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7 **Above- and belowground carbon stocks are decoupled in**  
8 **secondary tropical forests and are positively related to forest age**  
9 **and soil nutrients respectively**

10

11 RUNNING TITLE

12 Decoupled secondary tropical forest carbon stocks

13

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22

23 KEYWORDS

24 Aboveground biomass; Belowground biomass; Carbon storage; Forest restoration; Land-use change;

25 Necromass; Neotropics; Soil; Succession

26

27 ABSTRACT

28 Reducing atmospheric CO<sub>2</sub> is an international priority. One way to assist stabilising and reducing  
29 CO<sub>2</sub> is to promote secondary tropical forest regrowth on abandoned agricultural land. However,  
30 relationships between above- and belowground carbon stocks with secondary forest age and specific  
31 soil nutrients remain unclear. Current global estimates for CO<sub>2</sub> uptake and sequestration in secondary  
32 tropical forests focus on aboveground biomass and are parameterised using relatively coarse metrics  
33 of soil fertility. Here, we estimate total carbon stocks across a chronosequence of regenerating  
34 secondary forest stands (40–120 years old) in Panama, and assess the relationships between both  
35 above- and belowground carbon stocks with stand age and specific soil nutrients. We estimated  
36 carbon stocks in aboveground biomass, necromass, root biomass, and soil. We found that the two  
37 largest carbon pools - aboveground biomass and soil – have distinct relationships with stand age and  
38 soil fertility. Aboveground biomass contained ~61-97 Mg C ha<sup>-1</sup> (24-39 % total carbon stocks) and  
39 significantly increased with stand age, but showed no relationship with soil nutrients. Soil carbon  
40 stocks contained ~128-206 Mg C ha<sup>-1</sup> (52-70 % total stocks) and were unrelated to stand age, but  
41 were positively related to soil nitrogen. Root biomass carbon stocks tracked patterns exhibited by  
42 aboveground biomass. Necromass carbon stocks did not increase with stand age, but stocks were held  
43 in larger pieces of deadwood in older stands. Comparing our estimates to published data from younger  
44 and older secondary forests in the surrounding landscape, we show that soil carbon recovers within 40  
45 years of forest regeneration, but aboveground biomass carbon stocks continue to increase past 100  
46 years. Above- and belowground carbon stocks appear to be decoupled in secondary tropical forests.  
47 Paired measures of above- and belowground carbon stocks are necessary to reduce uncertainty in  
48 large-scale models of atmospheric CO<sub>2</sub> uptake and storage by secondary forests.

49

## 50 1. INTRODUCTION

51 Tropical forests are a persistent sink of atmospheric CO<sub>2</sub> and store 55 % of global terrestrial carbon,  
52 estimated at  $471 \pm 93$  petagrams (Pg; Pan et al., 2011). In an era of unprecedented anthropogenic  
53 greenhouse gas emissions resulting in pervasive changes in global climatic patterns, maintaining  
54 tropical forest cover is key to stabilising the global carbon balance (Grace, Mitchard, & Gloor, 2014;

55 Yadvinder Malhi & Grace, 2000). Deforestation and conversion to agriculture removes aboveground  
56 biomass, shifts plant composition and function, and alters soil nutrient levels and local precipitation  
57 (Dent, DeWalt, & Denslow, 2013; Grace et al., 2014). Such changes drive increased carbon turnover  
58 and emissions estimated at 1-2 petagrams of carbon per year ( $\text{Pg C year}^{-1}$ ; Houghton, Byers, &  
59 Nassikas, 2015; Pan et al., 2011).

60

61 Approximately 50 % of global tropical forest cover is now degraded or regenerating secondary forest,  
62 rather than old-growth forest (FAO, 2016). Secondary forests are therefore increasingly important for  
63 the provision of tropical forest ecosystem services, such as uptake of atmospheric  $\text{CO}_2$  and long-term  
64 carbon storage (Chazdon et al., 2016). Recent pan-tropical analyses have shown that aboveground  
65 biomass and carbon stocks of regenerating secondary tropical forests accumulate to  $34.53 \pm 1.84 \text{ Mg}$   
66  $\text{C ha}^{-1}$  by 20 years of regrowth, rising to  $133.89 \pm 4.67 \text{ Mg C ha}^{-1}$  by 100 years of regrowth  
67 (Anderson-Teixeira, Wang, McGarvey, & LeBauer, 2016). This rapid accumulation of carbon  
68 represents an estimated net carbon sink of  $\sim 1\text{-}3 \text{ Pg C year}^{-1}$  (Houghton et al., 2015; Pan et al., 2011).

69

70 In the Neotropics, regenerating secondary forests (1-100 years old) take up  $\text{CO}_2$  at 11 times the rate of  
71 old-growth forests, and during the first 20 years of secondary forest regeneration the rate of uptake is  
72  $3.05 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  (Poorter et al., 2016). Indeed, the total accumulation of carbon over 40 years of  
73 secondary forest regrowth on former agricultural land in tropical Latin America is equivalent to  $\sim 20$   
74 years (1993 – 2014) of carbon emissions from fossil fuels and industrial processes across the region  
75 (Chazdon et al., 2016). The preservation of intact old-growth tropical forests and existing secondary  
76 forests, alongside the promotion of secondary forest regrowth on abandoned land, could therefore  
77 constitute a powerful tool in policies aimed at mitigating climate change such as the Bonn Challenge  
78 and REDD+ (Berenguer et al., 2014; Chazdon et al., 2016).

79

80 The quantity of carbon stored within tropical forests is determined by feedbacks between plant net  
81 primary production (NPP), soil fertility and climate. At regional scales, NPP of old-growth and

82 secondary tropical forests increases with precipitation and soil fertility (Anderson-Teixeira et al.,  
83 2016; Malhi et al., 2004; Malhi et al., 2009; Poorter et al., 2016). The spatial heterogeneity of  
84 available soil nutrients (such as nitrogen, phosphorus and potassium; Wright et al., 2011), topography  
85 (Grimm, Behrens, Märker, & Elsenbeer, 2008), and plant composition (Batterman et al., 2013;  
86 Jobbagy & Jackson, 2000) can be important determinants of forest carbon stocks at finer spatial  
87 scales.

88

89 Considerable uncertainty surrounds the relationship between carbon stocks in different carbon pools  
90 and secondary forest stand age; although above-ground biomass tends to increase over succession,  
91 field studies report increases, decreases and unchanged soil carbon over similar time-scales (reviewed  
92 in Powers & Marín-Spiotta (2017)). Current large-scale estimates of carbon uptake and stocks in  
93 secondary forests often consider only aboveground biomass (Poorter et al., 2016) or soil carbon (Don,  
94 Schumacher, & Freibauer, 2011), and rarely include multiple above- and belowground carbon pools  
95 (but see Anderson-Teixeira et al. (2016)). Considering both above- and belowground carbon stocks in  
96 concert is essential to understand how total forest carbon accumulates as forests regenerate,  
97 particularly when planning forest conservation policies aimed at promoting carbon uptake and  
98 sequestration (Chazdon et al., 2016; Powers & Marín-Spiotta, 2017). Furthermore, present estimates  
99 of the importance of soil nutrients in determining aboveground carbon stock accumulation are based  
100 on soil cation exchange capacity (CEC; Poorter et al. (2016)). Soil CEC can be a relatively coarse  
101 metric of soil fertility if site-specific values are unavailable (Nachtergaele, van Velthuisen, Verelst, &  
102 Wiberg, 2012). Therefore, we may be underestimating the importance of specific soil nutrients, such  
103 as N and P, in determining secondary forest above- and belowground carbon stock accumulation  
104 (Powers & Marín-Spiotta, 2017).

105

106 To better understand how regenerating secondary forests may contribute to reducing atmospheric CO<sub>2</sub>  
107 through carbon uptake and long-term sequestration, we urgently need more detailed understanding of  
108 the process of carbon accumulation and the relative importance of different carbon pools as secondary

109 forests develop (Chazdon et al., 2016). Specifically, we need to measure above- and belowground  
110 carbon stock estimates with plot-level data for targeted soil nutrients (Powers & Marín-Spiotta, 2017).  
111 Additionally, our knowledge of carbon stocks in intermediate (~60-90 years) and older (>100 years)  
112 secondary forests is limited (Anderson-Teixeira et al., 2016). Such information is vital to enhance  
113 predictive power regarding the long-term value of secondary forests in strategies to mitigate climate  
114 change (Chazdon et al., 2016), while contextualising the exceptional value of maintaining intact  
115 primary tropical forests and their existing carbon stocks (Grace et al., 2014).

116

117 The aim of our study was to assess the effect of forest stand age and specific soil nutrients on carbon  
118 storage within different secondary tropical forest carbon pools. We use a chronosequence in central  
119 Panama – which has the unique advantage of consistent rainfall and pH across sites and spans the  
120 longest trajectory of secondary forest regeneration in the Neotropics (40 – 120 years; Rozendaal et al.,  
121 2019) – to estimate carbon stocks in above- and belowground biomass and necromass. Specifically,  
122 we ask 1) do all carbon pools increase consistently with forest age? And 2) what is the relative  
123 importance of forest age and soil nutrients for carbon stock accumulation in different carbon pools?  
124 Answers to these questions will further elucidate patterns of total carbon accumulation over secondary  
125 forest regeneration and how they vary among different above- and belowground carbon pools.  
126 Furthermore, we will be better able to demonstrate the role specific soil nutrients play in carbon  
127 accumulation in regenerating tropical forests. Parameterising large-scale models of carbon uptake and  
128 storage within regenerating secondary tropical forests is key to demonstrating the importance of  
129 secondary forests in national and international carbon mitigation strategies and forest restoration goals  
130 (Chazdon et al., 2016).

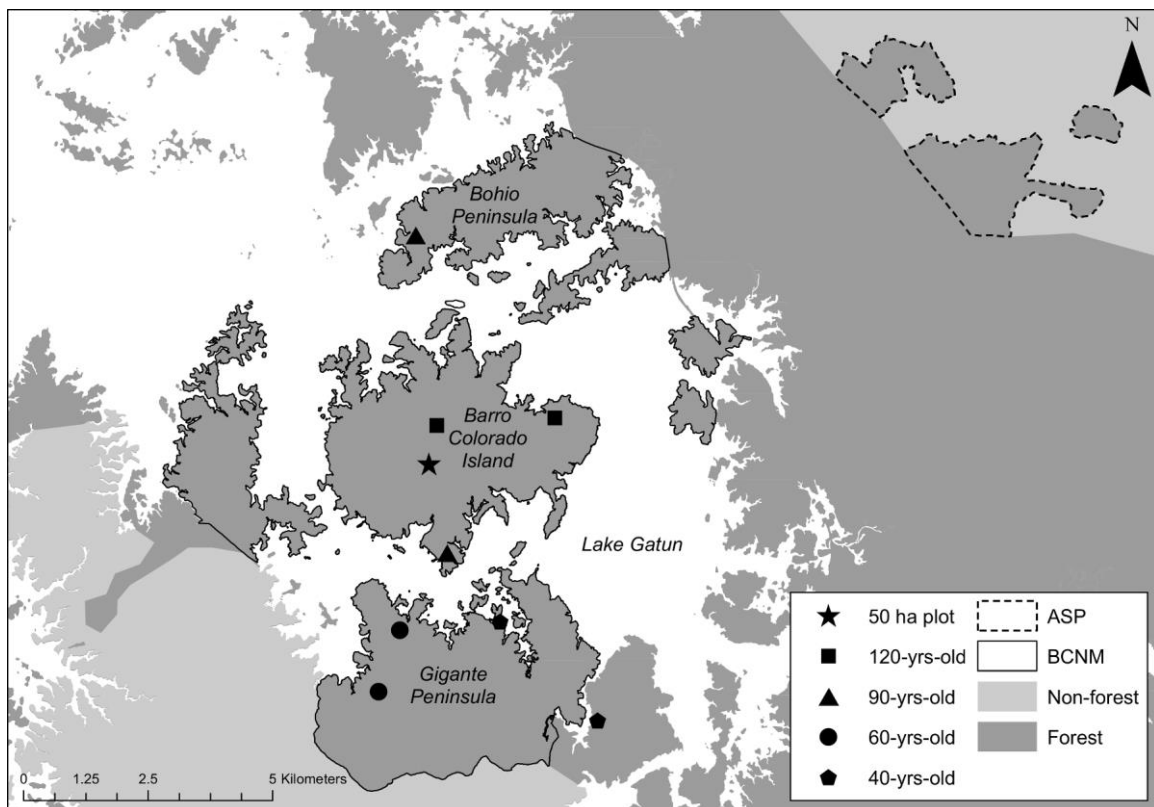
## 131 2. MATERIALS AND METHODS

### 132 2.1 Study area

133 This study was conducted across a 40–120 year secondary forest chronosequence located in central  
134 Panama within the Barro Colorado Nature Monument (BCNM) and includes sites on Barro Colorado

135 Island (BCI; 9°9' N, 79°51' W) and nearby mainland peninsulas (Fig. 1; Denslow & Guzman, 2000).  
 136 The BCNM comprises a mosaic of old-growth and secondary tropical forests of different ages, which  
 137 are the product of forest regrowth following successive episodes of agricultural land abandonment  
 138 between the 1880s and 1979 (Denslow & Guzman, 2000; E. G. J. Leigh, Rand, & Windsor, 1982).  
 139 We define old-growth stands as those with no indication of historical logging or cultivation (Piperno,  
 140 1990). The region receives ~2600 mm of rainfall annually, predominantly during a 7-month wet  
 141 season from May to December (Leigh et al., 1982). Geologically, the BCNM is a patchwork of  
 142 volcanic and sedimentary parent material that has weathered to form clay-rich oxisols and silty-clay  
 143 alfisols (Baillie, Elsenbeer, Barthold, Grimm, & Stallard, 2007; Yavitt, 2000).

144



145

146 **Fig. 1:** Geography of the eight 1-ha chronosequence study plots within the Barro Colorado  
 147 Nature Monument (BCNM), Panama. Chronosequence forest stands span 40-120 years of  
 148 forest regeneration since agricultural land abandonment. The Barro Colorado Island (BCI) 50-  
 149 ha plot comprises old-growth forest. ASP = Agua Salud Project, which comprises secondary

150 forest stands 5 to 15 years old. Map modified from Mayhew, Tobias, Bunnefeld, & Dent  
151 (2019).

152

## 153 2.2 Chronosequence plots

154 All data were collected within a network of eight permanent secondary forest plots representing two  
155 independent replicate 1-ha plots (50 x 200 m) in each of 40, 60, 90 and 120-year-old secondary forest  
156 stands (Fig 1; see Denslow & Guzman, 2000 and Dent et al., 2013 for further details). Stand ages  
157 were estimated using historical records, aerial photographs and interviews with long-time residents  
158 (for details see Denslow & Guzman 2000). Stands selected for plot establishment were a minimum of  
159 1.3 km apart (mean  $\pm$  SD = 4.65  $\pm$  2.28 km), were previously small-holdings farmed for fruit  
160 production and/or cattle pasture, and have not been subjected to further disturbance since land  
161 abandonment. Plots are located on different geological substrates but have similar values for soil pH  
162 and bulk density (see Denslow & Guzman (2000) for detailed plot characteristics). Due to limitations  
163 imposed by the landscape composition and land-use history, secondary forest plot age was closely  
164 linked with geology: all younger plots (aged 40 and 60 years) were exclusively associated with  
165 basaltic substrates, and older plots (aged 90 to 120 years) were associated with sedimentary substrates  
166 (Denslow & Guzman, 2000).

## 167 2.3 Carbon pool data collection and calculation

168 All trees and palms  $\geq$ 10 cm diameter at breast height (DBH) were measured for diameter and  
169 identified to species-level between 2011 and 2014, following census protocols established by the  
170 Forest Global Earth Observatory (ForestGEO; Condit, 2008). Soil sampling and necromass  
171 inventories were undertaken between February and May 2015, following protocols established for the  
172 ForestGEO 50-ha plot on BCI (Larjavaara & Muller-Landau, 2009; Turner, 2010).

173

### 174 *Above- and belowground biomass and community-weighted mean wood density*

175 We followed methods in Poorter et al. (2016) for estimating aboveground biomass for all trees and  
176 palms from diameter data and species-specific wood density values, compiled for trees and palms in

177 the BCNM (Wright et al., 2010). If a species-specific wood density value was not available for an  
178 individual, we used the genus-level mean wood density. We estimated the aboveground biomass of  
179 each individual using the allometric equation developed by Chave et al. (2014; equation 7, which  
180 incorporates a constant specific to temperature and water stress of the study area). Lack of height data  
181 precluded our use of a palm-specific allometric equation (Goodman et al., 2013). It was not feasible to  
182 physically remove any large tree roots from plots in order to estimate belowground root biomass, due  
183 to the consequential impacts to trees and long-term aboveground biomass monitoring. Thus, we  
184 estimated root biomass for each individual from DBH and wood density values using an allometric  
185 equation developed within Panamanian secondary forests (Sinacore et al., 2017). To obtain carbon  
186 stock estimates from above- and belowground biomass estimates, we assumed 47.4 % of biomass to  
187 be carbon and so multiplied biomass estimates by 0.474 (Martin & Thomas, 2011). We depart from  
188 the methods of Poorter et al. (2016) by using 47.4 % rather than 50 %, because the values of Martin &  
189 Thomas (2011) were tested in the BCNM, increasing our confidence in this value. Our aboveground  
190 biomass carbon stock calculations will therefore be lower than Poorter et al. (2016). For each plot, we  
191 generated a per-hectare estimate of total carbon stocks ( $\text{Mg C ha}^{-1}$ ) for the aboveground and root  
192 biomass carbon pools, by summing the estimated carbon stocks held in each individual. We also  
193 generated plot-level estimates for total basal area ( $\text{m}^2$ ) from DBH measurements, and we calculated  
194 plot-level community-weighted mean wood density by summing wood density values across all  
195 individuals and dividing by the number of individuals.

196

#### 197 *Necromass*

198 Fallen dead wood ( $\geq 10$  cm diameter) was inventoried along 1000 m of parallel transects located  
199 within each 1-ha plot (5 x 200 m transects, spaced at 10 m intervals) using the line-intercept method  
200 (Larjavaara & Muller-Landau, 2009). The diameter of all deadwood bisecting a transect was recorded,  
201 along with its orientation (Larjavaara & Muller-Landau, 2011). All standing deadwood  $\geq 10$  cm  
202 diameter (diameter at 1.3 m if  $\geq 1.3$  m high or diameter at the mid-point of the stump if  $< 1.3$  m high)  
203 was inventoried throughout 1-ha plots, with diameter and height recorded. For fallen and standing



204 deadwood  $\geq 20$  cm diameter, we estimated wood density non-destructively using a penetrometer and a  
205 relationship developed for deadwood  $\geq 20$  cm diameter within the BCNM (Larjavaara & Muller-  
206 Landau, 2010). For deadwood  $< 20$  cm diameter, a plot-level mean wood density was used, derived  
207 from the  $\geq 20$  cm diameter deadwood. Carbon stocks within each piece of fallen necromass were  
208 summed for each transect, as was necromass abundance and volume (Larjavaara & Muller-Landau,  
209 2011). Plot-level total necromass carbon stock estimates were generated by summing carbon stocks of  
210 individual pieces of standing and fallen deadwood.

211

### 212 *Soil sampling*

213 Within each 1-ha forest plot, soil samples were collected along two, parallel 200 m transects, spaced  
214 30 m apart. Five sampling points were located at 40 m intervals along each transect, giving 10  
215 sampling points per plot. Soil was collected from 0-10 cm and 10-20 cm at all 10 sampling points,  
216 while at alternate sampling points ( $n = 5$ ) deeper soils from 20-50 cm and 50-100 cm were also  
217 collected. Sampling generated 30 samples per plot (0-10 cm,  $n = 10$ ; 10-20 cm,  $n = 10$ ; 20-50 cm,  $n =$   
218 5; and 50-100 cm,  $n = 5$ ). If a sampling point was disturbed by animals (for example, tracks or  
219 burrows), sampling was carried out at the closest undisturbed area. Obvious surface litter, including  
220 decaying but recognisable leaves and twigs, was removed at the sampling point; any surface roots  
221 were left intact.

222

223 Soil cores from 0-10 cm and 10-20 cm depths were taken using a 2-inch-diameter, fixed-volume  
224 auger. If stones or roots interrupted coring, then the roots were cut or sampling was started again  
225 within 1.5 m of the original sampling point. The entire sample, including roots and stones, was taken  
226 back to the lab for processing. Soils from 20-50 cm and 50-100 cm depths were sampled using a  
227 Dutch auger. If coring was interrupted by stones and the depth achieved was  $< 80$  % of the required  
228 depth, sampling was started again within 1.5 m of the original sampling point. If the depth achieved  
229 was  $\geq 80$  % of the required depth, the exact depth achieved was recorded. Soil from each core was  
230 homogenised in the field, with a 500 g subsample taken back to the lab for processing.

231

232 For all soil samples, we removed all roots (>2mm diameter) and stones by hand, air-dried the soil in  
233 an air-conditioned laboratory for a minimum of five days, and calculated sample-specific bulk  
234 densities corrected for stone fraction (SI1). Due to the coring technique used for 20-50 cm and 50-100  
235 cm cores, core-specific bulk density values could not be obtained. Instead, we used bulk density  
236 values and estimated stone fraction from soil pits located close to each 1-ha plot (B. Turner pers.  
237 comm; H. Elsenbeer pers. comm.).

238

239 Only soil cores that reached  $\geq 80$  % of the required depth were used for soil carbon analyses so as not  
240 to bias the carbon and nutrient concentration data for each depth interval. Individual soil samples were  
241 ground and analysed for percentage carbon and nitrogen using a CN analyser (Elementar Vario III  
242 EL). Available phosphorus was extracted using 0.5M NaHCO<sub>3</sub> buffered at pH 8.5, and content  
243 determined colorimetrically by the molybdenum blue method. Phosphorus data were only obtained for  
244 0-10cm and 10-20cm soil depths. Soils within the chronosequence stands have relatively low pH (i.e.  
245 <7); therefore, we did not expect carbonates to be present and assumed that carbon concentration  
246 values were equivalent to soil organic carbon (Denslow & Guzman, 2000; Grimm et al., 2008). Soil  
247 carbon stock estimates were generated by correcting percentage carbon values using soil bulk density  
248 values for each sample (please see SI1 for full details). Estimates for soil carbon stocks, available  
249 phosphorus, and percentage nitrogen at each soil depth, as well as totals for each in soil 0-100 cm  
250 depth, were calculated using equations outlined in SI1.

251

#### 252 2.4 Integrating carbon stock data from the surrounding landscape

253 Using published data, we compiled values of aboveground biomass carbon and soil carbon stocks  
254 from secondary and old-growth forest sites within the surrounding landscape. The additional data  
255 included sites with much younger secondary forests of 5 to 15 years regrowth in the Agua Salud  
256 chronosequence (Neumann-Cosel, Zimmermann, Hall, van Breugel, & Elsenbeer, 2011) and old-

257 growth forests on BCI (Chave et al., 2003; Grimm et al., 2008; Fig. 1). Carbon stock data for  
258 necromass and root biomass have not been published for these other sites.

259

## 260 2.5 Data analyses

261 We used a combination of generalised linear (GLMs) and generalised linear mixed effects models  
262 (GLMMs) for analyses of each carbon pool using R (version 3.6.1; (R Core Team, 2019) and the  
263 ‘glmmTMB’ package (Magnusson et al., 2019). Predictor variables included in models, such as forest  
264 stand age and specific soil nutrients, varied depending on the response variable and relevance to the  
265 hypothesis being tested (Table S2.1). Prior to analysis, continuous predictor variables were rescaled  
266 (mean-centred and standardised by two standard deviations; Gelman & Su, 2016; Schielzeth, 2010) to  
267 enable direct comparison of effect sizes. The distribution of response variables was visually inspected  
268 and the appropriate distribution selected for models (Bolker, 2008); Table S2.1).

269

270 For each response variable, the potential co-linearity of predictor variables was assessed using a  
271 Pearson’s correlation matrix, with significant correlation taken as  $r > 0.7$  ( $P < 0.05$ ). Belowground root  
272 biomass was estimated from aboveground biomass and therefore these variables were not included  
273 together as predictor variables in analyses. Prior ‘land use’ and ‘substrate geology’ were both fitted as  
274 random effects to account for potential variation arising from these plot-level characteristics (Bolker  
275 et al., 2009).

276 Models were simplified by comparing AICc values using the R package ‘MuMin’ (Barton, 2017),  
277 whereby a difference of  $< 2$  between model AICc values indicated that models were not significantly  
278 different (Burnham & Anderson, 2002). Interactions between predictor variables were tested for and  
279 removed if non-significant. Specific considerations made during analyses of each carbon pool are  
280 outlined in the following sections.

281

### 282 *Above- and belowground biomass*

283 Total plot-level aboveground biomass, basal area, community-weighted mean wood density and  
284 carbon stocks, and belowground root biomass and carbon stocks were modelled using GLMs with a  
285 normal distribution. Each of these variables were modelled as a response to forest stand age, and plot-  
286 level mean available phosphorus and plot-level mean percentage nitrogen (0-100 cms; Table S2.1). As  
287 these were plot-level analyses, fitting random effects for ‘land use’ and ‘substrate geology’ was not  
288 possible due to over-parameterising models.

289

#### 290 *Necromass*

291 Transect-level carbon stock estimates were modelled using GLMMs, fitting ‘plot’ as a random effect  
292 to account for potential pseudoreplication of transect-level data. Necromass diameter class (<20 cm or  
293 >20 cm) and forest age were fitted with an interaction term, and included alongside necromass  
294 abundance and volume in analyses of carbon stocks. Necromass carbon stocks and volume were  
295 modelled using a Gamma distribution, and necromass abundance modelled using a Poisson  
296 distribution (Table S2.1).

297

#### 298 *Soil*

299 Soil carbon stock estimates from each sample were modelled using GLMMs, fitting ‘substrate  
300 geology’ and ‘land use’, as well as ‘plot’ and ‘sampling point’ as random effects to account for plot-  
301 level variation in topography and wider landscape characteristics. Soil carbon stocks, percentage  
302 carbon, percentage nitrogen, available phosphorus, and the C:N ratio were modelled with soil depth  
303 and forest stand age (Table S2.1). Percentage carbon and percentage nitrogen were modelled using a  
304 Beta distribution and carbon stocks, C:N ratio and available phosphorus were modelled using a  
305 Gamma distribution. Available P was not included as a predictor variable for soil carbon stocks  
306 because available P data were only available for 0-10cm and 10-20cm depths. However we assessed  
307 the relationship between soil carbon stocks and available P for the top two soil depths and found no  
308 significant relationship ( $z = -0.86$ ,  $P=0.39$ ).

309

310 3. RESULTS

311 3.1 Carbon stocks and contributions to total forest carbon

312 Total carbon stocks ranged from ~245 – 298 Mg C ha<sup>-1</sup> across the chronosequence (Table 1). Soil  
313 carbon constituted the greatest percentage of total forest carbon stocks (52 – 70 %) followed by  
314 aboveground biomass (24 – 39 %; Table 1).

315

316 **Table 1:** Total forest carbon and mean carbon stocks for above- and belowground carbon  
 317 pools, across secondary tropical forest stands of 40-120 years; 95 % confidence intervals  
 318 are presented in brackets. The percentage contributions to total forest carbon stocks are  
 319 presented in italics.  
 320

Forest age (years)		40	60	90	120
Mean carbon stocks (Mg ha <sup>-1</sup> )	Aboveground biomass	61.35 (59.82-62.88) <i>24.37</i>	75.11 (73.50-76.71) <i>25.21</i>	96.25 (85.60-106.91) <i>39.23</i>	96.86 (87.76-106.00) <i>32.86</i>
	Necromass	1.72 (1.51-1.93) <i>0.68</i>	2.42 (1.99-2.85) <i>0.81</i>	3.63 (2.46-4.53) <i>1.37</i>	3.34 (2.62-4.06) <i>1.13</i>
	Belowground biomass	12.48 (11.50-13.46) <i>4.96</i>	14.75 (13.86-15.64) <i>4.95</i>	17.45 (17.23-17.66) <i>7.11</i>	18.96 (13.06-24.86) <i>6.43</i>
	Soil (0-100 cm)	176.22 (172.2-180.30) <i>69.99</i>	205.70 (200.4-211.00) <i>69.03</i>	128.04 (118.20-123.90) <i>52.18</i>	175.60 (172.40-178.80) <i>59.57</i>
	Total	251.77 (245.03-258.57)	297.98 (289.75-306.20)	245.37 (223.49-253.00)	294.76 (275.84-313.72)

321

### 322 3.2 Above- and belowground biomass and carbon stocks

323 Mean carbon stocks held in aboveground biomass of trees  $\geq 10$  cm DBH ranged from ~61 – 97 Mg  
 324 ha<sup>-1</sup>. The total basal area of trees and aboveground carbon stocks significantly increased with forest  
 325 age; however, the community-weighted mean wood density of forest stands showed no significant  
 326 relationship with forest age (Fig. 2b; Table 2). Soil nutrients (% N and available P; Table 2) were not  
 327 significant predictors of basal area, aboveground carbon stocks, nor community-weighted mean wood  
 328 density, and were not related to forest age (Table 2). Estimated carbon stocks in root biomass ranged  
 329 from ~12-19 Mg C ha<sup>-1</sup> and significantly increased with forest age, but not soil nutrients (Table 2).

330

331 **Table 2:** Coefficient estimates for fixed effects within best-fit generalised linear models (GLMs) and  
332 generalised linear mixed-effects models (GLMMs). Marginal  $R^2$  ( $R^2_m$ ) represents the degree of model  
333 fit contributed by the fixed effects alone, while the conditional  $R^2$  ( $R^2_c$ ) shows the degree of model fit  
334 considering both random and fixed effects included within models (computed using  
335 ‘r.squaredGLMM’ in the ‘MuMin’ R package; Barton 2016).  $R^2$  values were not computed for models  
336 using a Beta distribution (see Table S2.1).  
337 \* $t$ -value computed rather than  $z$ -value.

Carbon pool	Variable	Fixed effects	Estimate	Std. error	z-value	$R^2_m$	$R^2_c$
Aboveground biomass	C stock (Mg ha <sup>-1</sup> )*	Intercept	82.39	2.57	32.02	0.81	-
		Forest age (years)	30.06	5.5	5.46		
	Basal area (m <sup>2</sup> )*	Intercept	21.45	0.71	30.14	0.6	-
		Forest age (years)	5	1.52	3.26		
	Community-weighted mean wood density (g cm <sup>-3</sup> )*	Intercept	0.59	0.006	91.64	0.26	-
		Forest age (years)	0.02	0.01	1.55		
Necromass	C stock (Mg ha <sup>-1</sup> ) (considering fallen necromass only)	Intercept	-0.36	0.08	-4.45	0.83	-
		Forest age (years)	-0.30	0.16	-1.86		
		Volume	1.61	0.16	9.81		
		Abundance	0.52	0.14	3.80		
		Forest age : diameter >20 cm	0.61	0.24	2.54		
	Volume (m <sup>3</sup> ha <sup>-1</sup> )	Intercept	1.91	0.16	12.18	0.36	-
		Diameter class	1.15	0.22	5.21		
		Abundance	0.94	0.25	3.75		
	Abundance	Intercept	1.46	0.08	18.64	0.04	-
		Forest age (years)	-0.43	0.15	-2.79		
		Diameter class	0.58	0.13	-4.4		
		Forest age : > 20 cm	0.95	0.26	3.66		
Belowground biomass	C stock (Mg ha <sup>-1</sup> )*	Intercept	19.53	0.56	34.55	0.86	-
		Forest age (years)	7.88	1.30	6.05		
Soil	C stock (Mg ha <sup>-1</sup> )	Intercept	3.76	0.06	57.99	0.45	0.57
		% N	0.69	0.05	13.60		
	% C	Intercept	-3.36	0.05	-61.80	-	-
		% N	0.84	0.05	16.26		
		Depth 10-20 cm	-0.22	0.04	-5.00		
		20-50 cm	-0.88	0.07	-12.49		

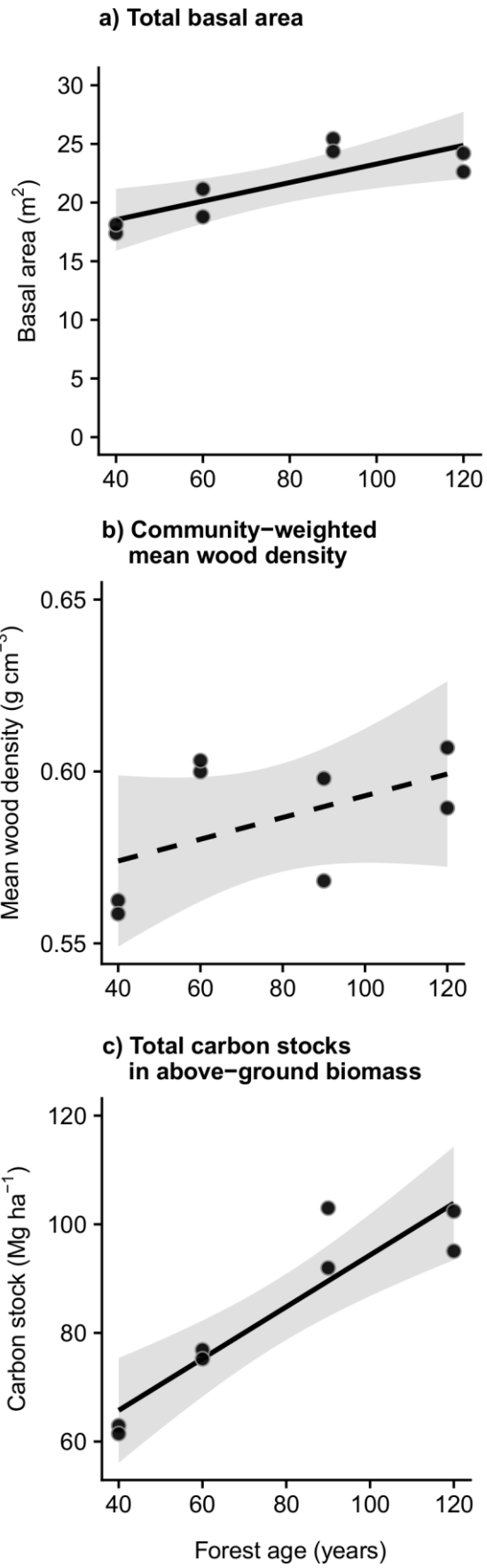
		50-100 cm	-1.49	0.10	-15.16		
	% N	Intercept	-0.17	0.11	-1.58	-	-
		Soil depth: 10-20 cm	-0.75	0.07	-10.00		
		20-50 cm	-1.33	0.10	-13.87		
		50-100 cm	-1.80	0.11	-16.27		
	Available P (mg kg <sup>-1</sup> )	Intercept	1.58	0.23	6.73	0.08	0.17
		% N	0.21	0.31	0.67		
		Soil depth: 10-20cm	-0.81	0.28	-2.9		
	C:N	Intercept	2.41	0.06	37.36	0.51	0.60
		Soil depth: 10-20 cm	-0.13	0.06	-2.34		
		20-50 cm	-0.49	0.06	-7.66		
		50-100 cm	-0.99	0.07	-15.23		

338

### 339 3.3 Necromass volume, abundance and carbon stocks

340 Across the chronosequence, total necromass carbon stocks ranged from 1.72 – 3.63 Mg ha<sup>-1</sup>. Stand  
341 age alone was not a significant predictor of necromass carbon stocks. However, there was a  
342 significant interaction between stand age and necromass diameter, such that carbon stocks were  
343 increasingly held in larger (>20 cm) deadwood in older secondary forests >90 years. Larger  
344 deadwood made a greater contribution to the total necromass volume in older stands, while the  
345 contribution of smaller deadwood (10-20 cm) decreased with stand age (Fig. 3; Table 2). Necromass  
346 carbon stocks significantly increased with higher values of necromass volume and abundance (Table  
347 2). Overall, necromass carbon stocks were predominantly contained within fallen deadwood (~80-  
348 95%) compared to standing deadwood.



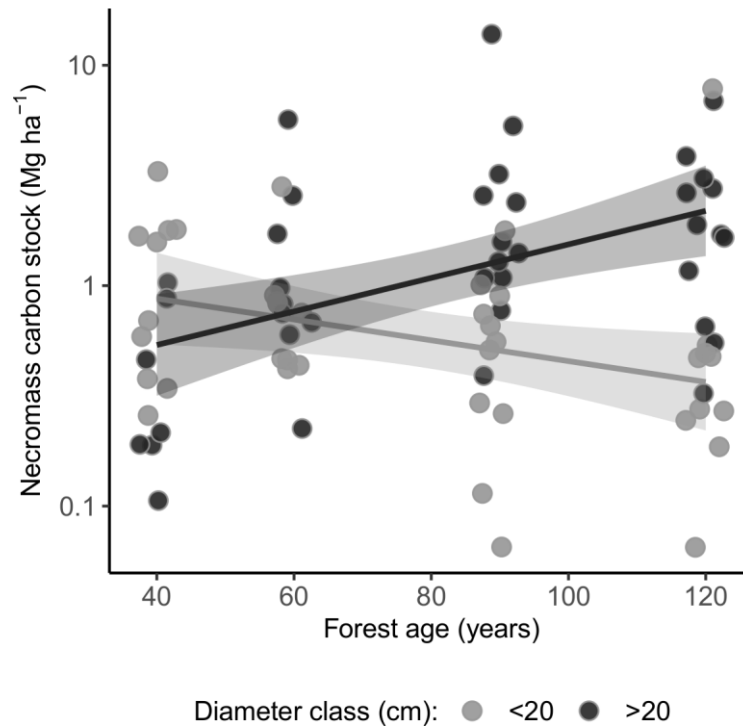


349

350

351 **Fig. 2:** Relationship between total basal area, community-weighted mean wood density, and  
 352 aboveground biomass carbon stocks for trees  $\geq 10$  cm DBH across eight 1-ha forest plots of  
 353 varying age. Solid regression lines indicate a significant relationship, with 95 % confidence  
 354 intervals represented by grey shading; dashed lines indicate a non-significant trend (Table 2).

355



356

357

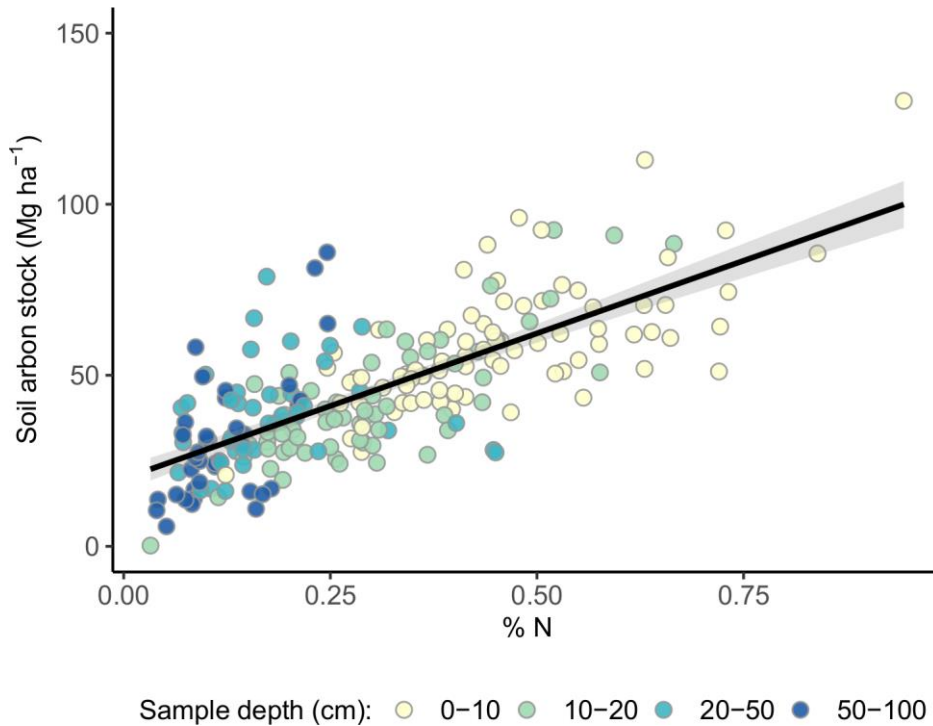
358 **Fig. 3:** Necromass carbon stocks in large ( $>20$  cm diameter) and small (10-20cm diameter)  
 359 deadwood in secondary forest stands of 40-120 years. Predicted values and 95 % confidence  
 360 intervals are plotted as solid lines and grey shading respectively. A  $\log_{10}$  scale is used on the y-  
 361 axis to aid visual clarity. Data represent fallen necromass only (Table 2).

362

### 363 3.4 Soil carbon stocks

364 Mean total soil carbon stocks ranged from  $\sim 176 - 206$  Mg C  $\text{ha}^{-1}$  in each stand across the  
 365 chronosequence (Table 1). The concentration of soil carbon (% C) and total soil carbon stocks  
 366 (Mg C  $\text{ha}^{-1}$ ) did not vary significantly across forest ages (Fig. S2.1; Table 2). Percentage C  
 367 significantly declined with depth, but this was not reflected in carbon stocks due to changes in  
 368 soil bulk density (SI1), and carbon stocks did not significantly change with soil depth (Fig.

369 S2.1; Table S2.3). Soil carbon stocks were significantly positively related to % N (Fig. 4; Table  
370 2), but were not related to available P or aboveground biomass (Table 2). Forest stand age did  
371 not predict % N in soils, nor available P (Table 2; Table S2.2), however % N decreased with  
372 soil depth, as did the C:N ratio and available P (Fig. S2.2; Table 2). Prior land use and substrate  
373 geology explained no variation in soil carbon or nutrient concentrations (Table S2.1).  
374



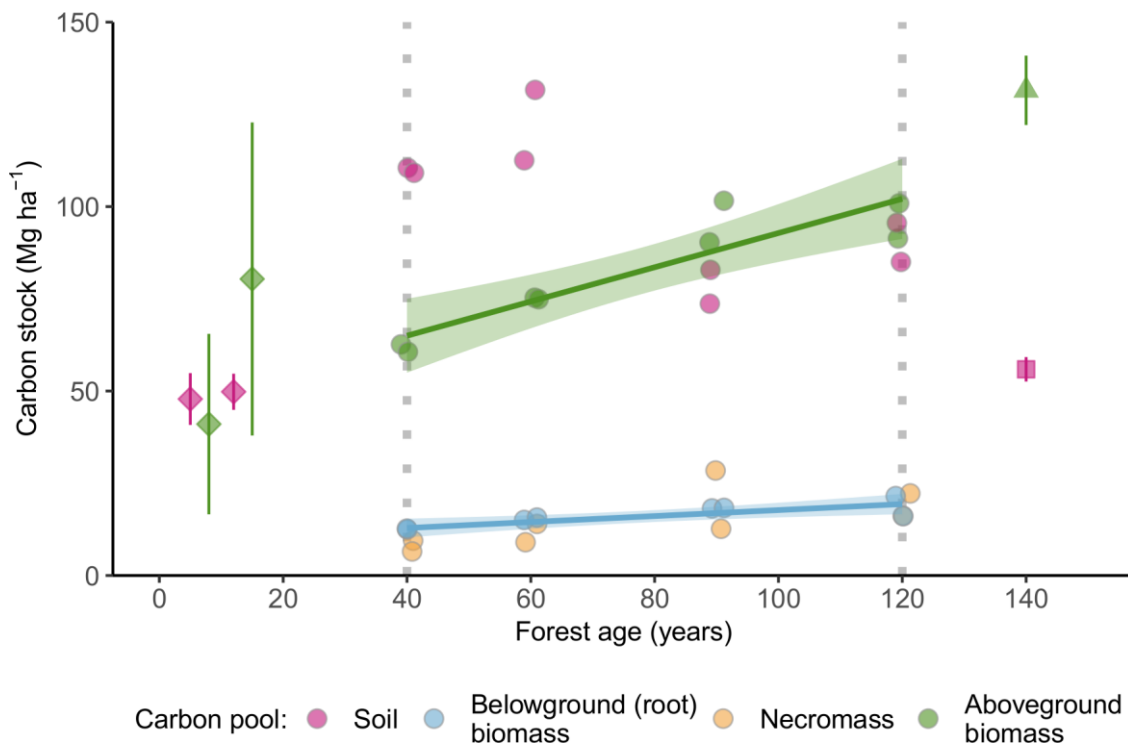
375 Sample depth (cm): 0-10 10-20 20-50 50-100  
376 **Fig. 4:** Relationship between soil carbon stocks and soil N concentration (% N) within  
377 soils 0-100 cm. The black line corresponds to predicted values, with 95 % confidence  
378 intervals indicated by grey shading. Points relate to individual sampling points.

379

### 380 3.5 Landscape-scale context of the 40-120 year chronosequence carbon pools

381 Aboveground biomass carbon stocks in our 40-year-old forest stands were within the range of  
382 values from nearby young secondary forests (5-15 years; Fig. 5). Estimated aboveground  
383 carbon stocks in old-growth forest were slightly higher than those of our 120-year-old stands,  
384 indicating that aboveground biomass may still be on a trajectory of recovery beyond 120 years  
385 (Fig. 5). Conversely, our chronosequence soil carbon stock estimates were significantly higher

386 than those for young secondary forests, but confidence intervals overlapped with those for old-  
 387 growth forests indicating that our soil carbon estimates were within the range of variation for  
 388 old-growth forests (Fig. 5). When viewed at the landscape scale, aboveground carbon stocks  
 389 appear to increase with forest age, whereas soil carbon stocks do not show a clear trajectory of  
 390 change in relation to forest age.  
 391



392 **Fig. 5:** Overview of carbon stocks at the landscape-scale. Carbon stock estimates from  
 393 the eight 1-ha chronosequence plots in this study are shown within the grey dotted  
 394 boundaries, with significant relationships between carbon pools and forest age denoted  
 395 by solid regression lines; 95 % confidence intervals are shown as shaded areas.  
 396 Additionally, soil carbon and aboveground carbon stocks are reported from nearby Agua  
 397 Salud for young secondary forests 5-15 years old (diamonds; Neumann-Cosel et al.,  
 398 2011). Soil carbon stocks (square; Grimm et al. (2008)) and aboveground carbon stocks  
 399 (triangle; Chave et al., 2003)) are plotted for old-growth forest on BCI (Fig. 1); an 95 %  
 400 confidence intervals are indicated by vertical bars. Points are coloured by carbon pool.  
 401

402 Only soil carbon stocks 0-20 cm in depth are reported to allow comparison between  
403 studies.

404

#### 405 4. DISCUSSION

406 We found that above- and belowground carbon stocks are decoupled in their relationships with forest  
407 stand age and soil nutrient status: carbon stocks in aboveground biomass increased with secondary  
408 forest age but showed no relationship with soil nutrients, while conversely, soil carbon stocks were  
409 positively related to soil nutrients (specifically % N) but not stand age. The soil carbon pool  
410 contributed 52 – 70 % of total forest carbon, and when viewed at the landscape scale, 40-year-old  
411 secondary forests had attained soil carbon stocks equivalent to those reported for old-growth forests.  
412 Aboveground biomass contributed 24 - 39 % of total forest carbon, and after 100 years of regrowth,  
413 was close to recovery towards old-growth forest biomass and may still be on a trajectory of recovery  
414 beyond 120 years.

415

##### 416 4.1 Effect of forest age on carbon stocks

417 As in other studies, we found that over tropical forest succession, aboveground and root biomass  
418 carbon stocks increased predictably and tracked forest age (Powers & Marín-Spiotta, 2017). However,  
419 as root biomass is estimated from aboveground biomass in our study, there remains some uncertainty  
420 regarding carbon stocks in this carbon pool (Sierra et al., 2007). Community-weighted mean wood  
421 density showed no relationship with stand age and was slightly higher than old-growth forests on BCI  
422 (basal-area-weighted mean wood density =  $0.51 \pm 0.16$ ; Muller-Landau, 2004), indicating that our  
423 secondary forest stands have recovered this key functional trait during forest regeneration, in contrast  
424 to recent findings from Amazonian secondary forests (Berenguer et al., 2018). We found no  
425 relationship between forest stand age and necromass volume, abundance, and carbon stocks.  
426 However, both the volume and carbon stock of necromass was increasingly contributed by larger  
427 diameter (>20 cm) deadwood in older forest stands >90 years (DeWalt, Maliakal, & Denslow, 2003).  
428 The decomposition rate for larger diameter necromass is lower than for small necromass; deadwood

429 of ~20 cm diameter takes an estimated 18 years to lose 95 % of its mass at a rate of 0.19 year<sup>-1</sup>  
430 (Chambers, Higuchi, Schimel, Ferreira, & Melack, 2000). Thus, the increasing abundance of large  
431 necromass in older secondary forests suggests that the necromass carbon pool in secondary forests  
432 >90 years could be more stable and retain carbon for longer than in younger forests (Carey, Brown,  
433 Gillespie, & Lugo, 1994).

434

435 Patterns in soil carbon dynamics are highly variable (Powers & Marín-Spiotta, 2017). Early studies  
436 assumed that patterns of soil carbon would mimic those of aboveground biomass (Detwiler, 1986),  
437 but results from field studies are inconsistent, with studies reporting increased, decreased or  
438 unchanged soil carbon stocks across tropical secondary forest succession (Powers & Marín-Spiotta,  
439 2017). Secondary forest stand age did not predict soil carbon stocks in our study, and the confidence  
440 intervals of our 0-10cm and 10-20cm soil carbon stocks overlapped with those reported for a  
441 comparable study of soil carbon (i.e. 0-10 cm and 10-20 cm soil layers) in old-growth forests on BCI  
442 (Grimm et al., 2008), indicating that our soil carbon stocks were similar to this old-growth forest  
443 stand. When using comparable soil data (i.e., the 0-10 cm and 10-20 cm soil layers), soils underlying  
444 our 40-year stands held significantly more carbon than reported for nearby young secondary forests  
445 (Neumann-Cosel et al., 2011) pointing towards rapid accumulation of soil carbon within the first 40  
446 years of secondary forest regeneration (Poorter et al., 2016; Powers, 2004). Some evidence suggests  
447 that stand age may be most influential on soil carbon stock recovery during the first 10-30 years of  
448 succession, along with additional factors that we could not include in analyses (such as composition  
449 of the regenerating forest; Batterman et al., 2013; Berenguer et al., 2014). We found that prior land  
450 use and substrate geology explained no variation in soil carbon stocks. The implications of complex  
451 land use histories and underlying geology for biogeochemical cycles across secondary forest  
452 regeneration are thoroughly reviewed in Powers & Marín-Spiotta (2017).

453

454 4.2 Effect of soil nutrients on carbon stocks

455 Across the chronosequence, aboveground biomass accumulation was not related to soil nutrients (% N  
456 and available P). A lack of relationship between aboveground biomass recovery and broad-scale soil  
457 nutrient availability (CEC) has been shown in a pan-Neotropical analysis of secondary forest biomass  
458 accumulation (Poorter et al., 2016). However, at finer spatial scales, soil nutrients have been shown to  
459 be an important limiting factor for biomass accumulation in trees <10 cm DBH and root biomass  
460 (Powers & Pérez-Aviles, 2013; Wright et al., 2011). Thus, soil nutrient status could be important in  
461 determining the trajectory of biomass accumulation in younger secondary forest stands <40 years.

462

463 Carbon and nitrogen are tightly coupled in tropical forest soils due to stoichiometric relationships in  
464 both vegetation and soil (Yang & Luo, 2011). Our finding that soil nitrogen concentration (% N) is  
465 the strongest correlate of soil carbon stocks across the chronosequence aligns with other studies of C  
466 and N accumulation across regenerating forests (Li, Niu, & Luo, 2012; Yang & Luo, 2011). Both % C  
467 and % N significantly declined with soil depth; however, when integrated with soil bulk density data,  
468 this pattern did not translate to a reduction in soil carbon stocks with soil depth (Grimm et al., 2008).  
469 Thus, we highlight the necessity of correcting % C data using soil bulk density when estimating soil  
470 carbon stocks (Li et al., 2012). That carbon stocks did not decline with soil depth highlights the  
471 importance of deeper tropical soils for carbon storage, and suggests that estimates of the contribution  
472 of soil carbon to total forest carbon stocks are improved by including carbon stock estimates from  
473 deeper soils (Jobbagy & Jackson, 2000; Ngo et al., 2013).

474

#### 475 4.3 Contribution of different carbon pools to total forest carbon stocks at local and landscape scales

476 When integrated with additional landscape-scale data on aboveground biomass carbon stocks, our  
477 data show a trajectory of aboveground biomass accumulation towards that of old-growth forests (Fig.  
478 5; Mascaro et al., 2011; Mascaro, Asner, Dent, DeWalt, & Denslow, 2012). However, carbon in  
479 aboveground biomass of our oldest secondary forest sites (120 years) was lower than nearby old-  
480 growth forest, suggesting that biomass recovery may continue past 120 years. Across our sites, total  
481 carbon stocks held in aboveground biomass ranged from ~61 – 97 Mg ha<sup>-1</sup>, which is lower than

482 predicted for similar-aged secondary forests in a recent pan-Neotropical analysis, likely due to  
483 characteristics of our study area such as the pronounced dry season or differences in tree community  
484 composition (Poorter et al., 2016).

485

486 In contrast to aboveground biomass, soil carbon stocks were variable across the wider landscape, but  
487 our data suggest that soil carbon has recovered to old-growth levels within 40 years of forest regrowth  
488 following agricultural abandonment (Powers, 2004; Powers & Marín-Spiotta, 2017). Our study  
489 showed that soil contributed 52 - 70 % of total forest carbon stocks, which contrasts with other  
490 estimates of carbon pool contributions, whereby aboveground biomass contributed the greatest  
491 proportion (56 %) of total forest carbon stocks compared to 32 % in soil (Pan et al., 2011). However,  
492 this difference is likely due to our soil carbon estimates incorporating deeper soils (0-100 cm).

493

494 The necromass carbon pool held 1.7 - 3.6 Mg C ha<sup>-1</sup>, similar to other Neotropical forests (Fonseca,  
495 Benayas, & Alice, 2011; Sierra et al., 2007) and for 20-100 year secondary forests pan-tropically (~5  
496 Mg C ha<sup>-1</sup>; Anderson-Teixeira et al., 2016). Our necromass carbon stock estimates are also similar to  
497 those in old growth forests on BCI (4.6 [3.1-6.39] Mg C ha<sup>-1</sup>; H. Muller-Landau, pers. comm.).  
498 However, the necromass carbon stock estimates from our 120-year-old stands and the BCI 50-ha plot  
499 are lower than for other old-growth tropical forests pan-tropically (~17 Mg C ha<sup>-1</sup>; Anderson-Teixeira  
500 et al., 2016).

501

#### 502 4.4 Implications for global carbon modelling

503 Above-and belowground carbon stocks in this system appear to be decoupled. Aboveground carbon  
504 accumulates over time due to inputs from NPP, unless there are substantial disturbances such as  
505 deforestation (Powers & Marín-Spiotta, 2017). In contrast, soil carbon is influenced both by NPP, soil  
506 micro-organisms and abiotic factors such as geology, climate and topography that can affect soil  
507 nutrients (Jackson et al., 2017). Given that soil contributed the greatest proportion of total secondary  
508 forest carbon in our study, we emphasise that global models of the value of secondary forests for



509 carbon accumulation and storage must include soil carbon estimates. Moreover, our study shows that  
510 models of carbon accumulation through secondary forest regeneration can be better calibrated by  
511 including site-level data on soil nutrient availability, alongside forest stand age, leading to improved  
512 predictive power of large-scale models of secondary forest carbon accumulation (Chazdon et al.,  
513 2016; Powers & Marín-Spiotta, 2017). Our study demonstrates the importance of detailed soil nutrient  
514 and carbon stock information for parameterising global models of the significant contribution  
515 increasing secondary tropical forest cover can make to climate change mitigation.

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529

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