

1 **Forest carbon dynamics in Papua New Guinea; isolating the influence of selective-**
2 **logging and El Niño**

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6

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24 **Authorship**

25 Julian C. Fox performed research, analysed data, and wrote the paper. Ghislain
26 Vieilledent contributed new methods and models, analysed data and contributed to
27 writing of the paper. Rodney J. Keenan conceived of the study and contributed to writing
28 of the paper. Cossey K. Yosi and Joe N. Pokana were responsible for data collection, data
29 analysis, and contributed to writing of the paper.

30

31 **Abstract**

32 Assessment of forest carbon (C) stock and sequestration and the influence of
33 forest harvesting and climatic variations are important issues in global forest ecology.
34 Quantitative studies of the C balance of tropical forests, such as those in Papua New
35 Guinea (PNG), are also required for climate change mitigation initiatives such as
36 REDD+. We develop a hierarchical Bayesian model (HBM) of aboveground forest C
37 stock and sequestration in primary, selectively-harvested, and El Niño Southern
38 Oscillation (ENSO) effected lowland tropical forest from 15 years of permanent sample
39 plot (PSP) census data for PNG.

40 HBM parameters indicated; C stock in aboveground live biomass (AGLB) of 137
41 ± 9 (95% CI) MgC ha⁻¹ in primary forest, compared with 62 ± 18 MgC ha⁻¹ for
42 selectively-harvested forest (55% difference); C sequestration in primary forest of 0.23 \pm
43 1.70 MgC ha⁻¹yr⁻¹ which was lower than in selectively-harvested forest, 1.12 \pm 3.41 MgC
44 ha⁻¹yr⁻¹; ENSO induced fire resulted in significant C emissions (-6.87 \pm 3.94 MgC ha⁻¹yr⁻¹
45 ¹). High variability between PSPs in C stock and C sequestration rates, and
46 autocorrelation among remeasurements of individual PSPs, necessitated random plot
47 effects for both stock and sequestration. The HBM approach allowed inclusion of
48 hierarchical autocorrelation, providing valid confidence intervals on model parameters
49 and efficient estimation. Model parameters have revealed the C balance of PNG's forests
50 and can be used as quantitative inputs for climate change mitigation initiatives.

51

52 **Key words:** Biomass, Sequestration, Degradation, Selective-harvesting, REDD+,
53 Carbon, Bayesian, Hierarchical.

54 **Introduction**

55 Tropical forests cover 10% of global land area but remain a scientific frontier due
56 to structural and biological complexity and high temporal variability associated with
57 complex successional processes (Chambers et al. 2001). A constraint is the limited
58 number of long-term studies quantifying tropical forest dynamics and the impacts of
59 anthropogenic and natural disturbances, such as harvesting and fire (Clark et al. 2001b;
60 Lewis et al. 2009). Long-term studies, whilst difficult to maintain, especially in
61 developing countries, are essential to the development and testing of hypotheses
62 regarding processes and rates of ecological recovery following disturbance, both
63 anthropogenic and natural (Taylor et al. 2008). In this study we report on a spatially and
64 temporally extensive Permanent Sample Plot (PSP) network in forests in Papua New
65 Guinea (PNG) and examine the impact of selective-harvesting and the El Niño-Southern
66 Oscillation (ENSO) induced fires on forest carbon (C) and C sequestration. To achieve
67 this, we develop a hierarchical Bayesian model (HBM) and derive parameters that can be
68 used to estimate the C and CO₂ balance of selective-harvesting, forest regeneration and
69 degradation after fire which are important inputs for climate change mitigation initiatives.

70 There is still considerable debate over carbon dynamics in primary tropical
71 forests. Field measurements of C stock change suggest that primary tropical forests are a
72 significant C sink (Phillips et al. 1998; Baker et al. 2004a). For example, Lewis et al.
73 (2009) examined C stock development for PSPs in Africa and reported that primary forest
74 is on average sequestering 0.63 MgC ha⁻¹ with 95% confidence interval (CI) 0.22–0.94.
75 The study of Lewis et al. (2009) is consistent with other studies on the C balance of
76 forests, in that they combine PSP measurements across time and space, and report an

77 average and a 95% CI. Other authors suggest that primary forest should be in
78 equilibrium with C sequestration in growth largely balanced by C emissions due
79 mortality and decomposition (Clark 2001b; Wright 2005; Sierra et al. 2007). The role of
80 recovering forest as a C source or a C sink remains poorly understood (Grassi et al. 2008;
81 Olander et al. 2008; Ramankutty et al. 2007), and there is contention over the extent and
82 recovery of forests in PNG after selective-harvesting (Shearman et al. 2009; Filer et al.
83 2010; Shearman et al. 2010). Studies elsewhere suggest that species differences in wood
84 density are an important consideration in assessing rates of carbon sequestration in
85 tropical regrowth forests (Enquist et al. 1999; Malhi et al. 2004). Other disturbances have
86 also been important in PNG forests. In 1997 and 1998, the 20th century's most intense El
87 Niño Southern Oscillation (ENSO) event provoked severe droughts across equatorial
88 tropical forests which induced forest fires and severely affected C stock (Nepstad et al.
89 2004). Catastrophic mortality events such as fires drive tropical forest structure and
90 dynamics (Connell 1978; Johns 1986, 1989), and their impact needs further investigation
91 (Phillips et al. 2004).

92 Tropical forests play a crucial role in the global C cycle through the storage and
93 sequestration of C in living forest biomass. This has been recognised in international
94 climate change negotiations with the initiative to include reduced CO₂ emissions from
95 deforestation and forest degradation (REDD+) coupled with the enhancement of forest C
96 stocks through forest restoration, sustainable forest management and forest conservation
97 in developing tropical countries (UNFCCC 2009). REDD+ can potentially offer
98 economic, environmental and social benefits with the intersection of carbon markets,

99 climate and environmental protection and, if implemented appropriately, could provide
100 wider social and economic opportunities for indigenous people.

101 PNG has over 28 M ha of tropical forests which have been subject to a high rate
102 of conversion due to timber harvesting and agriculture (Shearman et al. 2008, Filer et al.
103 2009), and has therefore become a focus of REDD+ initiatives. However, significant
104 policy, institutional and technical challenges need to be overcome before REDD+
105 becomes operational. Technical challenges include: estimation of forest C stock in
106 different forest stratum (Gibbs et al. 2007; Fox et al. 2010); change in these stocks due to
107 forest harvesting (Kauffman et al. 2009) and forest fires (Phillips et al. 2004); and
108 estimating rates of C sequestration in primary and regenerating forests across the forest
109 estate (Olander et al. 2008). Purchasers of reduced emission credits (whether they be
110 international organisations, other countries or corporate entities) will require assurance
111 that estimates of C stock, C sequestration, and reductions in net CO₂ emissions are
112 accurate and precise. All these challenges have high scientific currency given the urgency
113 of climate change mitigation coupled with the loss of biodiversity associated with
114 deforestation and degradation in the tropics (Venter et al. 2009).

115 Given the importance of discussions on the global carbon balance and the climate
116 mitigation potential of tropical forests, there is a need to identify improved statistical
117 approaches that go beyond simply averaging across datasets and constructing 95% CIs.
118 One of the challenges with statistical analysis of PSP data is autocorrelation between
119 measurements. Autocorrelation eventuates when spatial, temporal, or hierarchical
120 variation cannot be captured by deterministic model structures (such as a simple mean)
121 reducing estimation efficiency and biasing hypothesis tests on estimated parameters or

122 inferences on the average such as a 95% CI (Fox et al. 2001). It is likely that
123 autocorrelation is pervasive in models of forest C stock and sequestration, as they are
124 parameterised using data that has an implicit hierarchical structure; trees are nested
125 within plots which are repeatedly measured through time and/or space. Furthermore,
126 studies have observed strong spatial and temporal variation in C stocks (Rolin 2005;
127 Malhi and Wright 2004); however, examination of the literature reveals that these
128 variations are rarely accounted for. This is significant given that these models are being
129 used to estimate the C balance of forests and more recently, as quantitative input to
130 forest-based climate change mitigation initiatives.

131 Hierarchical Bayesian models (HBMs) can facilitate the explicit modeling of
132 autocorrelation (Clark 2005; Clark and Gelfand 2006; Cressie et al. 2009). The objective
133 of this study is to test the HBM approach for modelling forest C stock and sequestration
134 in PNG's forests.

135 **Materials and Methods**

136 *PNGFRI Permanent Sample Plots*

137 The PNG Forest Research Institute (PNGFRI) established a system of PSPs in the
138 early 1990s, some in forest immediately after selective-harvesting, and others in primary
139 forest across PNG (Figure 1). Plot measurements spanned the ENSO event which induced
140 fires in many lowland tropical forests in PNG in 1997 and 1998 (Barr 1999). The same
141 ENSO event was observed to cause drought and increased tree mortality in Sarawak
142 (Nakagawa et al. 2000), and in the Amazon (Cochrane et al. 1999; Laurance et al. 2004).
143 These PSPs are described in detail elsewhere (Fox et al. 2010). In summary, the PSPs
144 consist of 133, 1 ha (100 m x 100 m) plots, a majority of which (121) were established in

145 selectively-harvested forests, while 12 plots were established in primary forests. To
 146 supplement our limited sample in primary forest we included an additional 22
 147 measurements of aboveground C as collated by Bryan et al. (2010). In total, we used 411
 148 measurements of aboveground C in selectively-harvested forests and 44 measurements in
 149 primary forest.

150 Figure 1 near here

151 Aboveground live biomass (AGLB) was estimated using the method of Fox et al.
 152 (2010) and the wet forest allometry of Chave et al. (2005). For tree i , we denoted D_i the
 153 diameter in centimeters (cm), H_i the total height in meters (m), and q_i the wood specific
 154 gravity in grams per cubic centimeter (g cm^{-3}) derived from Eddowes (1977). For plot j
 155 at date d , we denoted I_{jd} the total number of trees with $\text{DBH} \geq 10$ cm and we computed
 156 AGLB_{jd} , the aboveground living biomass (Eqn. 1). Consistent with previous studies,
 157 AGLB will be reported in megagrams per hectare (Mg ha^{-1}). For further details of the
 158 error correction methodology and biometric modelling used to estimate AGLB, refer to
 159 Fox et al. (2010).

$$160 \quad \text{AGLB}_{jd} = \sum_{i=1}^{I_{jd}} \left[0.0776 \times (q_i D_i^2 H_i)^{0.94} \right] \quad (1)$$

161 The C content of biomass is reported assuming that dry biomass is 50% C (Clark
 162 et al. 2001a, Houghton et al. 2001, Malhi et al. 2004). We then computed C_{jd} , the carbon
 163 stock of plot j at date d and applied a multiplier (1.1) to estimate the contribution of
 164 stems with $\text{DBH} < 10$ cm (Fox et al. 2010) (2).

$$165 \quad C_{jd} = \frac{1}{2} (\text{AGLB}_{jd}) \times 1.1 \quad (2)$$

166 Details of allometry and AGLB calculations for supplementary primary forest
167 data can be found in Bryan et al. (2010). Note that Bryan et al. (2010) also used the
168 allometry of Chave et al. (2005) to estimate aboveground biomass. To make
169 measurements from Bryan et al. compatible with the PSPs, the AGLB component of C
170 stock is identified using the multiplier 0.88 for lowland and 0.78 for montane forest
171 (Bryan et al. 2010).

172 *Hierarchical Bayesian model for C dynamics*

173 We modelled C stock and sequestration using a hierarchical state-space Bayesian
174 model (Cressie et al. 2009). We benchmark all sequential measurements using a starting
175 date t_0 which corresponds to either the first measurement for primary (undisturbed) plots
176 or the date of disturbance (selective-harvesting or 1998 for fire affected plots) for
177 disturbed plots. Benchmarking plots in this way we can test for differences in the C stock
178 and C sequestration rates for the three types of plots. We use random plot effects to
179 account for the hierarchical structure of the data, and to incorporate year of measurement
180 as a random effect to account for temporal autocorrelation.

181 We use the notation $N(\mu, V)$ to define the Normal distribution with mean μ and
182 variance V and the notation $IG(s, r)$ to defined the Inverse-Gamma distribution with
183 shape s and rate r . We assumed that C_{jd} was normally distributed, with variance σ^2
184 and with mean equal to a linear function of t with intercept a and slope b . The intercept
185 a indicated the initial C stock, while the slope b indicated the sequestration rate reported
186 in megagrams C per hectare per year ($\text{MgC ha}^{-1}\text{yr}^{-1}$) (3).

$$187 \quad C_{jd} \sim N(a_j + b_j t, \sigma^2) \quad (3)$$

188

189 *The full model (Model 1)*

190 We fitted a full model (denoted Model 1) inclusive of (i) fixed effect $\alpha_{\{a,b\},S}$ for plot
191 status S ($S = P$ for primary forest, H for selectively-harvested and B for burnt plots) on
192 both the slope b and the intercept a , (ii) fixed effect $\gamma_{\{a,b\},\{A,T,R\}}$ for altitude A , mean
193 annual temperature T and annual rainfall R on both the slope and the intercept, (iii) plot
194 random effects $\beta_{\{a,b\}}$ on both the slope and the intercept, and (iv) annual random
195 effects δ_a on the year of measurement for temporal autocorrelation. Elevation,
196 temperature and precipitation were derived from the global high resolution climate
197 surfaces of Hijmans et al. (2005) and were normalized using the function
198 $f(x) = [x - E(x)]/[SD(x)]$ in order to facilitate Markov Chain Monte Carlo (MCMC)
199 convergence.

200 The intercept a and slope b for Model 1 can be defined as follows;

$$201 \quad a_j = \alpha_{a,S} + \beta_{a,j} + \gamma_{a,A}f(A) + \gamma_{a,T}f(T) + \gamma_{a,R}f(R) + \delta_{a,d} \quad (4)$$

$$202 \quad b_j = \alpha_{b,S} + \beta_{b,j} + \gamma_{b,A}f(A) + \gamma_{b,T}f(T) + \gamma_{b,R}f(R) \quad (5)$$

203 We assumed a hierarchical structure for the model defining first-level priors for the plot
204 random effects: $\beta_{\{a,b\}} \sim N(0, V_{\{a,b\},\beta})$ and for the annual random effects: $\delta_{a,d} \sim N(0, V_{a,\delta})$.
205 Second-level priors were assumed to be non-informative with large variances. For
206 parameters denoted $\alpha : \alpha \sim N(0, 1.0 \times 10^6)$, for parameters denoted $\gamma : \gamma \sim N(0, 1.0 \times 10^6)$,
207 for variance parameters denoted V and $\sigma^2 : V, \sigma^2 \sim IG(1.0 \times 10^{-3}, 1.0 \times 10^{-3})$.

208 *Model fitting*

209 Conditional posterior for each parameter was obtained using a Gibbs sampler (Gelfand
210 1990) available through the JAGS software ([http://www-](http://www-fis.iarc.fr/~martyn/software/jags/)
211 [fis.iarc.fr/~martyn/software/jags/http://www-fis.iarc.fr/~martyn/software/jags/](http://www-fis.iarc.fr/~martyn/software/jags/)). We ran
212 two MCMC simulations of 200 000 iterations. The ‘burn-in’ period was set to
213 100 000 iterations and the ‘thinning’ to 1/200. We then obtained 1 000 estimations for
214 each parameter. We checked chain convergence using the Gelman Rubin statistic
215 (Gelman 2003).

216 *Model comparison*

217 We compared the full Model (Model 1) with two simpler models, denoted Model 2 and
218 Model 3. Model 2 included only (i) fixed effects $\alpha_{\{a,b\},S}$ of plot status S on the slope
219 and intercept and (ii) random plot effects $\beta_{\{a,b\}}$ on the slope and the intercept. In Model
220 2 covariates for Altitude, Precipitation and Temperature were not included, and neither
221 was the random effect on the year of measurement. Model 3 included only fixed effects
222 $\alpha_{\{a,b\},S}$ of the plot status S on the slope and intercept. Model 3 did not include any
223 random effects and is analogous to a classical approach.

224 The DIC (Deviance Information Criterion) was used to compare models. The DIC is the
225 sum of the mean deviance (with Deviance = $-2 \log(\text{Likelihood})$) and the number of
226 parameters pD. A difference of more than 10 is taken as a rough index of difference
227 between two models and rules out the model with the higher DIC (Spiegelhalter 2002).
228 When DIC difference is less than 10, the best model is the one with the lower number of
229 parameters pD, in accordance with the parsimony principle.

230 *Parameter significance*

231 From the posterior distribution of each parameter, we computed a credible 95%
232 confidence interval. If the interval included zero, we assumed that the parameter was not
233 significantly different from zero.

234 *Predictive posterior of the carbon stock*

235 We computed the predictive posterior π of $c(t)$, the carbon stock at time t (6). The
236 predictive posterior included variability in the process (e.g. plot variability) and
237 parameter uncertainty. We denoted Θ the vector of parameters.

238
$$\pi(C(t)) = \int_{\Theta} \pi(C(t)|\Theta)\pi(\Theta)d\Theta \quad (6)$$

239 **Results**

240 *PNG PSP data structure*

241 There were a range of trends in C stock observed on the PSPs. For example, there was an
242 exponential trend for Giluwe01 and Oomsi02 (Figure 2); a concave curvature with
243 increasing sequestration after disturbance for Pasma01 and Umbuk01; and a linear trend
244 for Mokol01 and Wasap01. Some PSPs exhibited high rates of C sequestration (above 3
245 MgC ha⁻¹yr⁻¹; Wasap01, Mokol01, Oomsi02), while others (Giluw01, Pasma01,
246 Umbuk01) indicated lower rates below 1.7 MgC ha⁻¹yr⁻¹. A simple linear model was
247 found to provide the best generalised fit for C stock change.

248 Figure 2 near here

249 PSPs that were affected by ENSO induced fires in 1997/1998 generally had reduced C
250 stock in live biomass in subsequent measures due to mortality; some PSPs recovered

251 from fire (UMBOI01, WCOST04, VAILA02), while other PSPs continued to degrade
252 after fire (KAPUL02, IVAIN02, ORLAK01, Figure 3).

253 Figure 3 near here

254 To examine mean trends and variability in the PNG PSP data we constructed a graph
255 (Figure 4) with measurements benchmarked against either the first measurement for
256 primary plots or the date of disturbance (selective-harvesting or 1998 for fire affected
257 plots) for disturbed plots.

258 Figure 4 near here

259 C stock and sequestration is highly variable across the PSPs. C stock in primary forest
260 PSPs is generally (but not uniformly) higher than in selectively-harvested and burnt PSPs.

261 C sequestration is generally positive on selectively-harvested PSPs and negative on PSPs
262 burnt in 1997 or 1998 (Figure 4).

263 *HBM Model selection*

264 The estimated variation (assessed using DIC) is equivalent for models 1 and 2, which
265 both include random effects, but is far larger for Model 3, which only includes fixed
266 effects (Table 1). Despite having the same DIC, Model 2 is superior to Model 1 because
267 it is more parsimonious, having fewer parameters ($pD=210$). None of the parameters for
268 Altitude, Rainfall and Temperature, nor random effects on the year of measurement
269 (temporal autocorrelation), were significantly different to zero. Therefore Model 2 was
270 the preferred model for estimating C stock and sequestration.

271 Table 1 near here

272 *Parameter estimates*

273 Table 2 and Figure 5 near here

274 The HBM approach was used to determine C stock at t_0 and the average C sequestration
275 across re-measurements for primary, harvested and ENSO burnt PSPs (Table 2 and
276 Figure 5). C stock in primary forest ($137 \pm 9 \text{ MgC ha}^{-1}$) is significantly higher than in
277 harvested ($62 \pm 18 \text{ MgC ha}^{-1}$) and burnt ($70 \pm 26 \text{ MgC ha}^{-1}$) forest (Table 2). C
278 sequestration in harvested forest ($1.12 \pm 3.41 \text{ MgC ha}^{-1}\text{yr}^{-1}$) is higher than C sequestration
279 in primary forest (0.23 ± 1.70), but neither were significantly different to zero. C
280 sequestration in burnt forest (-6.87 ± 3.98) is significantly negative. If we assume that
281 primary and selectively-harvested forest C stock are representative averages across forest
282 types and regions, then the change in C stock due to selective-harvesting (ΔC_{SH}) is on
283 average 75 MgC ha^{-1} (55%). We can construct an additive 95% CI for ΔC_{SH} as 75 ± 25
284 MgC ha^{-1} (or $55\% \pm 18\%$)

285 There was a significant variance in the plot random effect for both the intercept (C
286 stock at t_0 ; $V_{a,\beta} = 641.4$) and the slope (C sequestration rate; $V_{b,\beta} = 1.29$) indicating that
287 plot to plot variation in C stock at t_0 and C sequestration was high. The insignificance of
288 covariates for temperature, rainfall, and altitude suggest that this was not driven by
289 environmental conditions, but rather differences in forest types and species composition
290 and the degree of disturbance from selective-harvesting or fire.

291 Comparing confidence intervals for the parameters (Table 2) when random plot
292 effects are included (Model 2) and excluded (Model 3) indicates that confidence intervals
293 are narrower for all parameters for Model 3. This creates a false impression of precision
294 in parameter estimates. When hierarchical variability is included in Model 2, confidence
295 intervals that reflect the true precision of parameter estimates result. Model 2 also
296 explained far more variability in the data as indicated by the lower deviance (Table 1).

297 This is due to the high plot to plot variability in the intercept and slope which is captured
298 using random parameters.

299 **Discussion**

300 Selective-harvesting results in the displacement of living forest biomass to non-
301 living biomass, a component of which is taken off site as wood products with the
302 remaining displacement termed collateral damage and becoming decomposing residue on
303 the forest floor (Blanc et al. 2009). Collateral damage in tropical forest harvesting can be
304 large and consists of crown material, peripheral trees that are damaged during tree felling
305 and that subsequently die, and tree boles used for bridge, road and deck construction
306 (Johns et al. 1996; Feldpausch 2005). The enhanced pool of decomposing residue
307 resulting from collateral damage in disturbed forest can be a significant source of CO₂
308 emissions (Keller et al. 2004, Feldpausch 2005).

309 Although our sample of primary forest plots is small, we can estimate the change
310 in C stock due to selective-harvesting ($75 \pm 25 \text{ MgC ha}^{-1}$). This provides an estimate of
311 the displacement of living aboveground biomass to collateral damage and wood products.
312 However, our comparison is unbalanced and unmatched; we have far more observations
313 in selectively-harvested forest, and plots were not designed for this comparison; matched
314 plots in adjoining primary and selectively-harvested forest would provide a more valid
315 comparison. Nevertheless, an initial estimate of 55% reduction in AGLB could be a
316 useful indicative figure for calculations of reductions in forest C due to commercial
317 selective-harvesting in PNG. Similar reductions have been observed elsewhere, with
318 surprising consistency; Lasco et al. (2006); Tangki and Chappell (2008); Feldpausch et

319 al. (2005); and Gerwing (2002) all observed 50% reductions in AGB in the Philippines,
320 Borneo, Southern Amazon, and Brazilian Amazon respectively.

321 Estimated change in C stock due to selective-harvesting can be used for
322 preliminary national estimates of harvesting related emissions. PNG Forest Authority
323 estimate that the area subject to selectively-harvesting between 1961, when commercial
324 selective-harvesting commenced, and 2002 is approximately 3.4 million (M) hectares
325 (PNGFA 2007). Based on our estimate of C reduction due to harvesting this equates to a
326 total and average annual displacement of 255 ± 85 MtC and 6 ± 2 MtC yr⁻¹ from living to
327 non-living AGB respectively. Over this period approximately 43 M m³ of logs have been
328 removed from PNG's native forests (Bank of PNG (various); SGS (various)). If we
329 assume 33% recovery of raw logs into timber products, and an average wood density of
330 0.58 g cm^{-3} (Fox et al. 2010), then approximately 5 MtC will have been stored in timber
331 products over this time. By this supposition, approximately 250 ± 85 MtC is either
332 collateral damage left in the forest to decompose or is sawmilling residue. Decomposition
333 of biomass in tropical forests occurs rapidly with woody material completely decomposed
334 with the C fraction emitted as CO₂ after 15 years (Keller et al. 2004; Chambers et al.
335 2000). Assuming complete decomposition of collateral damage and sawmilling residue
336 (which is often combusted), approximately 917 ± 312 Mt CO₂ has been emitted due to
337 selective-harvesting in PNG between 1961 and 2002. The year to year variability in
338 emissions will be high due to variability in the rate of timber harvesting, particularly over
339 the last 10 years (Bank of PNG 2009).

340 There is high variability in previous estimates of C sequestration in secondary
341 tropical forest. Some studies indicate less than $2.5 \text{ MgC ha}^{-1}\text{yr}^{-1}$ (Brown and Lugo 1990);

342 while others indicate sequestration of between 7.5 and 10 MgC ha⁻¹yr⁻¹ (Hughes et al.
343 1999; Scatena et al. 1996); with many studies falling in the middle of this range with
344 sequestration between 2.5 and 7.5 MgC ha⁻¹yr⁻¹ (Fehse et al. 2002; Uhl and Jordan 1984).
345 Many of these studies were for heavily disturbed forest in early successional phases
346 where sequestration is dominated by the growth of pioneers (Fehse et al. 2002). Our
347 analysis included species-specific wood densities (Fox et al. 2010) to capture the true C
348 contribution of low wood density pioneers (Baker et al. 2004a). A very large 95% CI (\pm
349 3.41) on the parameter indicated similar variability in C sequestration after selective-
350 harvesting, possibly due to variation in successional stage, forest type, level of
351 disturbance, edaphic conditions and the climatic regime in the period following
352 disturbance. On average, observed C sequestration in regrowth in PNG was at the lower
353 end of the range described above (1.12 ± 3.41 MgC ha⁻¹yr⁻¹, generally below 5 MgC ha⁻¹
354 yr⁻¹). This may be due to the lower levels of disturbance relative to secondary forest
355 resulting from agriculture. Selective-harvesting will have resulted in variability in
356 successional stages between, and also within, the large one hectare PSPs. Gaps created
357 due to selective-harvesting will experience regeneration that can result in high
358 sequestration, while undisturbed areas of latter successional forest may experience little C
359 sequestration, or even negative sequestration due to mortality (Feeley et al. 2007). We
360 also need to be mindful of a possible bias in our sample of secondary forest toward forest
361 that contains future merchantable timber; heavily harvested secondary forest may have
362 been avoided (Fox et al. 2010).

363 The PSPs represent a valuable sample of selectively-harvested forest in the
364 Oceania region with good spatial and temporal representation (Fox et al. 2010). We

365 contend therefore that the average sequestration ($1.12 \text{ MgC ha}^{-1}\text{yr}^{-1}$), despite high
366 uncertainty (± 3.41), is a sound estimate for C recovery rates after selective-harvesting. If
367 we assume that the 3.4 M ha harvested between 1961 and 2002 is harvested at the annual
368 rate of 0.083 M ha, then the net C sequestered since harvesting began can be calculated as
369 $(41*1.12*0.083 + 40*1.12*0.083 + 39*1.12*0.083 \dots + 1*1.12*0.083)$ and is
370 approximately equal to 80 MtC or 294 MtCO₂ over this period. If we include parameter
371 uncertainty in this estimate the 95% CI for sequestered C is 80 ± 244 MtC. Despite this
372 high uncertainty, if the average sequestration occurred across selectively-harvested forest
373 it would offset approximately one third of the emissions from decomposition of collateral
374 damage and sawmilling residue (917 MtCO₂).

375 The observed uptake of C by primary tropical forests (Phillips et al. 1998) has
376 become a point of contention in recent years (Clark 2001b; Wright 2005). Results for the
377 limited number of plots in this study indicated a mean sequestration rate in primary forest
378 of $0.23 \pm 1.57 \text{ MgC ha}^{-1}\text{yr}^{-1}$. This figure is lower than biome averages for primary forest
379 ($0.44 \text{ MgC ha}^{-1}\text{yr}^{-1}$, Phillips et al. (1998); $0.61 \text{ MgC ha}^{-1}\text{yr}^{-1}$, Baker et al. (2004b)). These
380 higher than expected C sequestration rates for primary forest have led several authors to
381 suggest a pervasive alteration of primary tropical forest dynamics from global
382 environmental changes such as increased atmospheric CO₂ (Phillips et al. 1998; Baker et
383 al. 2004b; Lewis et al. 2009). Our limited sample suggests that PNG's primary forests are
384 not a net C sink, however, more samples are required to verify this.

385 The ENSO event of 1997/1998 caused a drying out of lowland tropical forests in
386 PNG, with large-scale wildfires causing widespread tree mortality. The estimated annual
387 C emission in AGLB after this event is $-6.87 (\pm 3.98) \text{ MgC ha}^{-1}\text{yr}^{-1}$. Balch et al. (2008)

388 report a similar loss of AGLB of $-8.5 \text{ MgC ha}^{-1}\text{yr}^{-1}$ for a large-scale fire experiment in
389 Amazonian forests. Some of the PSPs in this study were measured for 10 years after
390 ENSO-induced fires, and indicated that ΔC_B is ongoing with net C emissions 10 years
391 after the fire disturbance. Shearman et al. (2008) estimate that 350,000 ha has been
392 affected by fire between 1972 and 2002. Assuming that fire impacts the forest C dynamic
393 for 10 years, then emissions from fire affected forest over this period are approximately
394 $24 \pm 14 \text{ MtC}$ or $88 \pm 51 \text{ MtCO}_2$. Considering that ENSO events are predicted to become
395 more frequent and more severe under climate change, the significant emissions as
396 observed here have implications for global C cycles.

397 There has been speculation (Shearman et al. 2009) that PNG's secondary forests
398 are degraded to the extent that they are incapable of recovery. The present study suggests
399 otherwise, indicating that selectively-harvested forests are reasonably stocked after
400 harvesting ($62 \pm 18 \text{ MgC ha}^{-1}$), and are recovering C at the rate of $1.12 \pm 3.41 \text{ MgC ha}^{-1}$
401 yr^{-1} . The high variability indicates that some plots are degrading but the bulk of plots are
402 either maintaining or increasing biomass and carbon stock. If the average sequestration
403 rate is maintained at a linear rate, it would take approximately 65 years for harvested
404 forest to recover the 75 MgC ha^{-1} that was displaced during selective-harvesting.

405 We have used HBM model parameters inclusive of valid parameter uncertainties
406 for some initial estimates of CO_2 emissions from harvesting and fires. These estimates
407 can provide a quantitative basis for forest C accounting systems for PNG, and constitute
408 country specific information required for Tier 3 compliant greenhouse gas inventories of
409 forested land (IPCC 2006). Analysis of carbon dynamics in PNG forests can be based on
410 these estimates, published carbon book-keeping methods (e.g. Ramankutty et al. 2007;

411 Blanc et al. 2009) and elements of the Voluntary Carbon Standard (VCS 2008) to
412 construct an appropriate forest C accounting system for PNG. Note that the initial
413 emission estimates detailed in this paper include only aboveground C dynamics. A full C
414 account would need to be inclusive of under-storey plants, lianas and vines, woody
415 debris, litter, coarse and fine roots and soil C (Blanc et al. 2009).

416 In this study, hierarchical autocorrelation was highly significant due to high plot
417 to plot variability in both the intercept (C stock at t_0) and the slope (C sequestration).
418 This has important implications for carbon dynamic models. Deterministic model
419 structures fail to effectively explain these plot to plot differences, despite the inclusion of
420 environmental variables (altitude, rainfall, and temperature). Explaining structural
421 complexity and temporal variability in tropical forests is an ongoing scientific challenge
422 (Chambers et al. 2001). As our understanding of this complexity improves there will be
423 opportunities to include covariates in deterministic model structures that better explain
424 site to site and plot to plot variability. Until this occurs it seems prudent to use model
425 structures, such as HBM, that account for high site to site variability.

426 The HBM model structure used in this study has several advantages over
427 reporting averages and 95% confidence intervals. It avoided the presence of
428 autocorrelation in model residuals that result in biased estimates of standard errors of
429 parameter estimates (Johnston 1972), and bias in inference on averages or parameter
430 estimates such as 95% CIs. When we excluded plot level random effects (in Model 3) the
431 CIs for different parameters were considerably lower, creating a false impression of
432 precision. This is statistically well known. When positive autocorrelation is present
433 among residuals located on the same sampling unit (for example; several remeasurements

434 of a plot) then parameter CIs will be underestimated and hypothesis tests on the
435 significance will be biased upwards and the type I error rate will be inflated, i.e. too often
436 it will be concluded that the value is different from zero. Inferences on the parameters
437 and averages are particularly important in light of controversies on the C balance of
438 tropical forests. Many studies that have observed significant net C sequestration in
439 primary tropical forest have failed to account for autocorrelation resulting from
440 hierarchical data structures. When autocorrelation is incorporated, estimation efficiency
441 is improved, as each measurement is bringing information to the model, independent of
442 other measurements. Efficiency considerations are important in light of the cost of
443 tropical forest census. Given the importance of discussions on the global carbon balance
444 and the climate mitigation potential of tropical forests, we need improved statistical
445 methodology such as hierarchical Bayesian models which are more appropriate for
446 tropical forest data from repeated plot measurements.

447 In conclusion, we have reported defensible estimates of aboveground C and C
448 sequestration in primary, selective-harvested, and ENSO burnt forest using a HBM.
449 These estimates have improved our understanding of the forest C cycle in PNG, and
450 provide quantitative inputs for climate change mitigation initiatives such as REDD+.

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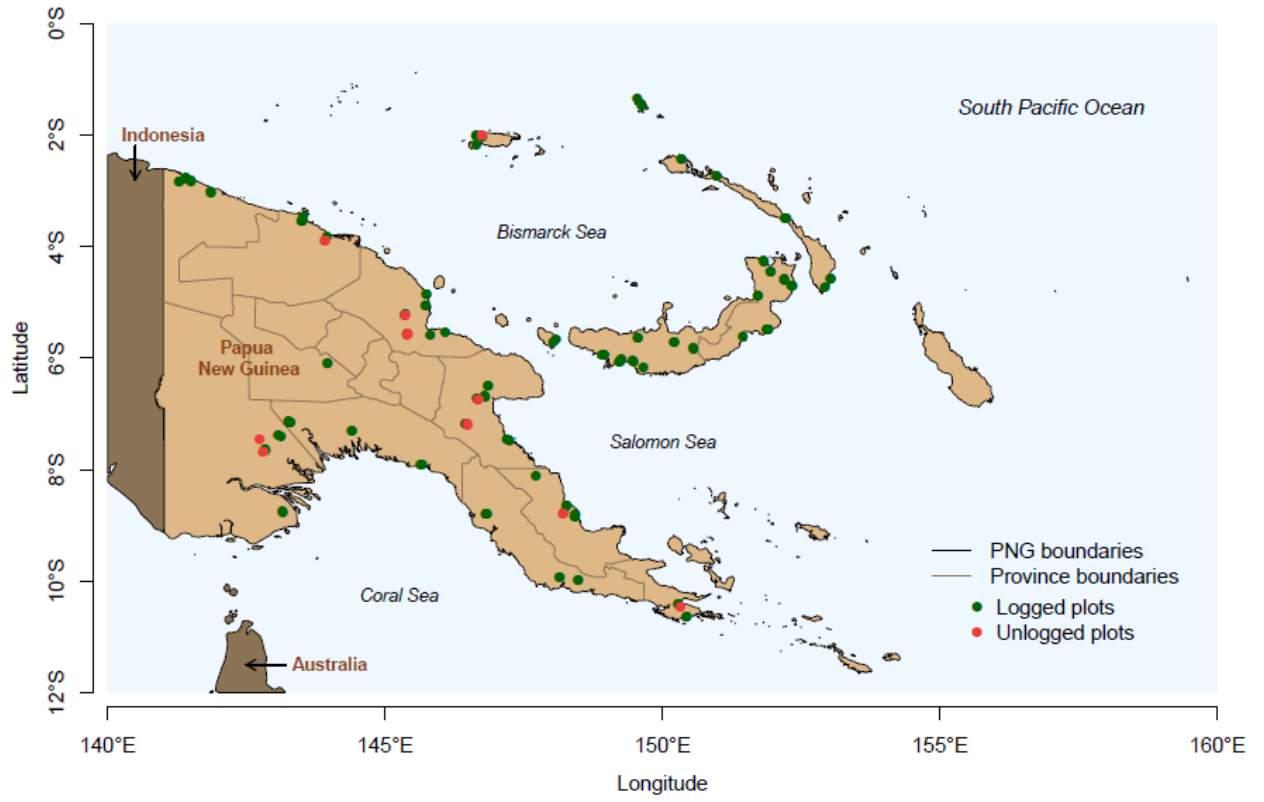
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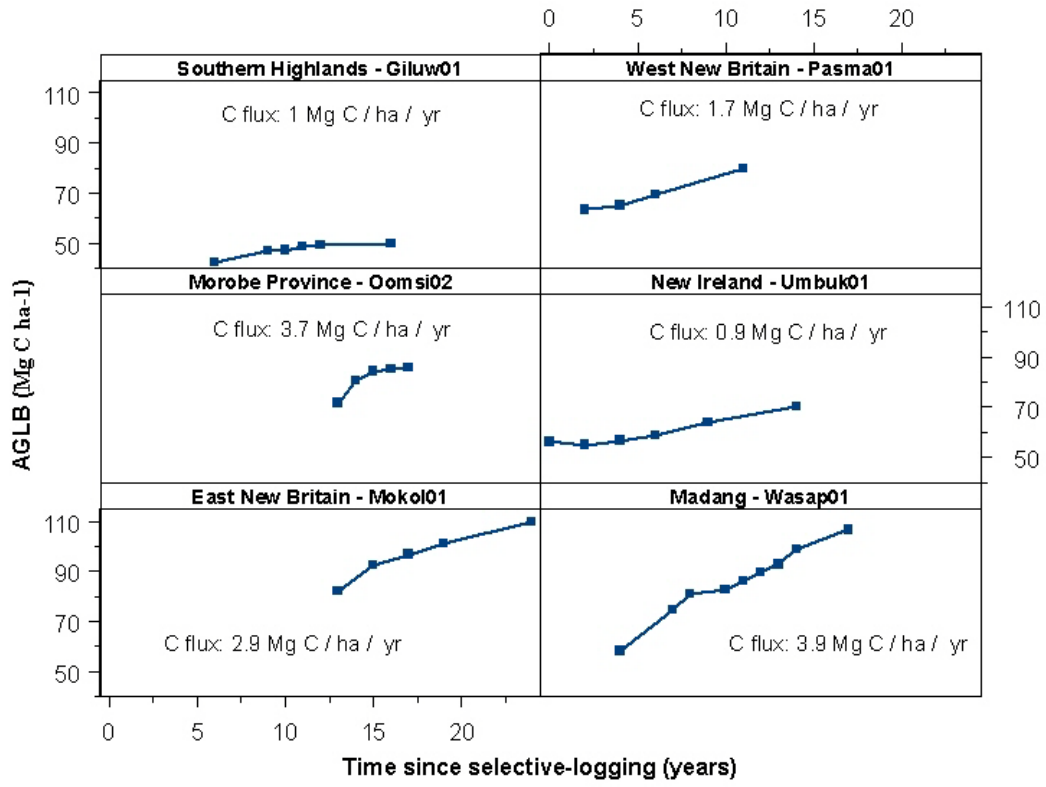
693 Figure 1
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697 Figure 2

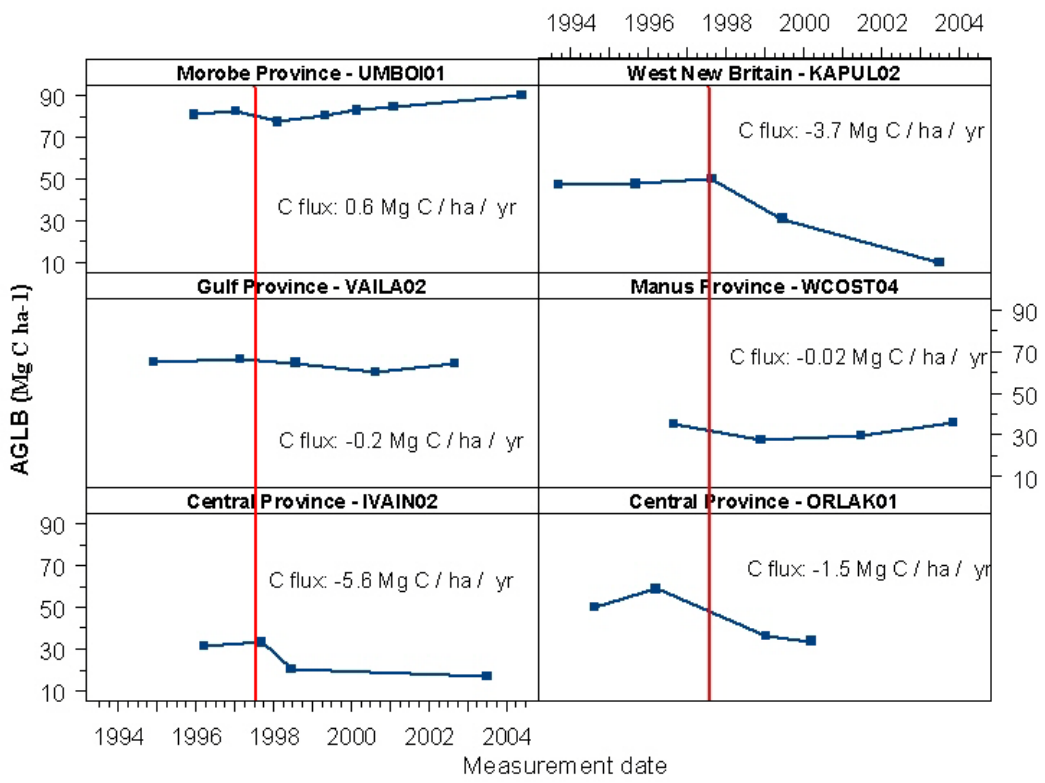


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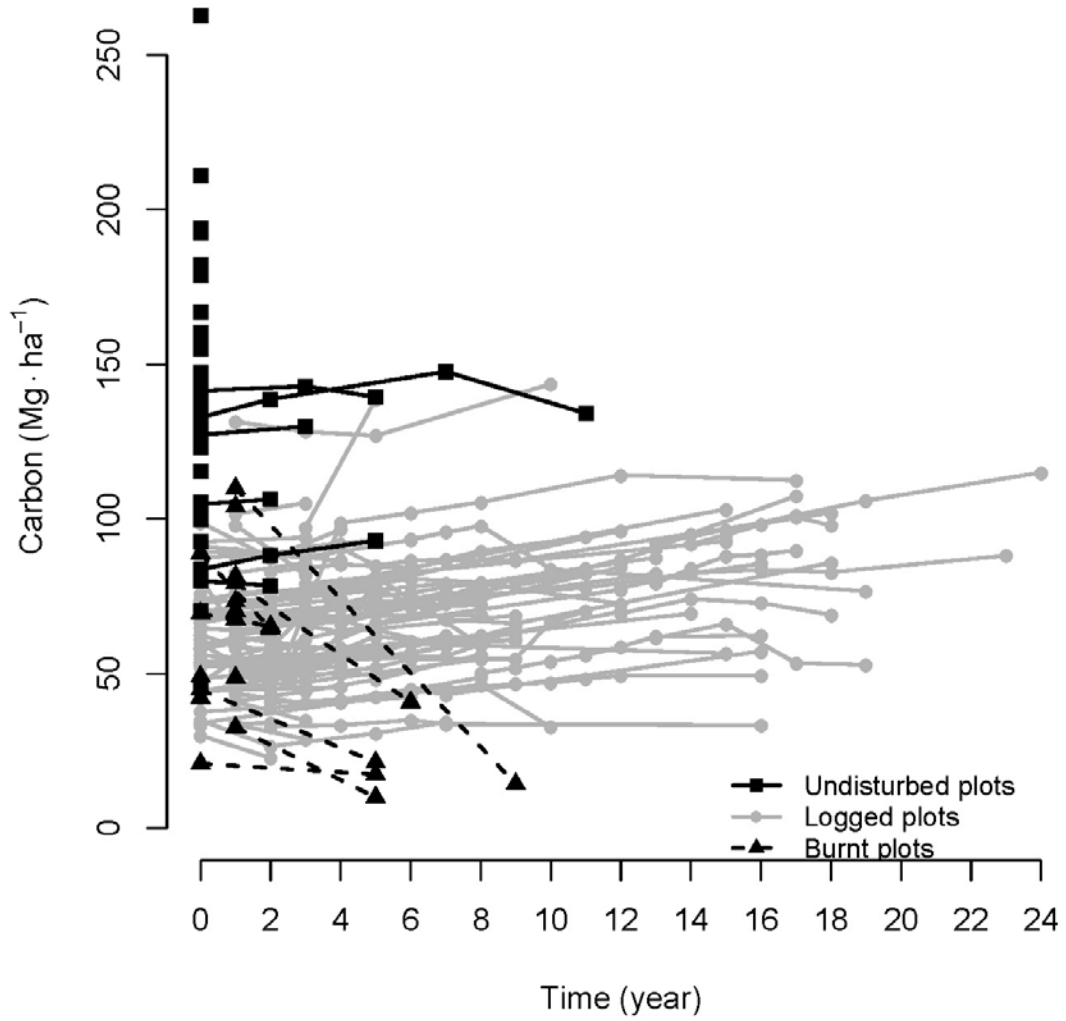
701 Figure 3



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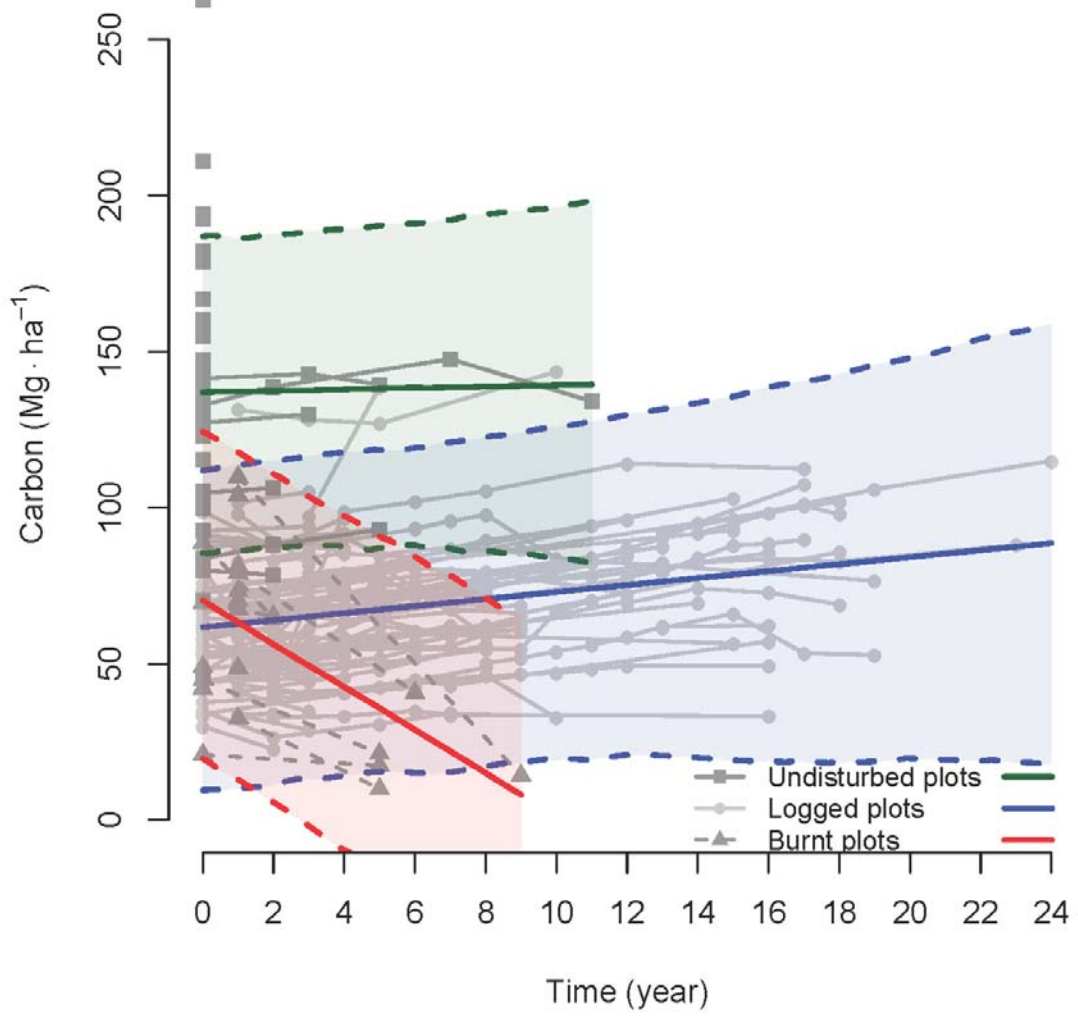
704 Figure 4



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707 Figure 5



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710 Figure Legends

711 Figure 1. Spatial distribution of PNGFRI PSPs across PNG

712 Figure 2. Trends in C stock after selective-harvesting

713 Figure 3. Trends in C stock for plots affected by ENSO induced fires of 1997 and 1998

714 Figure 4. PNG PSP data structure

715 Figure 5. Predicted posterior for Model 2 with 95% confidence intervals inclusive of

716 random plot variability on the intercept and slope

717

718

719 Table 1. Model comparison

	Deviance	pD	DIC
Model 1	2762	217	3060
Model 2	2777	210	3060
Model 3	4100	7	4107

720

721

722 Table 2. Parameter estimates for Model 2

Parameter	Explanation	Parameter estimate	95% CI	
			M2*	M3**
α_P	C stock t_0 – Primary	137.00 [#]	± 8.62	± 6.90
α_H	C stock t_0 – Harvested	61.74 [#]	± 18.34	± 7.53
α_B	C stock t_0 – Burnt	70.17 [#]	± 25.93	± 13.91
b_P	C sequestration - Primary	0.23	± 1.70	± 1.11
b_H	C sequestration - Harvested	1.12	± 3.41	± 2.93
b_B	C sequestration - Burnt	-6.87 [#]	± 3.98	± 3.10
$V_{a,\beta}$	Variance on plot random effect on intercept	641.40 [#]	± 140.17	
	Variance on plot random effect on slope	1.29 [#]	± 0.85	
σ^2	Variance	30.92 [#]	± 6.26	± 63.47

723 # Parameter estimate is significantly different to zero *Credible 95% confidence interval

724 CI for Model 2 inclusive of random plot effects **95% for Model 3 with no random

725 effects

