

Lianas and soil nutrients predict fine-scale distribution of above-ground biomass in a tropical moist forest

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Summary

1. Prediction of carbon dynamics in response to global climate change requires an understanding of the processes that govern the distribution of carbon stocks. Above-ground biomass (AGB) in tropical forests is regulated by variation in soil fertility, climate, species composition and topography at regional scales, but the drivers of fine-scale variation in tropical forest AGB are poorly understood. The factors that control the growth and mortality of individual trees may be obscured by the low resolution of studies at regional scales.

2. In this paper, we evaluated the effects of soil nutrients, topography and liana abundance on the fine-scale spatial distribution of AGB and density of trees for a lowland tropical moist forest in Panama using additive regression models.

3. Areas with larger values of AGB were negatively associated with the presence of lianas, which may reflect competition with lianas and/or the association of lianas with disturbed or open-canopy patches within forests. AGB was positively associated with soils possessing higher pH and K concentrations, reflecting the importance of below-ground resource availability on AGB independently of stem density.

4. *Synthesis.* Our results shed new light on the factors that influence fine-scale tree AGB and carbon stocks in tropical forests: liana abundance is the strongest predictor, having a negative impact on tree AGB. The availability of soil nutrients was also revealed as an important driver of fine-scale spatial variation in tree AGB.

Key-words: above-ground biomass spatial distribution, carbon dynamics, carbon stocks, INLA approach, liana, resource competition, soil nutrients, spatial statistics

Introduction

Tropical forests store 40–50% of total terrestrial carbon (Phillips *et al.* 2009). Consequently, determining carbon dynamics in tropical forests is a major goal of international climate policies (Pan *et al.* 2011; Dickson *et al.* 2012). Carbon stocks of live biomass in tropical forests reside mainly in the above-ground biomass (AGB) of trees, which therefore make a disproportionate contribution to the potential for ecosystem carbon storage and the regulation of atmospheric carbon dioxide concentrations (Schimel *et al.* 2001; Bunker *et al.* 2005; Saatchi *et al.* 2011). To address this issue, there has been a

major effort to calculate AGB stocks in tropical forests over recent decades (Clark & Kellner 2012), including the creation of plot networks (Malhi *et al.* 2002; Anderson-Teixeira *et al.* 2014), development of remote sensing methods to quantify AGB at continental scales (Asner *et al.* 2010), improvements to equations for estimating individual AGB (Feldpausch *et al.* 2012; Chave *et al.* 2014) and the development of methods for scaling from local to regional AGB values (Marvin *et al.* 2014).

One conclusion derived from the analysis of long-term plot data is that AGB stocks in intact tropical forests are increasing through time (Phillips *et al.* 1998; Baker *et al.* 2004a), possibly due to an increase in atmospheric carbon dioxide concentrations (Holtum & Winter 2010; Coomes, Burslem &

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Simonson 2014). However, this conclusion is challenged by data from well-characterized sites that display a decline in carbon storage due to decelerating growth (Feeley *et al.* 2007; Dong *et al.* 2012; Clark, Clark & Oberbauer 2013), and dendrochronological studies that provide no indication of an increase in tree growth rates over the past 100 years (van der Sleen *et al.* 2014; Groenendijk *et al.* 2015). The inconsistencies in the magnitude and direction of AGB change may reflect a divergence in response across spatial scales and geographic regions (Chave *et al.* 2008; Wright 2013), and it limits our capacity to forecast future changes in AGB in response to climate change predictions. The AGB of individual trees is influenced by interactions among neighbours and is therefore subject to the effects of competition, local community structure and resource availability. These factors may operate differentially in different regions through biogeographic effects determined by variation in local species pools and contrasting abiotic environments.

Despite the discrepancies among current studies of AGB dynamics in tropical forests, it is well-established that AGB increases through successional development and is therefore greater in relatively undisturbed primary forests than in secondary forests (Brown & Lugo 1982; Wright 2013). Hence, AGB increases after disturbance and reaches a maximum value that depends on local climate and resource availability in late succession. Among primary tropical forests, AGB at the regional scale responds to variation in soil fertility and soil physical properties (Laurance *et al.* 1999; Baker *et al.* 2004b), topography (Mascaro *et al.* 2011; Réjou-Méchain *et al.* 2014), climatic factors (Quesada *et al.* 2012; Lewis *et al.* 2013), interactions between soil and climatic factors (Quesada *et al.* 2012; Lewis *et al.* 2013), stand-level wood density (Baker *et al.* 2004b) and species composition (Laurance *et al.* 2004; Bunker *et al.* 2005; Poorter *et al.* 2015). Species composition and species richness may correlate with AGB through indirect effects mediated by these underlying environmental drivers or through variation in species' wood density (Chisholm *et al.* 2013; Poorter *et al.* 2015), although expected relationships, such as a positive relationship between AGB and community wood density, are not always observed and differ among regions and forest types (Slik *et al.* 2010; Ruiz-Jaen & Potvin 2011). A third potential explanation is that species richness might increase AGB through the expression of complementary niches among coexisting species (Tilman, Isbell & Cowles 2014; Poorter *et al.* 2015) although this hypothesis is also subject to doubt (Huston *et al.* 2000). In addition to all these factors, competition with lianas (woody vines) is a key biotic factor known to reduce tropical tree growth, survival and recruitment (Schnitzer & Carson 2010; van der Heijden, Powers & Schnitzer 2015), and it has recently been detected that an increase in liana abundance reduces carbon stocks in tropical forest (Durán & Gianoli 2013; Schnitzer *et al.* 2014; van der Heijden, Powers & Schnitzer 2015). Moreover, the presence of lianas within the forest is linked with areas with more recent or a higher frequency of disturbances (Dalling *et al.* 2012; Ledo & Schnitzer 2014). Lianas are not only direct competitors with trees

for resources but also indicative of areas with a recent history of disturbance (Schnitzer 2005). Furthermore, the role of disturbance in explaining spatial variation in AGB is often overlooked (but see Quesada *et al.* 2012), despite its importance in theoretical models (Chambers *et al.* 2004), possibly because disturbances are difficult to evaluate (Lewis *et al.* 2013).

A plausible explanation for discrepancies in the spatial distribution of AGB among tropical forests is that different studies have focused on different combinations of explanatory factors instead of considering them all simultaneously. A second potential explanation could be that the main factors controlling AGB are scale-dependent (Detto & Muller-Landau 2013; Poorter *et al.* 2015): climate and soils have been found to be the most important factors controlling AGB in most studies that evaluated the spatial distribution of AGB at continental scales of ~6 million ha (Quesada *et al.* 2012; Lewis *et al.* 2013), while topography has been revealed to be the key factor in many studies dealing with AGB spatial distribution at regional scales of ~1500 ha (Mascaro *et al.* 2011; Detto *et al.* 2013; Réjou-Méchain *et al.* 2014). In the Amazon basin, the interaction of climate, soil properties and species composition determines spatial variation in AGB (Baker *et al.* 2004b; Malhi *et al.* 2004; Quesada *et al.* 2012). African tropical forests have been less well studied, but current evidence suggests that AGB increases in response to the amount of rainfall during the dry season and on richer soils (Lewis *et al.* 2013). In a study in Borneo, AGB was found to vary with soil fertility, which had a stronger effect than stem density (Slik *et al.* 2010). Consequently, spatial variation in AGB is explained by a combination of factors, including soil and climate.

The studies of the spatial determinants of AGB in tropical forests reviewed above have been conducted at regional scales, whereas the correlates of fine-scale variation in AGB within plots are less well known. The demographic processes that govern AGB, tree growth and mortality are determined by interactions within individual tree neighbourhoods. Therefore, an improved mechanistic understanding of AGB change can emerge only through investigation of the demographic processes and fine-scale spatial dependencies that collectively determine their response at the regional scale. Individual tree growth and mortality depend on both biotic factors, including competition and interactions with pests (Peters 2003; Canham, LePage & Coates 2004), and abiotic factors, including resource availability or surrogates of resource availability such as topography (Clark *et al.* 2003; Dong *et al.* 2012; Uriarte *et al.* 2012). These factors all act at small spatial scales.

In this paper, we tested the hypothesis that the fine-scale distribution of AGB on a tropical forest plot is non-random with respect to biotic (stem density of trees, abundance of lianas) and abiotic (soil pH, nutrient availability and topography) variables. We aimed to identify the factors that determine spatial variation in AGB or to determine whether AGB is distributed randomly at scales up to 50 ha. To test these hypotheses, we fitted a spatially explicit model of fine-scale AGB variation to a set of spatial covariates. We

accounted for spatial autocorrelation in the AGB measurements by modelling the distribution of stem density simultaneously with the AGB distribution in a joint model and included a shared spatial random field that accounted for that spatial correlation. Clearly, AGB depends on the spatial distribution of the trees. Using a joint model with two responses – tree distribution and AGB – allows us to identify the factors governing either AGB or tree distribution separately while taking account of the aggregation of trees in space and the dependence of AGB on tree locations through a shared spatial field. With a simple model of AGB alone, the influence of explanatory variables on biomass storage and tree distribution would have been confounded. A joint, multiresponse model allows us to identify those factors, conditional on tree distribution. Using this model, we tested the effects of microtopography, soil resource availability and liana abundance (liana stem density) as explanatory spatial covariates. To fit the model, we used an integrated nested Laplace approximation (INLA; Rue, Martino & Chopin 2009), which is a computationally efficient method for fitting models in a Bayesian context that speeds up parameter estimation substantially.

Materials and methods

STUDY SITE

The study site was a 50-ha forest dynamics plot (Lat. 9.1543, Long. –79.8461) in seasonal lowland moist forest on Barro Colorado Island (BCI) in central Panama (Condit 1998; Hubbell *et al.* 1999). This plot was first censused in 1980–1982, and it has now been recensused on seven occasions in 1985 and at five-year intervals thereafter. At each census, all of the free-standing trees ≥ 1 cm in diameter at breast height (DBH) are remeasured, and new trees above this diameter limit are identified and measured. We used tree data from the sixth BCI tree census (2005), since this provided the best match to the single liana census conducted in 2007 (Schnitzer, Rutishauser & Aguilar 2008; Schnitzer *et al.* 2012). The forest on the BCI plot is representative of primary semi-deciduous lowland tropical forest in central Panama (Condit 1998; Hubbell *et al.* 1999). The BCI plot holds more than 200 000 stems, comprising 314 species (Hubbell *et al.* 1999). The mean basal area of stems ≥ 1 cm DBH is $31 \text{ m}^2 \text{ ha}^{-1}$ and mean AGB is $281 \pm 20 \text{ Mg ha}^{-1}$ (Chave *et al.* 2003). The plot comprises mostly old-growth forest, and distinct habitats have been defined within the plot (Harms *et al.* 2001): low plateau (50% of the plot), high plateau (14%), slope (23%), swamp (2%), streamside (3%), young forest (4%) and mixed habitats (5%). Mean annual temperature is 27°C and the mean annual rainfall of 2600 mm is distributed seasonally, with a strong dry period from December to April (Condit *et al.* 1999). The soil is Kandiodalfic Eutrudox, Isohyperthermic (USDA Soil Taxonomy) dominated by kaolinite clay (B. Turner, pers. comm).

SPATIAL COVARIATES

A map of the topography at $1 \text{ m} \times 1 \text{ m}$ resolution is available for the BCI plot (ctfs.arnarb.harvard.edu/Public/CTFSRPackage/index.php/web). That map was created from field measurements on a $20 \text{ m} \times 20 \text{ m}$ grid, where elevation was calculated for each quadrat as the mean of values at its four corners. Interpolation techniques

were used to generate the $1 \text{ m} \times 1 \text{ m}$ map available on the Web. This elevation map was used to create a digital elevation model (DEM) using the software QGIS v. 2.8 (Quantum 2013) from which we derived elevation, slope, curvature and hillshade (an index computed by QGIS from latitude, elevation and solar angles to reflect relative amount of canopy exposure to direct radiation; less exposed habitats such as gullies take higher values than more exposed environments).

Two data sets were obtained for 10 soil chemistry variables. The first was collected in 2005 (John *et al.* 2007) and comprises a grid of 300 points collected in a 50-m regular grid and including some extra points to capture variation at fine scales. The second data set was also collected in 2005 (J. Dalling & S. J. Wright, unpubl. data) and comprises data from 238 points located adjacent to seed traps on the BCI plot (Lebrija-Trejos *et al.* 2014). The sampling, processing and laboratory analysis were identical in both cases. The soils samples were collected from a depth of 0–10 cm, and cations and P were extracted using a Mehlich III solution and analysed using inductively coupled plasma spectroscopy. pH was measured on a 1:3 mixture of fresh soil and distilled water (John *et al.* 2007). The two data sets were pooled and screened for obvious outliers for each measured element (points with values $> \sim 100\%$ of their nearest neighbours), which were systematically removed. The final pooled data set comprised measurements of pH, Al, B, Ca, Cu, Fe, K, Mn, Mg and P for up to 537 points across the 50-ha plot.

A census of all lianas > 1 cm diameter at ground level was conducted in 2007 (Schnitzer, Rutishauser & Aguilar 2008; Schnitzer *et al.* 2012), and these data were used to generate maps representing liana abundance. Liana abundance was quantified as the sum of total individual liana basal area per quadrat, on the same spatial grids that we used in our models. Individual liana basal area was calculated using the diameter measured at 1.3 m from the rooting point (Schnitzer *et al.* 2012). We repeated the analysis using number of liana stems and AGB instead of basal area and the results were qualitatively identical but the fit to the data was less strong in both cases, so we report the results for the model with liana density measured as basal area density below.

CREATING DATA LAYERS

The AGB of all trees was estimated using the allometric equations recently developed by Chave *et al.* (2014), which were derived in part from data from Panama and Central America, unlike alternative equations in the recent literature (Feldpausch *et al.* 2012). We estimated AGB using Model 4 in (Chave *et al.* 2014), which computes AGB as a function of measurements of DBH from the tree census and tree height (H) estimated from DBH using allometric equations constructed from trees in central Panama (Appendix S1 in Supporting information). Previous work has suggested that including a term for tree height improves AGB estimation (Feldpausch *et al.* 2012). Wood density values were measured for trees in Central Panama (Wright *et al.* 2010). Estimated AGB per tree was then summed within subplots at spatial resolutions of $10 \text{ m} \times 10 \text{ m}$, $20 \text{ m} \times 20 \text{ m}$ and $50 \text{ m} \times 50 \text{ m}$ to create three discretized maps of tree AGB (Fig. 1). The mean number of trees and AGB of stems ≥ 1 cm DBH on the $10 \text{ m} \times 10 \text{ m}$ quadrats is $41.5 \text{ trees} \pm 11.8$ standard deviation and $2533 \pm 3913 \text{ kg}$ standard deviation, respectively (Fig. 1). Equivalent values for the $20 \text{ m} \times 20 \text{ m}$ and $50 \text{ m} \times 50 \text{ m}$ quadrats are 165.8 ± 33.0 trees and $10\,133 \pm 754 \text{ kg}$ and 1036.3 ± 121.7 trees and $63\,333 \pm 18\,890 \text{ kg}$, respectively (Fig. 1). Liana basal area was summed across all individuals within the same grid of plots at each

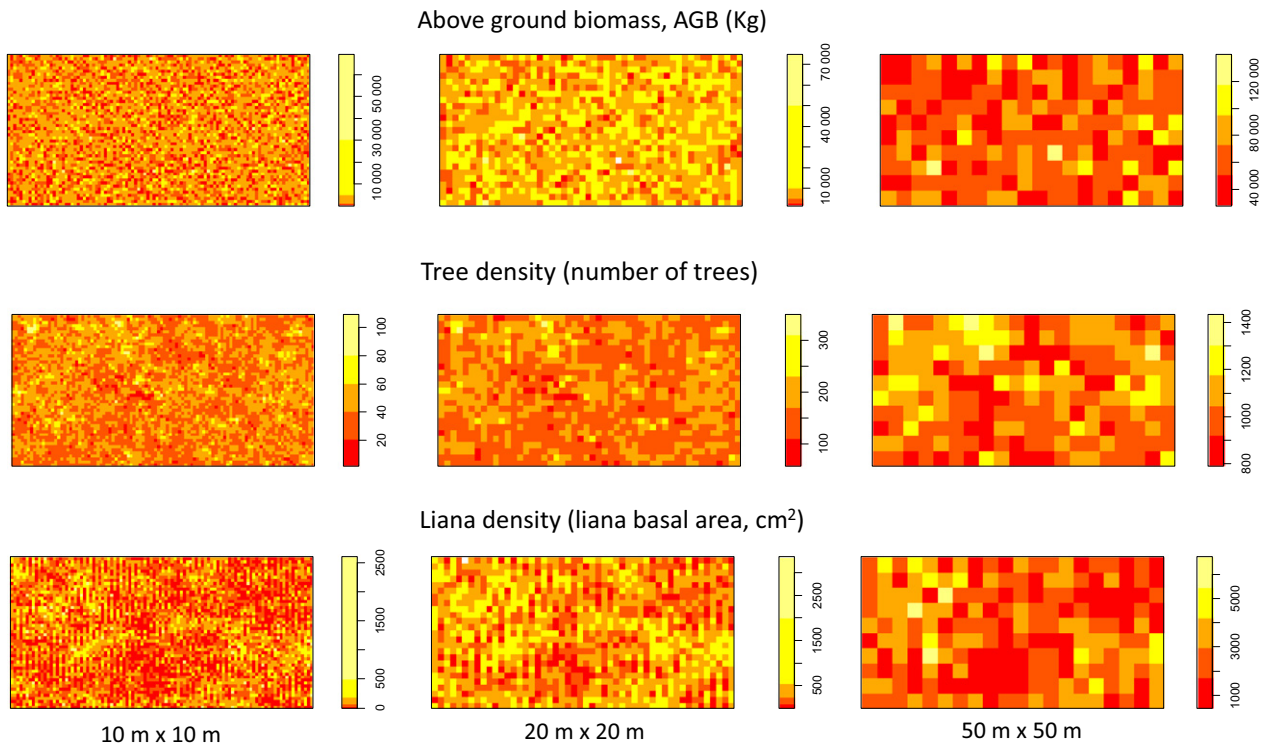


Fig. 1. Values of AGB (above) and stem density (below) in the different grids (a) $10\text{ m} \times 10\text{ m}$ (b) $20\text{ m} \times 20\text{ m}$ and (c) $50\text{ m} \times 50\text{ m}$ in the BCI plot.

of the three spatial resolutions. We obtained values of the four topography variables at the desired spatial resolution by creating three different DEMs at $10\text{ m} \times 10\text{ m}$, $20\text{ m} \times 20\text{ m}$ and $50\text{ m} \times 50\text{ m}$ using the Triangulated Irregular Network (TIN) interpolation method, available in the QGIS. We adopted a geostatistical approach to construct the spatial layers for the ten soil chemical variables. We calculated the empirical semi-variogram for each variable (Cressie 1993) and then used restricted maximum likelihood (REMS) to fit a spherical model semi-variogram to the data. Ordinary kriging was then used to extend the soil variables to the spatial resolutions of the grids ($10\text{ m} \times 10\text{ m}$, $20\text{ m} \times 20\text{ m}$, and $50\text{ m} \times 50\text{ m}$) using the fitted semi-variogram. These analyses were conducted using the `GEOR` package for R v 1.7-4.1 (Ribeiro & Diggle 2001).

MODEL DESCRIPTION AND FITTING

The response variables of interest here are total AGB of trees on quadrats of $10\text{ m} \times 10\text{ m}$, $20\text{ m} \times 20\text{ m}$ and $50\text{ m} \times 50\text{ m}$. However, AGB depends on tree position, so to evaluate the independent underlying causes of variation in AGB distribution, the effects of the spatial distribution of trees have to be removed. The modelling approach we take here accounts for the spatial distribution of trees and the inherent autocorrelation of demographic processes at small scales (Jansen, Meer & Bongers 2008), which may in turn produce some spatial structure in AGB. Ignoring the processes generating spatial autocorrelation would lead to explanatory variables becoming significant even though they are not (Legendre 1993; Kissling & Carl 2007).

We consider the data as a marked spatial point pattern where the locations of the trees form the ‘points’ and AGB for each tree are the marks, and we model the marks along with the spatial point pattern in a joint model. This implies that we have two response variables,

the spatial pattern (tree distribution) and the marks (AGB). We used a marked log Gaussian Cox point process model (Rue & Held 2005). Log Gaussian Cox processes are special cases of latent Gaussian models, which assume that the observations are independent given one or more latent fields. The latent fields explain the spatial dependence structure in the data by explicitly accounting for spatial autocorrelation through covariates and a spatially smooth random field (also referred to as a spatially structured effect), which accounts for the spatial autocorrelation in the data unexplained by the covariates (Illian *et al.* 2012). While AGB was the response variable of interest, we account for spatial autocorrelation in the AGB measurements by modelling the tree pattern simultaneously through the joint modelling approach. The random field was assumed to be a Gauss–Markov random field (GMRF; Rue & Held 2005). The GMRF has a local dependence structure, which speeds up computation and makes model fitting practically feasible. In our model, the same GMRF is shared between the two response variables (the marks and spatial point pattern). To fit the model, we use integrated nested Laplace approximation (INLA; Rue, Martino & Chopin 2009), which is a computationally efficient way of fitting models in a Bayesian context that speeds up parameter estimation substantially, and thus also enhances the feasibility of fitting of complex spatial models such as the marked point process we use here (Rue, Martino & Chopin 2009).

The data set comprised a regular grid with p rows and q columns. Since we have two response variables we have two latent fields, η and ν , that share a common random field $f_s(\cdot)$. Conditional on the latent field η , the number of points y_{ij} in grid cell s_{ij} ($i = 1, \dots, p$; $j = 1, \dots, q$) is assumed to be Poisson-distributed, that is $y_{ij} | \eta_{ij} \sim \text{Po}(|s_{ij}| \exp(\eta_{ij}))$, and conditional on the latent field ν , the value of the response variable AGB, a_{ij} , in that cell is assumed to be Gamma-distributed.

1 The latent field η_{ij} is given as:

$$\eta_{ij} = \alpha_{\eta} + \sum \beta_{pi} z_{ij} + f_s(s_{ij}) + e_{pij} \quad \text{eqn 1}$$

and

2 the latent field v_{ij} is given as:

$$v_{ij} = \alpha_v + \sum \beta_{mi} z_{ij} + f_s(s_{ij}) + e_{mij} \quad \text{eqn 2}$$

where α_{η} and α_v are intercept terms, β_k are parameters reflecting linear effects of explanatory covariates z_{kij} in grid (the corresponding grid size in each case), $f_s(s_{ij})$ is the spatially structured effect GMRF in grid cell s_{ij} , modelled using a two-dimensional random walk. The e_{ij} are unstructured, independent and identically distributed random variables (iid), that is error terms, following a normal distribution. Total AGB (v) was included as Kg per grid cell and tree density (η) as number of trees per quadrat. All the covariates were centred before being included in the model.

The proposed model was fitted using INLA through the R library R-INLA [47], which implies that inference was implemented in a Bayesian context. Hence, we needed to choose appropriate prior values in order to obtain the posterior distribution of the parameters that describe the model. We assigned Gaussian priors to the random terms in equations 1 and 2. For the spatial field, $f_s(s_{ij})$ we used a gamma prior for the precision and scale parameters, with distribution (0.1, 0.001) (see Saatchi *et al.* 2011 for more details). We chose a conservative value for the prior to ensure that the significant covariates were ecologically meaningful.

A stepwise approach to model selection was implemented as follows. We first fitted the model including all the covariates as linear terms (fixed effects), plus the spatial and error terms (random effects), at the three different grid sizes. However, because some of the covariates were correlated (Appendix S2), we then fitted models including each covariate separately, along with the spatial and error terms for both the spatial distribution of trees and AGB. We repeated the same set of models and included each covariate along with the quadratic value of the covariate, to look for quadratic effects. We selected the covariates that were significant at the 97.5% level in those individual models (the model including one covariate at a time, or a covariate with a quadratic term, Appendix S4). We fitted several models including systematically all different combinations of those relevant covariates. We calculated the Deviance Information Criterion (DIC) for each fitted model. We then followed a stepwise modelling approach: we initially included one covariate at a time and checked whether it was significant or not. Subsequently, we included different combinations of the covariates that were significant either for AGB or tree density and kept all significant variables in the model (Appendix S4). We started including combinations of pairs of significant covariates that were not correlated (Pearson's coefficient < 0.2). Then, we incremented one by one the number of covariates until all of the significant ones were included. In those combinations, we avoided variables that were correlated. In the resulting models, some of the covariates that were significant when included alone resulted in no significant variables when combined with others (Appendix S4). If different models had the same number of significant covariates, we chose the best model based on the DIC values, and will refer to this model as the final model from now on. We considered a model to be better than another model when their DIC values differed by 5 or more, as smaller differences are insufficient to distinguish among alternative models (Zuur *et al.* 2009). We made sure that the covariates included in the final models were uncorrelated (Pearson's coefficient < 0.2). The R code adopted for these analyses can be found in Appendix S3.

We derived a set of nested models from the final model to determine the relative importance of the significant factors. For each nested model, we included only one of the significant covariates as a fixed effect, along with the spatial and error terms. This approach assumes that the final model provides full explanatory power for the fixed variables and that the null model (including only the random effects) has zero explanatory power. We quantified this through changes in DIC among the final, null and nested models, where the difference in DIC between each nested model and the null model was expressed as a percentage of the difference in DIC between the final and null models.

Results

The final models (including all the significant covariates and the best models in terms of the DIC, Appendix S4) displayed different combinations of significant spatial covariates at the three spatial scales considered in these analyses (Fig. 2). The error field did not show any spatial structure for those models (Appendix S5), indicating that spatial autocorrelation had been captured by the covariates and the spatial field. The variables that were significant predictors of AGB at the 97.5% level were different to those that explained tree distribution for the three different grid sizes (Fig. 2).

A total of 58 models were compared at the largest spatial scale of 50 m \times 50 m (Appendix S4a). There were strong effects of liana stem density (negative) and soil pH (positive) on values of AGB (Fig. 2). Only one variable explained tree distribution: areas with lower soil P concentrations supported a higher density of tree stems. Including a term for liana stem density had the largest impact in terms of percentage reduction in the DIC relative to the null model (Fig. 2). The variables identified as significant either for tree density or AGB were not correlated. As can be seen in Appendix S4, including hillshade instead of P also resulted in a significant model with the same number of variables. However, we chose the best model based on the DIC and the model including P had lower DIC (Appendix S4); that is, it had more explanatory power. Yet, we could note here that hillshade was correlated with soil nutrients (Appendix S2).

We compared 76 models at a spatial scale of 20 m \times 20 m (Appendix S4b). An increase in the density of liana stems had a negative effect on values of AGB. An increase in soil K concentration contributed to higher values of AGB (Fig. 2). A quadratic effect of lianas was also significant (Fig. 2), indicating the existence of a maximal value of liana abundance which reduces tree AGB accumulation at this scale of study. Soil concentrations of P and Fe were significantly positively and negatively correlated with tree density, respectively (Fig. 2; Appendix S4b). The soil nutrients Fe and P were not correlated in our data set (Pearson correlation = 0.05; Appendix S4). Note that a second model including Mn² instead of Fe was also significant, but its DIC was higher. In addition, the effect of Mn was not significant, and Mn and K are positively correlated (Pearson correlation = 0.4; Appendix S2). Slope was identified as significant in some models (Appendix S4), but these were associated with models with higher DIC. As for analyses conducted at a

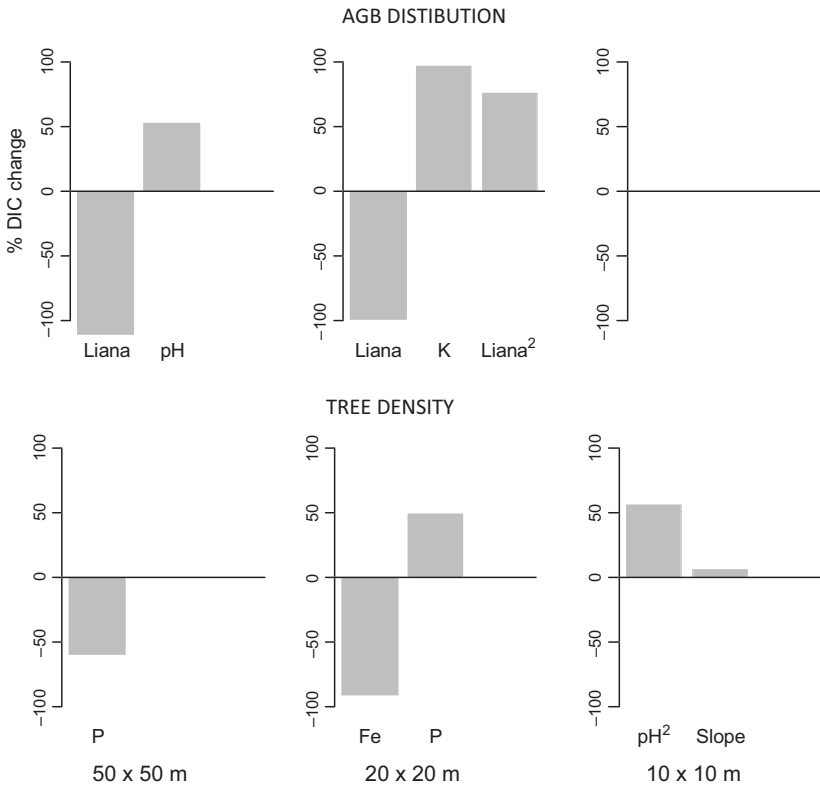


Fig. 2. Significant variables (at 97.5%) explaining AGB spatial distribution (above) and tree density (below) in the best model for grids of 50 m × 50 m, 20 m × 20 m and 10 m × 10 m on the BCI Forest Dynamics Plot. Positive associations are represented as positive values and negative associations as negative values in the histograms. The length of the bars indicate the explanatory power of the covariate, defined as the percentage change in DIC between the null model with random effects alone (0% DIC) and alternative models which include one significant covariate as a fixed effect (indicated along the x axis) along with the random spatial field and errors. The DIC of the final model is represented as 100%. Factors have been ordered from the most relevant (left to right) in terms of explanatory power for each grid size.

scale of 50 m × 50 m, slope is highly correlated with soil nutrients (Appendix S2).

We compared 66 models at the smallest scale of 10 m × 10 m (Appendix S4c). None of the covariates were significant in explaining the spatial distribution of AGB in trees (Fig. 2). Quadrats with a higher density of tree stems were associated with slopes and gullies, and had less acidic soils (as reflected in a quadratic relationship with pH). Including the terms for soil pH (quadratic term) had the greatest relative impact in terms of reducing values of DIC (Fig. 2).

Discussion

Our study demonstrates that fine-scale distribution of AGB was non-random with respect to biotic and abiotic variables on the BCI forest dynamics plot. Liana abundance (basal area of liana stems) is the strongest predictor of tree AGB at the fine scale represented by a grain of 100-m², 400-m² and 2500-m² quadrats within a single 50-ha plot. The availability of soil nutrients was also revealed as an important driver of spatial variation in AGB. Microtopographic variation across the plot was not a significant factor explaining differences on AGB when accounting for soil nutrients and liana density, although topography explained the distribution of stem density independently of AGB (Fig. 2). Uncovering these patterns was dependent on the spatially explicit modelling of fine-scale AGB variation while accounting for autocorrelation associated with spatial structure in stem density. In other words, we accounted for the dependence of tree density and AGB in the shared spatial random field, which allows us to

identify the particular factors that affect each of those variables individually.

EFFECTS OF LIANAS ON ABOVE-GROUND BIOMASS STOCKS

Our study shows that higher liana stem density is related to lower tree AGB. This result agrees and extends the findings in (Durán & Gianoli 2013) who found a negative correlation between carbon stored in large trees and the presence of lianas at plot level. Our methods accounted for additional variation through additional explanatory factors including tree density, topography and soil nutrients and demonstrate a greater importance of liana abundance over these alternative explanatory variables (Fig. 2). Two underlying ecological mechanisms could explain the lower AGB of trees in patches with greater liana abundance: (i) competition from lianas reduces tree growth, survivorship and biomass accumulation and/or (ii) lianas are indicators of patches with more frequent or more recent disturbance, where large trees are absent or less abundant.

Recent research at our study site supports the plausibility of both mechanisms, but strongly supports the capacity of lianas to reduce forest-level AGB. A liana removal experiment in the Gigante Peninsula, adjacent to BCI, found that liana infestation reduced net biomass accumulation by 76% (van der Heijden, Powers & Schnitzer 2015) due to decreased tree growth (explaining 48% of forest-level biomass accumulation reduction) and increased tree mortality (explaining 41% forest-level biomass accumulation reduction). Indeed evidence of lianas

reducing tree growth has been observed in American (van der Heijden & Phillips 2009; Ingwell *et al.* 2010) and Asian (Wright *et al.* 2015) tropical forests, and long-term experimental research suggests that lianas reduce the rate of carbon accumulation in forest gaps (Schnitzer *et al.* 2014). Lianas also delay tree recruitment in some gaps by suppressing tree regeneration and regrowth of canopy trees and thus keeping the canopy gaps open for longer (Schnitzer, Dalling & Carson 2000; Schnitzer & Carson 2010; Tymen *et al.* 2016). These results are consistent with the hypothesis that lianas reduce AGB accumulation in trees through direct competition.

Additionally, a positive relationship between liana abundance and soil fertility has been found in some other tropical forests (Schnitzer & Bongers 2002; Tymen *et al.* 2016), although this result is not consistent (Dalling *et al.* 2012; Ledo & Schnitzer 2014). Tymen *et al.* (2016) suggested that the higher nutrient concentration in soils of liana-infested forests may be the result of a release of nutrients from vegetation after a forest blowdown. The presence, abundance and distribution of lianas across the BCI plot are linked to patches with more frequent disturbance (Dalling *et al.* 2012; Ledo & Schnitzer 2014), which is also consistent with the relationship observed in our data because areas in which disturbances are more frequent are less likely to support the large trees that often dominate AGB (Slik *et al.* 2013).

While our results cannot distinguish between these explanations for the negative association between AGB in trees and liana abundance, experimental work at a nearby site indicates that lianas reduce forest-level AGB (van der Heijden & Phillips 2009; van der Heijden, Powers & Schnitzer 2015), in contrast, the role of lianas as indicators of prior disturbance remains uncertain. Moreover, our results allow us to discount the likelihood that the pattern is due entirely to the separation of lianas from large trees in recently disturbed patches, because an additional prediction of that mechanism would be a positive association between liana and tree abundance through intense recruitment of individuals of both life-forms in recently disturbed areas, unless lianas inhibit recruitment into the 1 cm DBH size class represented in the plot inventory. The explanation for the observed pattern may be a combination of both underlying mechanisms, but certainly a negative effect of lianas on tree growth and survival.

EFFECT OF SOIL NUTRIENTS ON ABOVE-GROUND BIOMASS STOCKS

Spatial distribution of AGB at a continental scale responds to climate and soil fertility (Quesada *et al.* 2012; Lewis *et al.* 2013). Climate was not considered in our study because at the scale of analysis (50 ha) little variation in rainfall or temperature would be expected. Nevertheless, richer soils enhanced AGB accumulation at the fine scales of our analysis (Fig. 1), which suggests that a positive relationship between measures of soil chemical fertility and AGB in trees extends from local to continental scales. This pattern supports a strong body of research suggesting that nutrient availability may limit AGB accumulation in tropical forests (Asner *et al.* 2004; Wright

et al. 2011; Wright 2013). We found that AGB storage is linked to variation in soil pH, with more AGB stored in vegetation growing on less acidic soils. We also observed that areas with higher values of soil K concentration support greater AGB (Fig. 2). This pattern is consistent with the findings of a long-term fertilization experiment on the Gigante Peninsula close to our study site, which has demonstrated that K addition increased stand-level biomass and production of fine root biomass, enhanced seedling tissue nutrient concentrations, reduced seedling root allocation and improved stomatal control and photosynthesis (Wright *et al.* 2011; Pasquini & Santiago 2012; Santiago *et al.* 2012; Wurzburger & Wright 2015). In the same experiment, P addition increased fine litter production and photosynthetic rates (Wright *et al.* 2011; Pasquini, Wright & Santiago 2015). These studies suggest that soil K and P concentrations have a fundamental role in regulating forest productivity, and our analyses suggest that they also contribute to variation in ecosystem-level AGB. On the other hand, Lewis *et al.* (2013) found a negative correlation between AGB and soil fertility measured as the sum of base cations among African tropical forests. Nevertheless, at the large scales of their analysis soil fertility is correlated with climate gradients, and it is therefore difficult to decouple the confounding effects of these factors on AGB storage. Lewis *et al.* (2013) concluded that more information on African forest is necessary to coherently understand factors contributing to AGB storage.

The emergence of soil pH as a key predictor of spatial variation in AGB follows from the association between soil acidity and numerous measures of soil chemical and biological fertility (Ashman & Puri 2013), including many factors that were not measured in the study, such as microbial activity and the availability of toxic elements. Soil pH may also be an indicator of exchangeable cation concentrations, as a decline in pH may cause an increase cation solubility and losses through leaching (Turner *et al.* 2013). It is also important to bear in mind that most of the soil nutrient concentrations were intercorrelated, including pH (Appendix S2), which indicates that the availability of multiple nutrients would increase or decrease in parallel with variation in soil pH (Ashman & Puri 2013). Soil fertility also varies with topographic variation (Appendix S2, Chadwick & Asner 2016). These correlations point to an underlying gradient in multiple soil chemical properties that governs the spatial distribution of AGB.

Our findings suggest that spatial variation in AGB may be linked to soil resource availability independently of patterns in stem density, which is indicative of soils driving differences in tree size class distributions and/or species composition (John *et al.* 2007). Other studies have determined that tree species distributions on the BCI plot are related to soil resource availability (Baldeck *et al.* 2013), which may contribute to differences in AGB (Poorter *et al.* 2015). We conclude that soil chemical and/or biological fertility acting at the individual tree scale contributes to spatial variation in AGB. This association may arise from spatial variation in factors such as species distributions, traits such as wood density that contribute to AGB, and/or a disproportionate development of larger trees in the most fertile sites.

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Data accessibility

The Barro Colorado Forest Census Plot Data are archived and openly available for download from the Smithsonian Institute DSpace repository (<http://dx.doi.org/10.5479/data.bci.20130603>; Condit *et al.* 2012)

Conflict of interest

The authors have no competing interests.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Fitted parameters of the DBH:H allometric equations for the Panamanian trees including all the individuals (General) and for each species with more than 60 individuals in the data set used.

Appendix S2. Linear Pearson's correlations among covariates (topography, soils nutrients and number of liana stems) at different grid sizes: (a) 50 m × 50 m (b) 20 m × 20 m and (c) 10 m × 10 m.

Appendix S3. R code for the analyses.

Appendix S4. DIC and log-likelihood (Loglik) values of the fitted models, including different combinations of covariates as fixed effects and the spatial field and error term as random effects at grid sizes: (a) 50 m × 50 m (b) 20 m × 20 m and (c) 10 m × 10 m.

Appendix S5. Residuals from the fitted best models at each grid size for both responses: tree distribution (above) and AGB (below).