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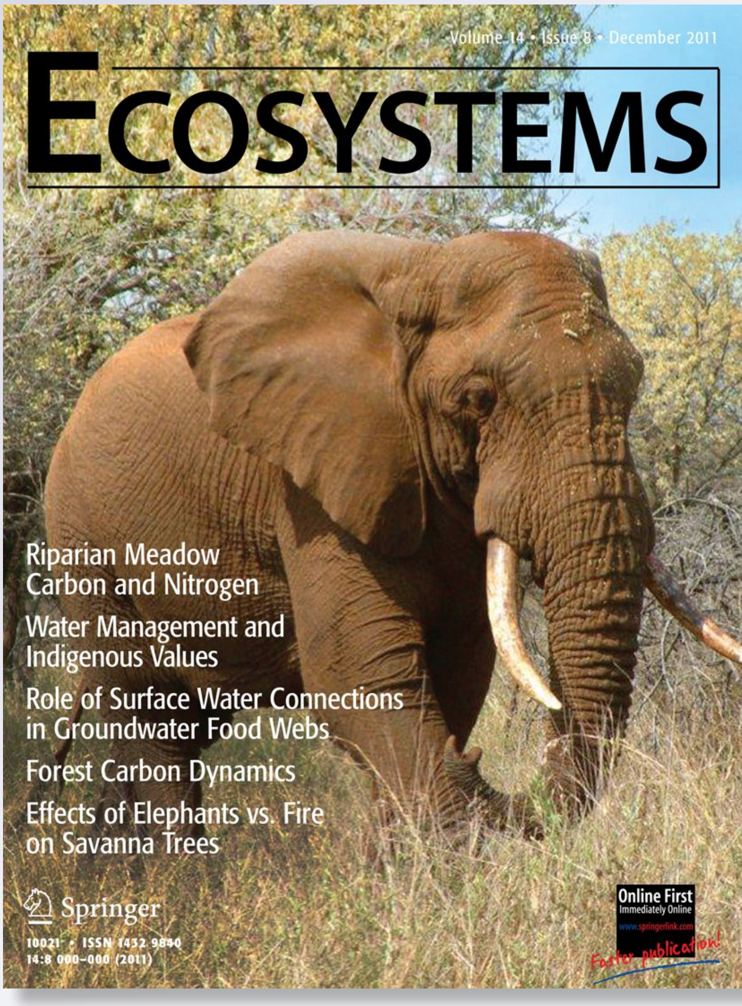

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Aboveground Forest Carbon Dynamics in Papua New Guinea: Isolating the Influence of Selective-Harvesting and El Niño

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Abstract

Assessment of forest carbon (C) stock and sequestration and the influence of forest harvesting and climatic variations are important issues in global forest ecology. Quantitative studies of the C balance of tropical forests, such as those in Papua New Guinea (PNG), are also required for forest-based climate change mitigation initiatives. We develop a hierarchical Bayesian model (HBM) of aboveground forest C stock and sequestration in primary, selectively harvested, and El Niño Southern Oscillation (ENSO)-effected lowland tropical forest from 15 years of Permanent Sample Plot (PSP) census data for PNG consisting of 121 plots in selectively harvested forest, and 35 plots in primary forest. Model parameters indicated: C stock in aboveground live biomass (AGLB) of 137 ± 9 (95% confidence interval (CI)) MgC ha^{-1} in primary forest, compared with 62 ± 18 MgC ha^{-1} for selectively harvested forest (55% difference); C sequestration in primary forest of 0.23 ± 1.70 MgC ha^{-1} y^{-1}, which was lower than in selectively harvested forest, 1.12 ± 3.41 MgC ha^{-1} y^{-1}; ENSO-induced fire resulted in significant C emissions (−6.87 ± 3.94 MgC ha^{-1} y^{-1}). High variability between PSPs in C stock and C sequestration rates necessitated random plot effects for both stock and sequestration. The HBM approach allowed inclusion of hierarchical autocorrelation, providing valid CIs on model parameters and efficient estimation. The HBM model has provided quantitative insights on the C balance of PNG's forests that can be used as inputs for climate change mitigation initiatives.

Key words: biomass; sequestration; degradation; selective-harvesting; REDD+; carbon; bayesian; hierarchical.

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Author Contributions: Julian C. Fox performed research, analyzed data, and wrote the paper. Ghislain Vieilledent contributed new methods and models, analyzed data and contributed to writing of the paper. Rodney J. Keenan conceived of the study and contributed to writing of the paper. Cossey K. Yosi and Joe N. Pokana were responsible for data collection, data analysis, and contributed to writing of the paper.

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Introduction

Tropical forests cover 10% of global land area but remain a scientific frontier due to structural and biological complexity and high temporal variability associated with complex successional processes (Chambers and others 2001). A constraint is the limited number of long-term studies quantifying tropical forest dynamics and the affects of anthropogenic and natural disturbances, such as harvesting and fire (Clark and others 2001b; Lewis and others 2009). Long-term studies, whilst difficult to maintain, especially in developing countries, are essential to the development and testing of hypotheses regarding processes and rates of ecological recovery following disturbance, both anthropogenic and natural (Taylor and others 2008). In this study, we report on a spatially and temporally extensive Permanent Sample Plot (PSP) network in the forests of Papua New Guinea (PNG) and examine the impact of selective-harvesting and the El Niño Southern Oscillation (ENSO)-induced fires on aboveground forest carbon (C) stock and C sequestration. To achieve this, we develop a hierarchical Bayesian model (HBM) and derive parameters that can be used to estimate the C and CO_2 balance of selective-harvesting, forest regeneration and degradation after fire, which are important inputs for climate change mitigation initiatives.

There is still considerable debate over carbon dynamics in primary tropical forests. Field measurements of C stock change suggest that primary tropical forests are a significant C sink (Phillips and others 1998; Baker and others 2004a). For example, Lewis and others (2009) examined C stock development for PSPs in Africa and reported that primary forest is on average sequestering C at the rate of 0.63 MgC ha^{-1} y^{-1} with a bootstrapped 95% confidence interval (CI) 0.22–0.94. The study of Lewis and others (2009) is consistent with other studies on the C balance of forests (Phillips and others 1998; Baker and others 2004a), in that they combine PSP measurements across time and space, and report an average and a 95% CI. This is despite studies observing strong spatial and site-based variability in C stock (for example Malhi and others 2006). Other authors suggest that primary forest should be in equilibrium with C sequestration in growth largely balanced by C emissions due to mortality and decomposition (Clark and others 2001b; Wright 2005; Sierra and others 2007). The role of recovering forest as a C source or a C sink remains poorly understood (Grassi and others 2008; Olander and others 2008; Ramankutty and others 2007), and there is a contention over the extent and recovery of forests in PNG after selective-harvesting (Shearman and others 2009; Filer and others 2009; Shearman and others 2010). Studies elsewhere suggest that species differences in wood density are an important consideration in assessing rates of carbon sequestration in tropical regrowth forests (Baker and others 2009; Malhi and others 2004). Other disturbances have also been important in PNG forests. In 1997 and 1998, the twentieth century's most intense ENSO event provoked severe droughts across equatorial tropical forests that induced forest fires and severely affected the C stock (Nepstad and others 2004). Catastrophic mortality events such as fires drive tropical forest structure and dynamics (Connell and Slatyer 1978; Johns 1986, 1989), and their impact needs further investigation (Phillips and others 2004).

Tropical forests play a crucial role in the global C cycle through the storage and sequestration of C in living forest biomass. This has been recognized with the international climate change mitigation initiative to reduce emissions from deforestation and forest degradation (REDD+) coupled with the enhancement of forest C stocks through forest restoration, sustainable forest management and forest conservation in developing tropical countries (UNFCCC 2009, 2010; Fox and others 2011b). Mitigation initiatives such as REDD+ can potentially offer economic, environmental and social benefits with the intersection of carbon markets, climate and environmental protection and, if implemented appropriately, could provide wider social and economic opportunities for indigenous people in developing tropical countries.

Papua New Guinea has approximately 33 million (M) ha of tropical forests (Shearman and others 2008), which have been subject to a high rate of conversion due to timber harvesting and agriculture (Shearman and others 2009; Filer and others 2009), and has, therefore, become a focus of REDD+ initiatives. However, significant policy, institutional and technical challenges need to be overcome before REDD+ becomes operational (Howes 2009; Melick 2010). Technical challenges include: estimation of forest C stock in different forest types (Gibbs and others 2007; Fox and others 2010); change in these stocks due to forest harvesting (Kauffman and others 2009) and forest fires (Phillips and others 2004); and estimating rates of C sequestration in primary and regenerating forests across the forest estate (Olander and others 2008). Fox and others (2010) presented a methodology for estimating forest C from PSPs, and reported the first estimates of forest carbon in lowland tropical forest in PNG. Bryan and others (2010) also reported estimates of forest carbon based on a range of data sources from PNG. However, it is the change in forest C pools over space and time and consequent emissions of carbon dioxide to, or removals from (uptake of C in living biomass), the atmosphere due to different land-use activities that are most important for REDD+ implementation (Gibbs and others 2007). Purchasers of reduced emission credits (whether they be international organizations, other countries or corporate entities) will require assurance that estimates of C stock, C sequestration and reductions in net CO_2 emissions are accurate and precise. All these challenges have high scientific currency given the urgency of climate change mitigation coupled with the loss of biodiversity associated with deforestation and degradation in the tropics (Venter and others 2009; Laurance and others 2011).

Given the importance of discussions on the global carbon balance and the climate mitigation potential of tropical forests, there is a need to identify improved statistical approaches that go beyond simply averaging across datasets and constructing 95% CIs. One of the challenges with statistical analysis of PSP data is autocorrelation between measurements. Autocorrelation results from spatial, temporal or hierarchical variation that is not captured by deterministic model structures (such as a simple mean) reducing estimation efficiency and biasing hypothesis tests on estimated parameters or inferences on the average such as a 95% CI (Fox and others 2001). It is likely that autocorrelation is pervasive in models of forest C stocks and sequestration, as they are parameterized using data that have an implicit hierarchical structure; trees are nested within plots, which are repeatedly measured through time and/or space. Furthermore, studies have observed strong spatial and temporal variation in C stocks (Malhi and Wright 2004); however, examination of the literature reveals that these variations are rarely accounted for. This is significant given that these models are being used to estimate the C balance of forests and more recently, as quantitative input to forest-based climate change mitigation initiatives.

Hierarchical Bayesian models (HBMs) can facilitate the explicit modelling of autocorrelation (Clark 2005; Clark and Gelfand 2006; Cressie and others 2009). The objective of this study is to test the HBM approach for modelling the forest carbon balance of PNG's forests; for isolating the influence of selective-harvesting and ENSO-induced fires; and providing ecological insights.

Materials and Methods

PSPs

The PNG Forest Research Institute (PNGFRI) established a system of PSPs in the early 1990s, some in forest immediately after selective-harvesting, and others in primary forest across PNG (Figure 1; Table 1). As can be observed in Table 1, some plot measurements in selectively harvested forest spanned the ENSO event, which induced fires in many lowland tropical forests in PNG in 1997 and 1998 (Barr 1999). The same ENSO event was observed to cause drought and increased tree mortality in Sarawak (Nakagawa and others 2000), and in the Amazon (Cochrane and others 1999; Laurance and others 2004). These PSPs are described in detail elsewhere (Fox and others 2010; Yosi and others 2011), however, the PSP system was designed to effectively sample the range of floristic compositions in lowland tropical forests in PNG (Alder 1998). PSPs

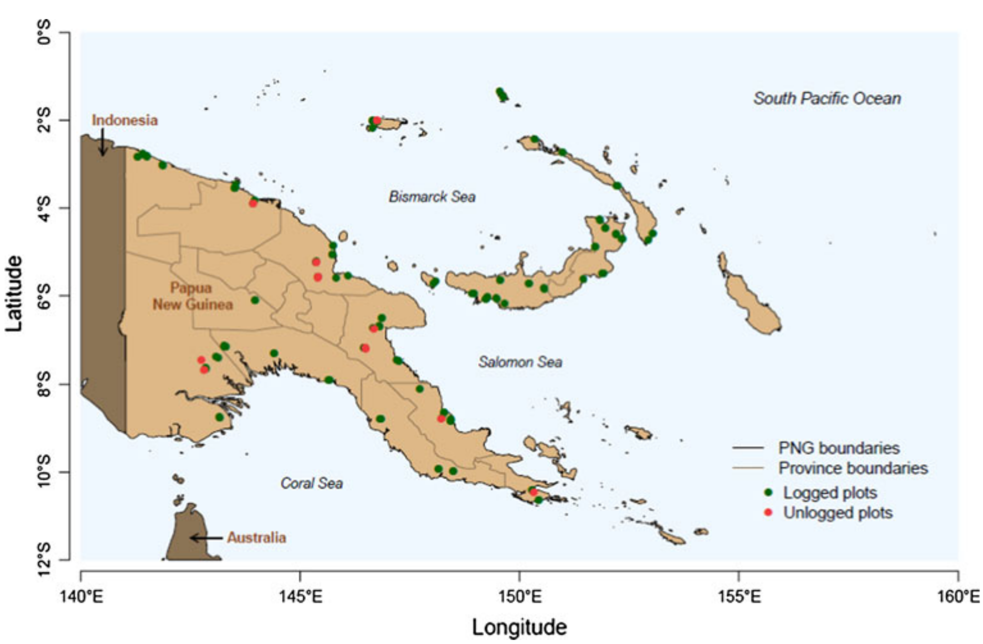

Figure 1. Spatial distribution of PSPs across Papua New Guinea. Note that each location may represent two or more PSPs.

Table 1. Number of Plots and Number of Measurements by Disturbance for the Papua New Guinea Forest Research Institute PSPs

Forest type	Disturbance	Plots	1 Census	2–4 Census	>4 Census	Total measurements
Harvested	ENSO fire	23	5	15	3	68
	None	98	17	53	28	354
Primary	None	13	7	6	0	21

ENSO, El Niño Southern Oscillation.

have been established and remeasured from 1990 onwards, at different intervals from annual census to 10 years between census (see Table 1). In summary, PSPs are 1 ha (100 m × 100 m) in size with all stems greater than 10 cm identified to the species level with diameter at breast height (1.3 m) measured in every census, and measured for height in the first census for each stem. Diameter was measured above the buttress, when a buttress was present. Stem heights for successive remeasurements were estimated using species-specific height-diameter models described in Fox and others (2010, 2011a). To supplement our limited sample in primary forest (Bryan and others 2011), we included an additional 22 plot measurements of aboveground C as collated by Bryan and others (2010). Each Bryan and others (2010) plot measurement was a single forest census (no repeated measurements) using similar measurement standards as the PSP dataset, that is, stems greater than 10 cm identified to the species level with DBHOB measured for diameter (above the buttress).

Aboveground live biomass (AGLB) was estimated using the wet forest allometry of Chave and others (2005); Eq. 1. The wet forest allometry of Chave and others (2005) includes biomass measurements from PNG (Edwards and Grubb 1977), and was successfully applied to PNG tree measurements in Fox and others (2010). For tree i, we denoted D_i the diameter in centimeters (cm), H_i the total height in meters (m) and q_i the wood specific gravity in grams per cubic centimeter (g cm^{-3}) for each species derived from Eddowes (1977) and the compilation for Asian tropical forest (IPCC 2006). For species with no wood density information (36% of the 686 tree species found in PNG), an average value of 0.477 across all species on PSPs was used (Brown 1997; Chave and others 2003). For plot j at date d, we denoted I_{jd} the total number of trees with DBH at least 10 cm and we computed AGLB$_{jd}$ the aboveground living biomass (Eq. 1). Consistent with previous studies, AGLB will be reported in megagrams per hectare (Mg ha^{-1}). For further details of the error correction methodology and biometric modelling used to estimate AGLB, refer to Fox and others (2010)

$$AGLB_{jd} = \sum_{i=1}^{I_{jd}} \left[0.0776 \times \left(q_i D_i^2 H_i\right)^{0.94}\right] \tag{1}$$

The C content of biomass is reported assuming that dry biomass is 50% C (Clark and others 2001a; Houghton and others 2001; Malhi and others 2004). We then computed C_{jd}, the carbon stock of plot j at date d and applied a multiplier (1.1) to estimate the contribution of stems with DBH less than 10 cm (Chave and others 2003; Baker and others 2004a; Fox and others 2010) (2).

$$C_{jd} = \frac{1}{2}\left(AGLB_{jd}\right) \times 1.1 \tag{2}$$

Details of allometry and AGLB calculations for supplementary primary forest data can be found in Bryan and others (2010). Note that Bryan and others (2010) also used the allometry of Chave and others (2005) to estimate aboveground biomass. Bryan and others (2010) applied a root to shoot ratio of 0.12 for lowland and 0.22 for montane forest to each AGLB estimate. To isolate the AGLB component of C stock, we used the multiplier 0.88 for lowland and 0.78 for montane forest. This resulted in compatible AGLB estimates from Bryan and others (2010) and as measured on the PSPs in this study.

Based on the PNG vegetation classification of Hammermaster and Saunders (1995), our final combined C stock database for PNG was composed of 138 plots in lowland tropical forest (0–1,000 m asl); 7 plots in lower-montane (1,000–2,000 m asl); and 11 plots in mid-montane forest (2,000–3,000 m asl).

Hierarchical Bayesian Model for C Dynamics

We modelled C stock and sequestration using a hierarchical state-space Bayesian model (Cressie and others 2009). We benchmark all sequential measurements using a starting date (d in Eq 1 and 2) as t_o, which corresponds to either the first measurement for primary (undisturbed) plots or the date of disturbance (selective-harvesting or year of fire disturbance (1997 or 1998) for fire affected plots) for disturbed plots. By benchmarking plots in this way, we can test for differences in the C stock and C sequestration rates for the three types of plots. We use random plot effects to account for the hierarchical structure of the data. We incorporate year of measurement as a random effect to account for temporal variation, that is, the influence of annual variations in environment and climate on stock and sequestration.

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

$$C_{jd} \sim N\left(a_j + b_j t, \sigma^2\right) \tag{3}$$

In Eq. 3, we present a linear model of C stock over time, however, studies have suggested that C stock in forest recovering from disturbance should follow an initially exponential trend with an asymptotic tendency as the forest approaches full recovery (Brown and Lugo 1990; Hughes and others 1999). Following this we fitted a modified Chapman-Richards (Zeide 1993) model to selectively harvested PSPs. The modified Eq. 4 is an asymptotic non-linear model, as applied to C accumulation after disturbance by Brack and others (2006) (Eq. 4);

$$C_{jd} \sim N\left(a_j + b_j\left(e^{-\frac{c_j}{t}}\right), \sigma^2\right) \tag{4}$$

where the intercept a indicated the initial C stock, parameter b indicated upper asymptote, and parameter c represents the shape of the curve to this asymptote (Brack and others 2006).

The Full Model (Model 1)

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

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

$$a_j = \alpha_{a,S} + \beta_{a,j} + \gamma_{a,A} f(A) + \gamma_{a,T} f(T) + \gamma_{a,R} f(R) + \delta_{a,d} \tag{5}$$

$$b_j = \alpha_{b,S} + \beta_{b,j} + \gamma_{b,A} f(A) + \gamma_{b,T} f(T) + \gamma_{b,R} f(R) \tag{6}$$

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

Model Fitting

The conditional posterior for each parameter was obtained using a Gibbs sampler (Gelfand and Smith 1990) available through the JAGS software (http://www-fis.iarc.fr/~martyn/software/jags/http://www-fis.iarc.fr/~martyn/software/jags/). We ran two MCMC simulations of 200,000 iterations. The 'burn-in' period was set to 100,000 iterations and the 'thinning' to 1/200. We then obtained 1,000 estimations for each parameter. We checked chain convergence using the Gelman Rubin statistic (Gelman and others 2003). We note that a hierarchical model with similar specification could have been fitted in the maximum likelihood framework using Generalized Linear Mixed Models, but an advantage of the Bayesian approach is the flexibility in model specification.

Model Comparison

We compared the full Model (Model 1) with two simpler models, denoted Model 2 and Model 3. Model 2 included only (i) fixed effects $\alpha_{\{a,b\},S}$ of plot status S on the slope and intercept and (ii) random plot effects $\beta_{\{a,b\}}$ on the slope and the intercept. In Model 2 covariates for Altitude, Precipitation and Temperature were not included, and neither was the random effect on the year of measurement. Examination of parameter estimates and model diagnostics for Model 1 indicated that neither environmental covariates nor the random effect on the year of measurement were significant (see 'Results' section). Model 3 included only fixed effects $\alpha_{\{a,b\},S}$ of the plot status S on the slope and intercept. Model 3 did not include any random effects and is analogous to a classical linear model.

The DIC (Deviance Information Criterion) was used to compare models. The DIC is the sum of the mean deviance (with Deviance = −2 log(likelihood)) and the number of parameters pD. A difference of more than 10 is taken as a rough index of difference between two models and rules out the model with the higher DIC (Spiegelhalter and others 2002). When the DIC difference is less than 10, the best model is the one with the lower number of parameters pD, in accordance with the parsimony principle.

Parameter Significance

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

Predictive Posterior of the Carbon Stock

We computed the predictive posterior π of $c(t)$, the carbon stock at time t (7). The predictive posterior included variability in the process (for example, plot variability) and parameter uncertainty. We denoted Θ the vector of parameters.

$$\pi(C(t)) = \int_{\Theta} \pi(C(t)|\Theta)\pi(\Theta)\mathrm{d}\Theta \tag{7}$$

Results

C Stock Trends Across PSP Remeasurements

Selectively Harvested PSPs

There were a range of trends in C stock observed on selectively harvested PSPs. For example, there was an exponential trend for Giluwe01 and Oomsi02 (Figure 2); a concave curvature with increasing sequestration after disturbance for Pasma01 and Umbuk01; and a linear trend for Mokol01 and Wasap01. Some PSPs exhibited high rates of C sequestration (above 3 MgC ha^{-1} y^{-1}; Wasap01, Mokol01, Oomsi02), whereas others (Giluw01, Pasma01 and Umbuk01) indicated lower rates below 1.7 MgC ha^{-1} y^{-1}. The modified Chapman-Richards (Eq. 4) provided no improvement in fit when compared to a linear model of C sequestration for selectively harvested PSPs. This is most likely because our measurement period (maximum of 23 years, but often below 15 years) was not long

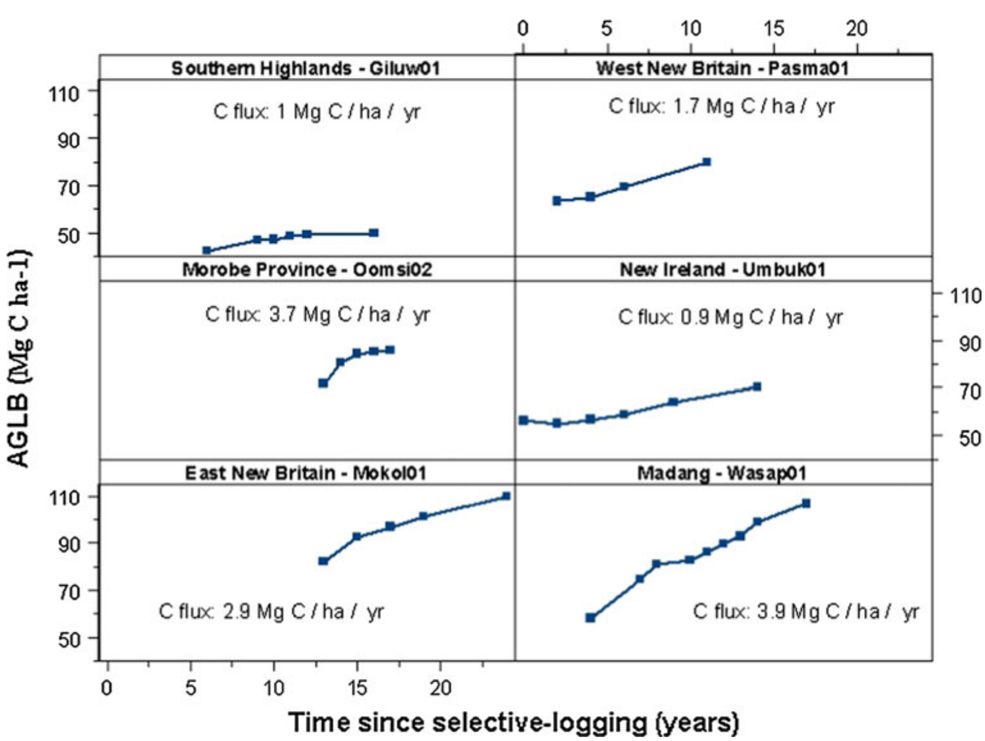

Figure 2. Trends in carbon stock of AGLB after selective-harvesting for selected PSPs.

enough for the expression of a sigmoidal or non-linear tendency in C stock change.

Overall Trends

To examine mean trends and variability in the PNG PSP data, we constructed a graph (Figure 3) with measurements benchmarked against either the first measurement for primary plots or the date of disturbance (selective-harvesting; 1997 or 1998 for fire affected plots) for disturbed plots.

C stock and sequestration are highly variable across the PSPs. Carbon stock in primary forest PSPs is generally (but not uniformly) higher than in selectively harvested and burned PSPs. Carbon sequestration is generally positive on selectively harvested PSPs and negative on PSPs burned in 1997 or 1998 (Figure 3).

HBM Model Selection

The estimated variation (assessed using DIC) is equivalent for models 1 and 2, which both include random effects, but is far larger for Model 3, which only includes fixed effects (Table 2). Despite having the same DIC, Model 2 is superior to Model 1 because it is more parsimonious, having fewer parameters (pD = 319). None of the parameters for Altitude, Rainfall and Temperature, nor random effects on the year of measurement (temporal variation), were significantly different from zero.

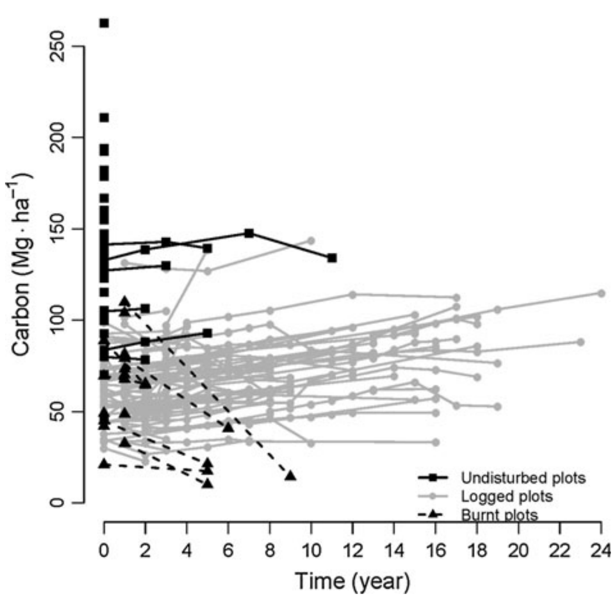

Figure 3. All data for permanent sample plot remeasurements. Note that time zero is the first measurement for primary plots; the date of selective-harvesting for harvested plots; or 1998 for fire affected plots.

Therefore, Model 2 was the preferred model for estimating C stock and sequestration.

Parameter Estimates

The HBM approach was used to determine C stock at t_0 and the average C sequestration across re-measurements for primary, harvested and ENSO-burned PSPs (Table 3; Figure 4). Carbon stock in primary forest (137 ± 9 MgC ha^{-1}) is significantly higher than in harvested (62 ± 18 MgC ha^{-1}) and burned (70 ± 26 MgC ha^{-1}) forest (Table 3). Carbon sequestration in harvested forest (1.12 ± 3.41 MgC ha^{-1} y^{-1}) is higher than C sequestration in primary forest (0.23 ± 1.70), but neither were significantly different from zero. Carbon sequestration in burned forest (−6.87 ± 3.98) is significantly negative. If we assume that primary and selectively harvested forest C stocks are representative averages across forest types and regions, then the reduction in C stock due to selective-harvesting (ΔC_{SH}) is on average 75 MgC ha^{-1} (55%). We can construct an additive 95% CI for ΔC_{SH} as 75 ± 25 MgC ha^{-1} (or 55 ± 18%).

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

Comparing CIs for the parameters (Table 3) when random plot effects are included (Model 2) and excluded (Model 3) indicates that CIs are narrower for all parameters for Model 3. This creates a false impression of precision in parameter estimates. When hierarchical variability is included in Model 2, CIs that reflect the true precision of parameter estimates result. Model 2 also explained far more variability in the data as indicated by the lower deviance (Table 2). This is due to the high

Table 2. Model Comparison

	Deviance	pD	DIC
Model 1	2827	343	3170
Model 2	2851	319	3170
Model 3	4100	7	4107

DIC, Deviance Information Criterion; pD, the number of parameters.

Table 3. Parameter Estimates for Model 2

Parameter	Explanation	Parameter estimate	95% CI M2[2]	95% CI M3[3]
a_P	C stock t_0—Primary	137.00[1]	±0.62	±6.90
a_H	C stock t_0—Harvested	61.74[1]	±18.34	±7.53
a_B	C stock t_0—Burned	70.17[1]	±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—Burned	−6.87[1]	±3.98	±3.10
$V_{a,\beta}$	Variance on plot random effect on intercept	641.40[1]	±140.17	
$V_{b,\beta}$	Variance on plot random effect on slope	1.29[1]	±0.85	
σ^2	Variance	30.92[1]	±6.26	±63.47

[1]Parameter estimate is significantly different from zero, [2] Credible 95% CI for Model 2 inclusive of random plot effects, [3] 95% CI for Model 3 with no random effects.

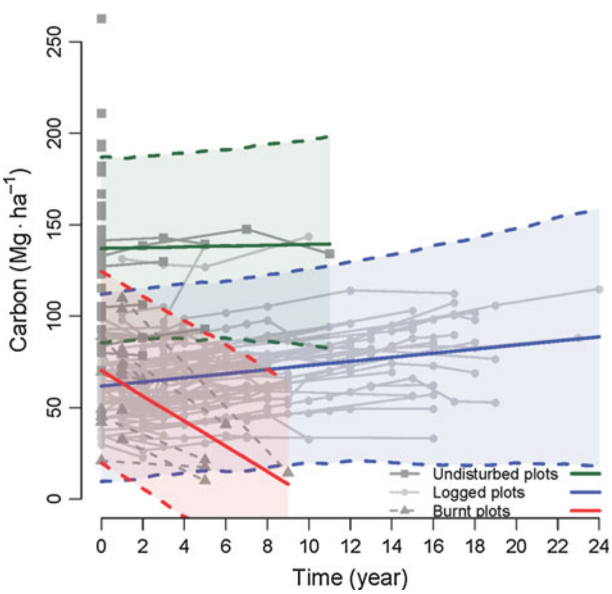

Figure 4. Predicted posterior for a hierarchical Bayesian model with *green solid line* for primary plots, *blue solid line* for selectively harvested plots, and *red solid line* for plots affected by El Niño Southern Oscillation-induced fires in either 1997 or 1998. *Dashed lines* in each posterior indicate 95% CIs inclusive of random plot variability on the intercept and slope (Color figure online).

plot to plot variability in the intercept and slope, which is captured using random parameters.

Discussion

Selective-harvesting results in the displacement of living forest biomass to non-living biomass, a component of which is taken off site as wood products with the remaining displacement termed collateral damage and becoming decomposing residue on the forest floor (Blanc and others 2009). Collateral damage in tropical forest harvesting can be large and consists of crown material, peripheral trees that are affected during tree felling and that subsequently die, and tree boles used for bridge, road and deck construction (Johns and others 1996; Feldpausch and others 2005). The enhanced pool of decomposing residue resulting from collateral damage in disturbed forest can be a significant source of CO_2 emissions (Keller and others 2004; Feldpausch and others 2005).

Although our sample of primary forest plots is small, we can estimate the reduction in C stock due to selective-harvesting (75 ± 25 MgC ha^{-1}). This provides an estimate of the displacement of living aboveground biomass to collateral damage and wood products. However, our comparison is unbalanced and unmatched; we have far more observations in selectively harvested forest, and plots were not designed for this comparison. Matched plots in adjoining primary and selectively harvested forest would provide a more valid comparison (Bryan and others 2011). Nevertheless, an initial estimate of a 55% reduction in AGLB is a useful indicative figure for calculations of reductions in aboveground forest C due to commercial selective-harvesting in PNG. Similar reductions have been observed elsewhere, with surprising consistency: Lasco and others (2006), Tangki and Chappell (2008), Feldpausch and others 2005 and Gerwing (2002) all observed 50% reductions in AGB in the Philippines, Borneo, Southern Amazon and Brazilian Amazon, respectively.

Estimated reduction in C stock due to selective-harvesting can be used for preliminary national estimates of harvesting related emissions. The PNG Forest Authority estimates that the area subject to selective-harvesting between 1961 and 2002 is approximately 3.4 million (M) hectares (PNGFA 2007). Based on our estimate of C reduction due to harvesting this equates to a total displacement of 255 ± 85 Teragram C (TgC; million MgC) and an average annual displacement of 6 ± 2 TgC y^{-1}

from living to non-living AGB. Over this period, approximately 43 M m^3 of logs have been removed from PNG's native forests (Bank of Papua New Guinea (Various years); SGS (Various years)). If we assume 33% recovery of raw logs into timber products (Blanc and others 2009), and an average wood density for exported logs of 0.58 g cm^{-3} (Fox and Keenan 2011), then approximately 5 TgC will have been stored in timber products over this time. By this supposition, approximately 250 ± 85 TgC is either collateral damage left in the forest to decompose or is sawmilling residue. Decomposition of biomass in tropical forests occurs rapidly with woody material completely decomposed with the C fraction emitted as CO_2 after 15 years (Keller and others 2004; Chambers and others 2000). Assuming complete decomposition of collateral damage and sawmilling residue (which is often combusted), approximately 917 ± 312 $TgCO_2$ has been emitted due to selective-harvesting in PNG between 1961 and 2002. The year to year variability in emissions will be high due to variability in the rate of timber harvesting, particularly over the last 10 years (Bank of Papua New Guinea 2009).

There is high variability in previous estimates of C sequestration in secondary tropical forest. Some studies indicate less than 2.5 MgC ha^{-1} y^{-1} (Brown and Lugo 1990), whereas others indicate sequestration of between 7.5 and 10 MgC ha^{-1} y^{-1} (Hughes and others 1999; Scatena and others 1993), with many studies falling in the middle of this range with sequestration between 2.5 and 7.5 MgC ha^{-1} y^{-1} (Fehse and others 2002; Uhl and Jordan 1984). Many of these studies were for heavily disturbed forest in early successional phases where sequestration is dominated by the growth of pioneers (Fehse and others 2002). Our analysis included species-specific wood densities (Fox and others 2010) to capture the true C contribution of low wood density pioneers (Baker and others 2004a). A very large 95% CI (±3.41) on the parameter indicated high variability in C sequestration after selective-harvesting, possibly due to variation in successional stage, forest type, level of disturbance, edaphic conditions and the climatic regime in the period following disturbance. On average, observed C sequestration in regrowth in PNG was at the lower end of the range described above (1.12 ± 3.41 MgC ha^{-1} y^{-1}, generally below 5 MgC ha^{-1} y^{-1}). This may be due to the lower levels of disturbance relative to secondary forest resulting from agriculture. Selective-harvesting will have resulted in variability in successional stages between, and also within, the large one hectare PSPs. Gaps created due to selective-harvesting will experience regeneration that can result in high sequestration, whereas undisturbed areas of latter successional forest may experience little C sequestration, or even negative sequestration due to mortality (Feeley and others 2007). We also need to be mindful of a possible bias in our sample of secondary forest towards forest that contains future merchantable timber; heavily harvested secondary forest may have been avoided (Fox and others 2010; Bryan and others 2011).

The PSPs represent a valuable sample of selectively harvested forest in the Oceania region with good spatial and temporal representation (Fox and others 2010; Yosi and others 2011). We contend, therefore, that the average sequestration (1.12 MgC ha^{-1} y^{-1}), despite high uncertainty (±3.41), is a sound estimate for C recovery rates after selective-harvesting. If we assume that the 3.4 M ha harvested between 1961 and 2002 is harvested at the annual rate of 0.083 M ha, then the net C sequestered since harvesting began can be calculated as (41*1.12*0.083 + 40*1.12*0.083 + 39*1.12*0.083….. 1*1.12*0.083) and is approximately equal to 80 TgC or 294 $TgCO_2$ over this period. If we include parameter uncertainty in this estimate, the 95% CI for sequestered C is 80 ± 244 TgC. Despite this high uncertainty, if the average sequestration occurred across selectively harvested forest it would offset approximately one third of the emissions from decomposition of collateral damage and sawmilling residue (917 $TgCO_2$).

There has been speculation (Shearman and others 2009) that PNG's secondary forests are degraded to the extent that they are incapable of recovery. The present study suggests otherwise, indicating that selectively harvested forests are reasonably stocked after harvesting (62 ± 18 MgC ha^{-1}), and are recovering C at the rate of 1.12 ± 3.41 MgC ha^{-1} y^{-1} (see also Yosi and others 2011). The high variability indicates that some plots are degrading but the bulk of plots are either maintaining or increasing biomass and carbon stock. If the average sequestration rate is maintained at a linear rate, it would take approximately 65 years for harvested forest to recover the 75 MgC ha^{-1} that was displaced during selective-harvesting.

The observed uptake of C by primary tropical forests (Phillips and others 1998) has become a point of contention in recent years (Clark and others 2001b; Wright 2005). Results for the limited number of plots (only six plots with remeasurements) in this study indicated a mean sequestration rate in primary forest of 0.23 ± 1.57 MgC ha^{-1} y^{-1}. This figure is lower than biome averages for primary forest (0.44 MgC ha^{-1} y^{-1}, Phillips and others 1998;

0.61 MgC ha^{-1} y^{-1}, Baker and others 2004b; 0.63 MgC ha^{-1} y^{-1}, Lewis and others 2009). These higher than expected C sequestration rates for primary forest have led several authors to suggest a pervasive alteration of primary tropical forest dynamics from global environmental changes such as increased atmospheric CO_2 (Phillips and others 1998; Baker and others 2004b; Lewis and others 2009). The sequestration rate for our limited sample of primary forest measurements was lower than other studies, but the CI included zero as well as previous estimates from Phillips and others (1998) and Baker and others (2004b). More plots and more measurements are required to understand the sequestration trend of primary forests of PNG.

The ENSO event of 1997/1998 caused a drying out of lowland tropical forests in PNG, with large-scale wildfires causing widespread tree mortality (Barr 1999; Yosi and others 2011). The estimated annual C emission in AGLB after this event is −6.87 (±3.98) MgC ha^{-1} y^{-1}. Balch and others (2008) report a similar loss of AGLB of −8.5 MgC ha^{-1} y^{-1} for a large-scale fire experiment in Amazonian forests. Some of the PSPs in this study were measured for 10 years after ENSO-induced fires, and indicated that degradation persists with net C emissions 10 years after the fire disturbance. The significant emissions associated with ENSO as observed here have implications for global C cycles.

We have used HBM model parameters inclusive of valid parameter uncertainties for some initial estimates of CO_2 emissions from harvesting and fires. These estimates can provide a quantitative basis for forest C accounting systems for PNG. Analysis of carbon dynamics in PNG forests can be based on these estimates, published forest carbon book-keeping methods (for example, Ramankutty and others 2007; Blanc and others 2009) and elements of the Voluntary Carbon Standard (VSC) (2008) to construct an appropriate forest C accounting system for PNG (See Fox and Keenan 2011; Hunt 2011; Coote and Fox 2011). Note that the initial emission estimates detailed in this paper include only aboveground C dynamics. A full C account would need to be inclusive of understory plants, lianas and vines, woody debris, litter, coarse and fine roots and soil C (Blanc and others 2009; Nimiago and others 2011; Nimiago 2011).

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

The HBM model structure used in this study has several advantages over reporting averages and 95% CIs. It avoided the presence of autocorrelation in model residuals that result in biased standard errors of parameter estimates (Johnston 1972), and bias in inference on averages or parameter estimates such as 95% CIs. When we excluded plot level random effects (in Model 3) the CIs for different parameters were considerably lower, creating a false impression of precision. This is statistically well known. When positive autocorrelation is present amongst residuals located on the same sampling unit (for example; several remeasurements of a plot) then parameter CIs will be underestimated and hypothesis tests on the significance will be biased upwards and the type I error rate will be inflated, that is, too often it will be concluded that the value is different from zero. Inferences on the parameters and averages are particularly important in light of controversies on the C balance of tropical forests. Many studies that have observed significant net C sequestration in primary tropical forest have failed to account for autocorrelation resulting from hierarchical data structures. When autocorrelation is incorporated, estimation efficiency is improved, as each measurement is bringing information to the model, independent of other measurements. Efficiency considerations are important in light of the cost of tropical forest census. Given the importance of discussions on the global carbon balance and the climate mitigation potential of tropical forests, we need improved statistical methodology such as hierarchical Bayesian models, which are more appropriate for tropical forest data from repeated plot measurements.

We have explicitly modeled uncertainties using a Bayesian approach, however, there are several sources of error which we were unable to include in our analysis such as errors in the field measurement of individual trees (Clark and others 2001a; Phillips and others 2002), and errors resulting from the application of a generalized allometric equation to estimate biomass from individual tree measurements (Chave and others 2004). These errors can be large and important, and are difficult to quantify, hence, in the future, the full error budget of forest C estimates should be quantified and incorporated into a Bayesian framework.

In conclusion, we have reported defensible estimates of aboveground C and C sequestration in primary, selective-harvested and ENSO-burned forest using a HBM. These estimates have improved our understanding of the forest C cycle in PNG with the recovery of selectively harvested forest found to be highly variable, but on average constituting a significant net C sequestration, in contrast to the extensive degradation inflicted by ENSO fires, with effected forest constituting a significant net C emission. They also provide quantitative inputs for climate change mitigation initiatives such as REDD+.

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