these ecological mechanisms that might explain differences in the responses of

281 species richness and community composition in secondary tropical forests, our study is subject to

282 some of the limitations of the literature we used in our analyses. The most important factor is likely to

283 be associated with distance-decay in community similarity [62]. Sites used in this study are likely to

284 vary in their distance from undisturbed reference sites and thus the proportion of species shared with

285 undisturbed forests would be expected to vary, even without any human disturbance [62, 63].

286 Unfortunately, very few studies give details of distances between secondary and reference sites. We

287 hope that future studies might record such landscape metrics. Despite this our findings suggest that

288 natural colonisation alone may not be sufficient to restore tropical forest plant biodiversity effectively

289 in less a century.

290

291 **(c) Comparative rates of carbon and biodiversity recovery**

292   Our results indicate that carbon pools and tree species richness recover more quickly than

293 epiphyte species richness, while undisturbed forest plant species do not accumulate over time in

294 secondary forests. Analyses of the carbon and biodiversity benefits of avoided deforestation have

295 often suggested synergistic relationships between these goals due to overlap of priority areas for

296 biodiversity conservation and carbon storage [64, 65]. In contrast, reforestation schemes that have the

297 primary aim of carbon sequestration have often been criticised as they may support relatively little

298 forest biodiversity [66]. Our study suggests a more nuanced relationship between biodiversity and

299 carbon in secondary tropical forests: while both carbon storage and conservation value increase as

300 secondary forests age, the trajectories of these increases differ. As a result of this, tropical forests

301 recovering from agricultural conversion are likely to have greater value for carbon storage and

302 sequestration than for biodiversity, especially during the first 100 years of development. These

303 differing rates of recovery should be acknowledged by policies targeting the recovery of biodiversity

304 and carbon in tropical forests.

305   The failure of species associated with undisturbed forest to colonise secondary forests

306   effectively is worrying for those aiming to conserve biodiversity in tropical forest landscapes subject

307   to human disturbance. These species are likely to be adapted to old-growth conditions and thus are

308   likely to be sensitive to human disturbance, have small ranges and populations [67] and as a result

309   they are likely to face greater threats of extinction [68]. This result clearly indicates that old growth

310   forests are vital for the conservation of some specialist species but also that if goals to conserve

311   species in human disturbed ecosystems are to be achieved we require novel solutions and further

312   research.

313

314   **Conclusion**

315   This study is the first integrated meta-analysis of both plant biodiversity and carbon pool

316   recovery in tropical secondary forests. We have shown that the recovery periods for the two differ

317   markedly. This has important implications for policies that target recovery of both carbon and

318   biodiversity, such as the Convention on Biological Diversity and REDD+. Carbon pools may take

319   approximately 80 years to recover following disturbance, faunal biodiversity 150 years [24] and plant

320   biodiversity well over 100 years. Thus, initiatives aiming to support recovery of both biodiversity and

321   carbon should not assume that the two are closely coupled. Enhancement of carbon stocks to the

322   values associated with local undisturbed forests appears possible through passive restoration.

323   However, in many situations active restoration involving human interventions (e.g. planting trees) or

324   other strategies such as increasing seed dispersal across the non-forest matrix by creating woodland

325   islets [69] may be required to enable long-term recovery of plant species community composition. In

326   addition further research into active restoration of tropical forests is required to identify novel

327   solutions to this problem.

328

337

338   Figure legends

339   Figure 1 – Recovery of aboveground biomass (n=326), belowground biomass (n=76) and soil

340   carbon (n=185) in secondary tropical forests, relative to undisturbed reference forests. Solid

341   lines represent model predictions, with different colours representing different disturbance

342   types. Parameters included in figures have AICc importance values >0.5. The horizontal

343   dashed line represents no difference between secondary and undisturbed forests.

344

345   Figure 2 – Recovery of epiphyte (n=65) and tree (n=204) species richness in secondary

346   tropical forests, relative to undisturbed reference forests. Solid lines represent model

347   predictions, with different colours representing different disturbance types. Parameters

348   included in figures have AICc importance values >0.5. The horizontal dashed line represents

349   no difference between secondary and undisturbed forests.

350

351   Figure 3 –Recovery of species associated with undisturbed tropical forest in secondary forest

352   (n=50). The horizontal dashed line represents no difference between secondary and

353   undisturbed forests.

354

355

356 **References**

357 1.   Gardner T.A., Barlow J., Sodhi N.S., Peres C.A. 2010 A multi-region assessment of
358 tropical forest biodiversity in a human-modified world. *Biological Conservation* **143**(10),
359 2293-2300. (doi:10.1016/j.biocon.2010.05.017).
360 2.   Dixon R.K., Solomon A.M., Brown S., Houghton R.A., Trexier M.C., Wisniewski J.
361 1994 Carbon pools and flux of global forest ecosystems. *Science* **263**(5144), 185-190.
362 3.   Gardner T.A., Barlow J., Chazdon R., Ewers R.M., Harvey C.A., Peres C.A., Sodhi
363 N.S. 2009 Prospects for tropical forest biodiversity in a human-modified world. *Ecology*
364 *Letters* **12**(6), 561-582. (doi:10.1111/j.1461-0248.2009.01294.x).
365 4.   Foley J.A., Asner G.P., Costa M.H., Coe M.T., DeFries R., Gibbs H.K., Howard E.A.,
366 Olson S., Patz J., Ramankutty N. 2007 Amazonia revealed: forest degradation and loss of
367 ecosystem goods and services in the Amazon Basin. *Frontiers in Ecology and the*
368 *Environment* **5**(1), 25-32.
369 5.   Gibbs H.K., Ruesch A.S., Achard F., Clayton M.K., Holmgren P., Ramankutty N.,
370 Foley J.A. 2010 Tropical forests were the primary sources of new agricultural land in the
371 1980s and 1990s. *Proceedings of the National Academy of Sciences* **107**(38), 16732-16737.
372 (doi:10.1073/pnas.0910275107).
373 6.   Sayer J., Chokkalingam U., Poulsen J. 2004 The restoration of forest biodiversity and
374 ecological values. *Forest ecology and management* **201**(1), 3-11.
375 7.   Calmon M., Brancalion P.H.S., Paese A., Aronson J., Castro P., da Silva S.C.,
376 Rodrigues R.R. 2011 Emerging Threats and Opportunities for Large-Scale Ecological
377 Restoration in the Atlantic Forest of Brazil. *Restoration Ecology* **19**(2), 154-158.
378 8.   Alexander S., Nelson C.R., Aronson J., Lamb D., Cliquet A., Erwin K.L., Finlayson
379 C.M., De Groot R.S., Harris J.A., Higgs E.S. 2011 Opportunities and challenges for
380 ecological restoration within REDD+. *Restoration Ecology* **19**(6), 683-689.
381 9.   CBD. 2010 Decision adopted by the conference of the parties to the convention on
382 biological diversity at its tenth meeting - The Strategic Plan for Biodiversity 2011-2020 and
383 the Aichi Biodiversity Targets.
384 10.   Silver W.L., Ostertag R., Lugo A.E. 2000 The Potential for Carbon Sequestration
385 Through Reforestation of Abandoned Tropical Agricultural and Pasture Lands. *Restoration*
386 *Ecology* **8**(4), 394-407. (doi:10.1046/j.1526-100x.2000.80054.x).
387 11.   Marín-Spiotta E., Sharma S. 2012 Carbon storage in successional and plantation
388 forest soils: a tropical analysis. *Global Ecology and Biogeography*, n/a-n/a.
389 (doi:10.1111/j.1466-8238.2012.00788.x).
390 12.   Anderson K.J., Allen A.P., Gillooly J.F., Brown J.H. 2006 Temperature-dependence of
391 biomass accumulation rates during secondary succession. *Ecology Letters* **9**(6), 673-682.
392 (doi:10.1111/j.1461-0248.2006.00914.x).
393 13.   Johnson C.M., Zarin D.J., Johnson A.H. 2000 Post-disturbance aboveground biomass
394 accumulation in global secondary forests. *Ecology* **81**(5), 1395-1401. (doi:10.1890/0012-
395 9658(2000)081[1395:pdabai]2.0.co;2).
396 14.   Brown S., Lugo A.E. 1990 Tropical secondary forests. *Journal of Tropical Ecology*
397 **6**(01), 1-32. (doi:doi:10.1017/S0266467400003989).
398 15.   Hughes R.F., Kauffman J.B., Jaramillo V.J. 1999 Biomass, Carbon, and Nutrient
399 Dynamics of Secondary Forests in a Humid Tropical Region of México. *Ecology* **80**(6),
400 1892-1907.
401 16.   Saldarriaga J.G., West D.C., Tharp M., Uhl C. 1988 Long-term chronosequence of
402 forest succession in the upper Rio Negro of Colombia and Venezuela. *The Journal of*
403 *Ecology*, 938-958.

404 17.	Cifuentes-Jara M. 2008 *Aboveground biomass and ecosystem carbon pools in tropical*
405 *secondary forests growing in six life zones of Costa Rica*, ProQuest.
406 18.	Read L., Lawrence D. 2003 Recovery of Biomass Following Shifting Cultivation in
407 Dry Tropical Forests of the Yucatan. *Ecological Applications* **13**(1), 85-97.
408 19.	Guo L.B., Gifford R.M. 2002 Soil carbon stocks and land use change: a meta analysis.
409 *Global Change Biology* **8**(4), 345-360. (doi:10.1046/j.1354-1013.2002.00486.x).
410 20.	Rhoades C.C., Eckert G.E., Coleman D.C. 2000 Soil Carbon Differences among
411 Forest, Agriculture, and Secondary Vegetation in Lower Montane Ecuador. *Ecological*
412 *Applications* **10**(2), 497-505.
413 21.	Neumann-Cosel L., Zimmermann B., Hall J.S., van Breugel M., Elsenbeer H. 2011
414 Soil carbon dynamics under young tropical secondary forests on former pastures—A case
415 study from Panama. *Forest ecology and management* **261**(10), 1625-1633.
416 (doi:10.1016/j.foreco.2010.07.023).
417 22.	Saynes V., Hidalgo C., Etchevers J.D., Campo J.E. 2005 Soil C and N dynamics in
418 primary and secondary seasonally dry tropical forests in Mexico. *Applied Soil Ecology* **29**(3),
419 282-289. (doi:10.1016/j.apsoil.2004.11.007).
420 23.	Dunn R.R. 2004 Recovery of faunal communities during tropical forest regeneration.
421 *Conservation Biology* **18**(2), 302-309.
422 24.	Dent D.H., Wright S.J. 2009 The future of tropical species in secondary forests: a
423 quantitative review. *Biological Conservation* **142**(12), 2833-2843.
424 25.	Chazdon R.L., Peres C.A., Dent D., Sheil D., Lugo A.E., Lamb D., Stork N.E., Miller
425 S.E. 2009 The Potential for Species Conservation in Tropical Secondary Forests.
426 *Conservation Biology* **23**(6), 1406-1417. (doi:10.1111/j.1523-1739.2009.01338.x).
427 26.	Corlett R.T. 1994 What is secondary forest? *Journal of Tropical Ecology* **10**(03), 445-
428 447.
429 27.	Newbold T., Scharlemann J.P.W., Butchart S.H.M., Şekercioğlu Ç.H., Alkemade R.,
430 Booth H., Purves D.W. 2013 Ecological traits affect the response of tropical forest bird
431 species to land-use intensity. *Proceedings of the Royal Society B: Biological Sciences*
432 **280**(1750). (doi:10.1098/rspb.2012.2131).
433 28.	Pullin A.S., Stewart G.B. 2006 Guidelines for systematic review in conservation and
434 environmental management. *Conservation Biology* **20**(6), 1647-1656.
435 29.	Gibson L., Lee T.M., Koh L.P., Brook B.W., Gardner T.A., Barlow J., Peres C.A.,
436 Bradshaw C.J.A., Laurance W.F., Lovejoy T.E., et al. 2011 Primary forests are irreplaceable
437 for sustaining tropical biodiversity. *Nature* **478**(7369), 378-381.
438 (doi:http://www.nature.com/nature/journal/v478/n7369/abs/nature10425.html#supplementary
439 -information).
440 30.	Holdridge L.R. 1967 *Life Zone Ecology*. San Jose, Tropical Science Center.
441 31.	Johnson E.A., Miyanishi K. 2008 Testing the assumptions of chronosequences in
442 succession. *Ecology Letters* **11**(5), 419-431.
443 32.	Baker T.R., Phillips O.L., Malhi Y., Almeida S., Arroyo L., Di Fiore A., Erwin T.,
444 Higuchi N., Killeen T.J., Laurance S.G. 2004 Increasing biomass in Amazonian forest plots.
445 *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*
446 **359**(1443), 353-365.
447 33.	Rey Benayas J.M., Newton A.C., Diaz A., Bullock J.M. 2009 Enhancement of
448 biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science*
449 **325**(5944), 1121-1124.
450 34.	Moreno-Mateos D., Power M.E., Comín F.A., Yockteng R. 2012 Structural and
451 Functional Loss in Restored Wetland Ecosystems. *PLoS Biol* **10**(1), e1001247.
452 (doi:10.1371/journal.pbio.1001247).

453   35.   Putz F.E., Zuidema P.A., Synnott T., Peña-Claros M., Pinard M.A., Sheil D., Vanclay
454   J.K., Sist P., Gourlet-Fleury S., Griscom B., et al. 2012 Sustaining conservation values in
455   selectively logged tropical forests: The attained and the attainable. *Conservation Letters*, no-
456   no. (doi:10.1111/j.1755-263X.2012.00242.x).
457   36.   Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J.R., Stevens M.H.H.,
458   White J.-S.S. 2009 Generalized linear mixed models: a practical guide for ecology and
459   evolution. *Trends in Ecology & Evolution* **24**(3), 127-135.
460   (doi:10.1016/j.tree.2008.10.008).
461   37.   Chave J., Andalo C., Brown S., Cairns M.A., Chambers J.Q., Eamus D., Fölster H.,
462   Fromard F., Higuchi N., Kira T., et al. 2005 Tree allometry and improved estimation of
463   carbon stocks and balance in tropical forests. *Oecologia* **145**(1), 87-99. (doi:10.1007/s00442-
464   005-0100-x).
465   38.   Barlow J., Gardner T.A., Araujo I.S., Ávila-Pires T.C., Bonaldo A.B., Costa J.E.,
466   Esposito M.C., Ferreira L.V., Hawes J., Hernandez M.I.M., et al. 2007 Quantifying the
467   biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the*
468   *National Academy of Sciences* **104**(47), 18555-18560. (doi:10.1073/pnas.0703333104).
469   39.   Chazdon R.L., Chao A., Colwell R.K., Lin S.-Y., Norden N., Letcher S.G., Clark
470   D.B., Finegan B., Arroyo J.P. 2011 A novel statistical method for classifying habitat
471   generalists and specialists. *Ecology* **92**(6), 1332-1343. (doi:10.1890/10-1345.1).
472   40.   Burnham K.P., Anderson D.R., Huyvaert K.P. 2011 AIC model selection and
473   multimodel inference in behavioral ecology: some background, observations, and
474   comparisons. *Behavioral ecology and sociobiology* **65**(1), 23-35.
475   41.   Nakagawa S., Schielzeth H. 2013 A general and simple method for obtaining R2 from
476   generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**(2), 133-142.
477   (doi:10.1111/j.2041-210x.2012.00261.x).
478   42.   R Development Core Team. 2011 *R: A Language and Environment for Statistical*
479   *Computing*. Vienna, Austria, R Foundation for Statistical Computing.
480   43.   Barton K. 2013 MuMIn: Multi-model inference. (1.9.5 ed.
481   44.   Wickham H. 2009 *ggplot2: elegant graphics for data analysis*. New York, Springer.
482   45.   Saatchi S.S., Harris N.L., Brown S., Lefsky M., Mitchard E.T.A., Salas W., Zutta
483   B.R., Buermann W., Lewis S.L., Hagen S., et al. 2011 Benchmark map of forest carbon
484   stocks in tropical regions across three continents. *Proceedings of the National Academy of*
485   *Sciences* **108**(24), 9899-9904. (doi:10.1073/pnas.1019576108).
486   46.   Guariguata M.R., Ostertag R. 2001 Neotropical secondary forest succession: changes
487   in structural and functional characteristics. *Forest ecology and management* **148**(1-3), 185-
488   206.
489   47.   Lindenmayer D.B., Laurance W.F., Franklin J.F., Likens G.E., Banks S.C., Blanchard
490   W., Gibbons P., Ikin K., Blair D., McBurney L., et al. 2013 New policies for old trees:
491   averting a global crisis in a keystone ecological structure. *Conservation Letters*, n/a-n/a.
492   (doi:10.1111/conl.12013).
493   48.   van Breugel M., Ransijn J., Craven D., Bongers F., Hall J.S. 2011 Estimating carbon
494   stock in secondary forests: Decisions and uncertainties associated with allometric biomass
495   models. *Forest ecology and management* **262**(8), 1648-1657.
496   (doi:http://dx.doi.org/10.1016/j.foreco.2011.07.018).
497   49.   Montgomery R.A., Chazdon R.L. 2001 Forest structure, canopy architecture, and light
498   transmittance in tropical wet forests. *Ecology* **82**(10), 2707-2718.
499   50.   Cairns M.A., Brown S., Helmer E.H., Baumgardner G.A. 1997 Root biomass
500   allocation in the world's upland forests. *Oecologia* **111**(1), 1-11.
501   51.   Fearnside P.M., Guimarães W.M. 1996 Carbon uptake by secondary forests in
502   Brazilian Amazonia. *Forest ecology and management* **80**(1), 35-46.

503   52.   Mokany K., Raison R., Prokushkin A.S. 2006 Critical analysis of root: shoot ratios in
504   terrestrial biomes. *Global Change Biology* **12**(1), 84-96.
505   53.   Don A., Schumacher J., Freibauer A. 2011 Impact of tropical land-use change on soil
506   organic carbon stocks – a meta-analysis. *Global Change Biology* **17**(4), 1658-1670.
507   (doi:10.1111/j.1365-2486.2010.02336.x).
508   54.   Marin-Spiotta E., Silver W.L., Swanston C.W., Ostertag R. 2009 Soil organic matter
509   dynamics during 80 years of reforestation of tropical pastures. *Global Change Biology* **15**(6),
510   1584-1597. (doi:10.1111/j.1365-2486.2008.01805.x).
511   55.   Chazdon R.L., Letcher S.G., van Breugel M., Martínez-Ramos M., Bongers F.,
512   Finegan B. 2007 Rates of change in tree communities of secondary Neotropical forests
513   following major disturbances. *Philosophical Transactions of the Royal Society B: Biological*
514   *Sciences* **362**(1478), 273-289. (doi:10.1098/rstb.2006.1990).
515   56.   Eaton J.M., Lawrence D. 2009 Loss of carbon sequestration potential after several
516   decades of shifting cultivation in the Southern Yucatán. *Forest ecology and management*
517   **258**(6), 949-958. (doi:10.1016/j.foreco.2008.10.019).
518   57.   Lawrence D. 2005 Biomass accumulation after 10–200 years of shifting cultivation in
519   Bornean rain forest. *Ecology* **86**(1), 26-33. (doi:10.1890/03-0564).
520   58.   KÖSter N., Friedrich K., Nieder J., Barthlott W. 2009 Conservation of Epiphyte
521   Diversity in an Andean Landscape Transformed by Human Land Use
522   Conservación de la Diversidad de Epífitas en una Paisaje Andino Transformado por Uso de
523   Suelo Humano. *Conservation Biology* **23**(4), 911-919. (doi:10.1111/j.1523-
524   1739.2008.01164.x).
525   59.   Woods C.L., DeWalt S.J. 2013 The Conservation Value of Secondary Forests for
526   Vascular Epiphytes in Central Panama. *Biotropica* **45**(1), 119-127. (doi:10.1111/j.1744-
527   7429.2012.00883.x).
528   60.   Benitez-Malvido J. 1998 Impact of Forest Fragmentation on Seedling Abundance in a
529   Tropical Rain Forest. *Conservation Biology* **12**(2), 380-389. (doi:10.1111/j.1523-
530   1739.1998.96295.x).
531   61.   Turner I.M., T. Corlett R. 1996 The conservation value of small, isolated fragments of
532   lowland tropical rain forest. *Trends in Ecology & Evolution* **11**(8), 330-333.
533   (doi:http://dx.doi.org/10.1016/0169-5347(96)10046-X).
534   62.   Condit R., Pitman N., Leigh E.G., Chave J., Terborgh J., Foster R.B., Núnez P.,
535   Aguilar S., Valencia R., Villa G. 2002 Beta-diversity in tropical forest trees. *Science*
536   **295**(5555), 666-669.
537   63.   Ramage B.S., Sheil D., Salim H.M., Fletcher C., Mustafa N.Z.A., Luruthusamay J.C.,
538   Harrison R.D., Butod E., Dzulkiply A.D., Kassim A.R. 2012 Pseudoreplication in tropical
539   forests and the resulting effects on biodiversity conservation. *Conservation Biology*.
540   64.   Ebeling J., Yasué M. 2008 Generating carbon finance through avoided deforestation
541   and its potential to create climatic, conservation and human development benefits.
542   *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**(1498), 1917-
543   1924. (doi:10.1098/rstb.2007.0029).
544   65.   Venter O., Meijaard E., Possingham H., Dennis R., Sheil D., Wich S., Hovani L.,
545   Wilson K. 2009 Carbon payments as a safeguard for threatened tropical mammals.
546   *Conservation Letters* **2**(3), 123-129. (doi:10.1111/j.1755-263X.2009.00059.x).
547   66.   Bekessy S.A., Wintle B.A. 2008 Using Carbon Investment to Grow the Biodiversity
548   Bank. *Conservation Biology* **22**(3), 510-513. (doi:10.1111/j.1523-1739.2008.00943.x).
549   67.   Gardner T.A., Barlow J., Parry L.W., Peres C.A. 2007 Predicting the Uncertain Future
550   of Tropical Forest Species in a Data Vacuum. *Biotropica* **39**(1), 25-30. (doi:10.1111/j.1744-
551   7429.2006.00228.x).

552   68.   IUCN SSC. 2001 IUCN Red List categories and criteria: version 3.1. *Prepared by the*
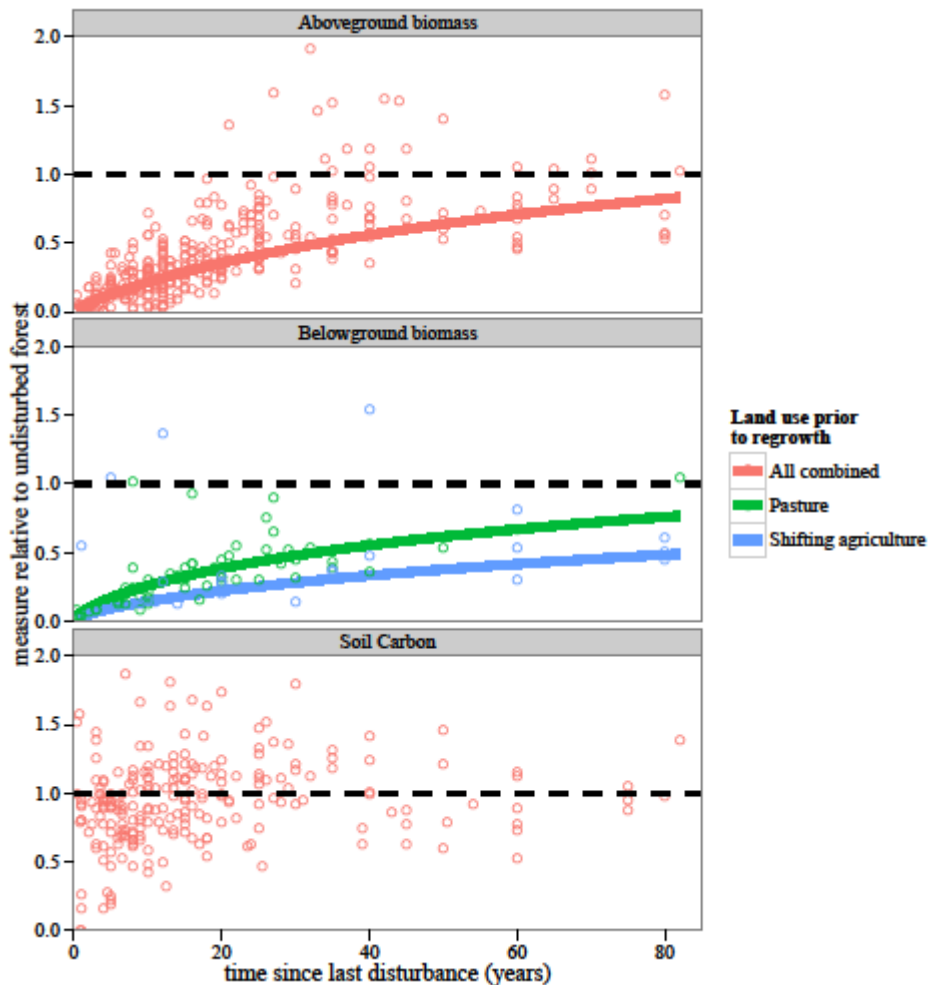553   *IUCN Species Survival Commission*.
554   69.   Benayas J.M.R., Bullock J.M., Newton A.C. 2008 Creating woodland islets to
555   reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology*
556   *and the Environment* **6**(6), 329-336.

557
558   Figures
559

560

561

562   Figure 1 - Recovery of above-ground biomass (n=326), below-ground biomass (n=76) and soil carbon

563   (n=185) in secondary tropical forests, relative to undis- turbed reference forests. Solid lines represent

564   model predictions, with different colours representing different disturbance types. Parameters

565   included in figures have AICc importance values greater than 0.5. The horizontal dashed line

566   represents no difference between secondary and undisturbed forests.
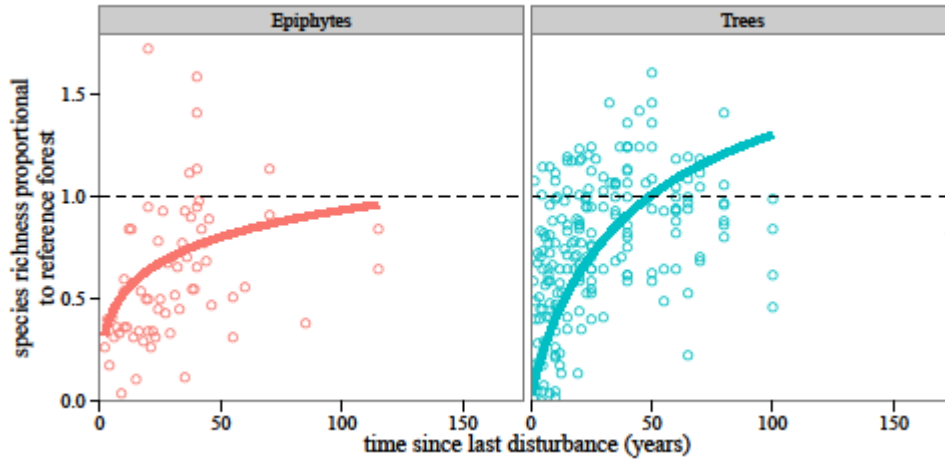
567

568 Figure 2 - Recovery of epiphyte (n=65) and tree (n=204) species richness in secondary tropical

569 forests, relative to undisturbed reference forests. Solid lines represent model predictions, with

570 different colours representing different disturbance types. Parameters included in figures have AICc

571 importance values greater than 0.5. The horizontal dashed line represents no difference between

572 secondary and undisturbed forests.
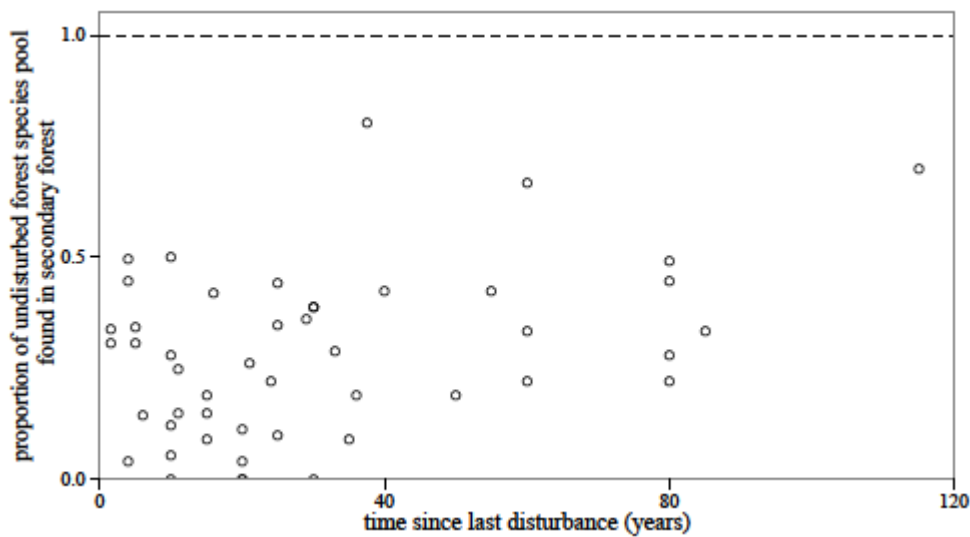
573

574 Figure 3 - Recovery of species associated with undisturbed tropical forest in secondary forest (n=50).

575 The horizontal dashed line represents no difference between secondary and undisturbed forests.