

Past human disturbances and soil fertility both influence the distribution of light-demanding tree species in a central African tropical forest

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Keywords: light-demanding species, moist tropical forests, past Human disturbances, shade-bearer species, soil charcoal abundance, soil properties, tree community assemblages, wood-specific gravity.

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This is the Postprint of the article published in Journal of Vegetation Science:

Vleminckx, J., Bauman, D., Demanet, M., Hardy, O. J., Doucet, J.-L., & Drouet, T. (2020). Past human disturbances and soil fertility both influence the distribution of light-demanding tree species in a Central African tropical forest. *Journal of Vegetation Science*, 31(3), 440–453.

<https://doi.org/10.1111/jvs.12861>

Abstract

Questions: In vast areas of central African forests, the upper canopy is presently dominated by light-demanding tree species. Here, we confront three hypotheses to explain this dominance: (1) these species have expanded their distribution because of widespread past slash-and-burn activities, as suggested by important charcoal amounts recorded in the soils of the region; (2) their abundance is rather explained by soil properties, as this guild establishes preferentially on favourable physico-chemical conditions for rapid growth; (3) soil properties have been substantially influenced by past human disturbances and those two effects cannot be disentangled.

Location: Pallisco-CIFM logging concession, south-eastern Cameroon (300 000 ha).

Methods: We quantified soil charcoal abundance and measured ten soil variables at the basis of 60 target trees that belonged to a list of three long-living pioneer light-demanding (LLP) and four shade-bearer (SB) species. We identified all stems with DBH \geq 20 cm distant of 15 m around each target tree. Species were characterised by their wood specific gravity (WSG) that reflected their light requirement. Multiple regression models were used to quantify and test the relative effects of charcoal abundance and soil variables on the mean WSG of the 60 tree communities, as well as the abundance of three guilds: LLP, SB, and non-pioneer light-demanders (NPLD).

Results: The mean WSG was the only response variable significantly explained by soil variables and charcoal abundance combined. It was significantly negatively associated to soil calcium and Mg content and to charcoal abundance, with soil and charcoal influencing the mean WSG independently.

Conclusion: Our results shed light on the relative influences of past human disturbances and edaphic factors on tree community composition in central African forests, a poorly documented subject, and pave the way for deeper similar investigation at the whole community scale as we focus on a limited number of species.

Introduction

Understanding how species are spatially assembled in natural communities is one of the main research interests in ecology. In tropical forest tree communities, the niche theory predicts that species composition results from the filtering of environmental conditions and niche differentiation (Maire et al. 2012), as well as density-dependence control mediated by natural enemies (Comita et al. 2014; Vleminckx et al. 2018). These theories have been challenged by neutral models suggesting that dispersal limitation and stochastic recruitment are the main factors explaining species distribution (Hubbell 2001). Nevertheless, there has been abundant support for niche models, especially regarding the role exerted by soil properties (e.g., John et al. 2007 and Condit et al. 2013 in the Neotropics, Russo et al. 2005 and Baldeck et al. 2016 in Southeast Asia, and Fayolle et al. 2012, Muledi et al. 2017 and Vleminckx et al. 2017 in Central Africa). Tree species turn-overs have been shown to correlate well with variations of soil nutrients' availability across space, notably calcium (Ca) (Muledi et al. 2017; Vleminckx et al. 2017), phosphorus (P) (Quesada et al. 2012), as well as along aluminium (Al) and manganese (Mn) toxicity gradients (Vitousek 2004; John et al. 2007).

Although more poorly studied, horizontal variations in light availability due to forest dynamics processes (natural tree fall gaps, Human disturbances) represent additional factors that may select different regeneration strategies and thus influence local composition (Hawthorne 1995; Senterre et al. 2005). Indeed, adaptations to well-lit conditions, occurring in forest openings, require costly mechanisms (e.g. high resource investment in photosynthetic metabolism) that would be counter-selective for plants in low-light conditions. As a consequence, we observe species that are able to grow

their entire lifespan under the shade of the canopy (“shade-bearer” species, hereafter SB) while at the opposite others require relatively well-lit conditions (“light-demanding” species, hereafter LD) to survive and reproduce. Because LD species usually display acquisitive strategies and higher growth rate, their competitive advantage compared to SB species may be magnified in fertile soil conditions (Ashton & Hall 1992). For instance, Ouédraogo et al. (2016) have demonstrated in moist semi-deciduous forests of the northern Congo Basin that nutrient-depleted substrates hosted more evergreen, slow-growing SB species than relatively nutrient-richer soils on which deciduous LD species were more abundant, despite variations in the seasonality.

LD species comprise several guilds associated to different forest successional stages: short-living pioneer (SLP) species are the first to establish in forest openings. They are progressively replaced by relatively slower-growing, long-living pioneers (LLP) after ca. 30 years (Poorter 2006). Intermediate behaviours exist between pioneers and shade-bearers, with species able to tolerate shade during their juvenile stage, while becoming more light-demanding as they reach the upper canopy (non-pioneer light-demanders, NPLD; Hawthorne 1995). We must also mention the so-called “cryptic pioneers” which are found as juvenile in forest gaps but can later persist when canopy closure increases above them. Therefore, spatial heterogeneity in the history of forest disturbance is likely to leave an imprint in the spatial distribution of these guilds, as well as in species traits reflecting light requirements. Such traits may involve, for instance, wood tissues which are likely to be lighter among fast-growing, light-demanders, than among shade-bearer species (Poorter et al. 2008; Wright et al. 2010). Previous studies have indeed suggested that the mean wood-specific gravity of a local tree community is associated to its successional stage in tropical forests, with old-growth forest communities producing denser wood than secondary forests (Fayolle et al. 2014; Plourde et al. 2015).

Forest openings may result from natural forest gaps created by storms or the fall of senescent trees, but also from human disturbances which have started to increase throughout the world by the development of agricultural activities at the beginning of the Holocene. Increasing amounts of archaeological evidence from different continents have emphasised important past human presence in large uninhabited forests of the humid tropics (Willis et al. 2004). A famous example is the *terra preta* soils, or Amazonian Dark Earth, an edaphic formation dating up to 4500 BP (Lima et al. 2002) and located in many parts of the Amazonian basin (Lehmann et al. 2003). These soils contain important amounts of potteries and bone fragments, supporting their human origin (Da Costa & Kern 1999), as well as charred organic remains (wood charcoal, seeds, ash) which enhance their nutrient-holding capacity and thereby soil fertility (Glaser & Birk 2012). The effect of past human disturbances on the present-day composition of tree communities on Amazon Dark Earth soils is thus closely linked to the effect that these disturbances had on soil properties (Quintero-Vallejo et al. 2015), and we cannot clearly disentangle human from edaphic influences on species assembly in this region. In a recent study, Odonne et al. (2019) have demonstrated that pre-Columbian human disturbances have favoured the establishment of edible-fruit trees in French Guiana forests. In South-East Asia, intensive field cultivation (crops, planting of trees) started to spread as early as 8000 years ago in Thailand (Kealhofer 2003) and 7000 years ago in the island of New-Guinea (Denham et al. 2003).

In central African forests, which remain poorly studied compared to Neotropical or south-eastern Asian forests, past human presence has been less well documented (Oslisly et al. 2013). Nevertheless, it has been well established that disturbances due to past slash-and-burn agriculture, causing openings ranging from a few hundreds of square meters to a few hectares, have widely occurred throughout the region (Brcic 2007; Biwolé et al. 2015). These activities reached their last paroxysm in a period stretching from about 100 to 300 years ago (Hubau 2013; Morin-Rivat et al. 2016), as suggested by the

important amounts of charcoals and archaeological remains dated from this period in the soil of these forests. These past human activities have likely left traces in the composition of present-day tree communities. Indeed, in vast uninhabited parts of central Africa, the upper canopy is presently dominated by light-demanding tree species, which cannot regenerate well underneath their own shade (Swaine & Hall 1988; Van Gernerden et al. 2003; Fayolle et al. 2014), while at the same time natural forest gaps are generally not large enough or the undergrowth too dense to allow significant regeneration (Rollet 1983; Doucet 2003). The present lack of regeneration of LD species could be explained by the sharp decrease of forest agricultural activities due to the migration of human populations from deep forest areas to roadsides at the beginning of the colonial period (early 20th century, Clist 2005). Therefore, we may hypothesize that these trees grew up in more open vegetation than today, and that the forest cover has become presently denser, which has progressively decreased their fitness for the benefit of shade-bearer species. This hypothesis has been reinforced by Morin-Rivat et al. (2017) who showed in western central African forests that light-demanding emergent species regenerated ca. 165 years ago (around 1850) after major anthropogenic disturbances, while nowadays their demographic structure typically follows a bell-shaped curve due to a lack of regeneration.

Despite studies emphasising links between past human disturbances and local dominance of some emergent LD species (e.g. Bourland et al. 2015), so far little is known regarding to what extent Human disturbances have modified forest stand composition in Central Africa compared to other environmental factors. In addition, we do not know whether past slash-and-burn practices have induced as much impact on soil properties as in the Amazon, and so whether soil and human influences on tree community assembly can be disentangled or not.

Some regions of south-eastern Cameroon offer ideal conditions to investigate the impact of past human disturbances on tree species composition, as we encounter a mosaic of forest patches characterised by different proportions of LD and SB guilds, and thus potentially reflecting spatial variations in the age and the degree of past Human disturbances. In these regions, however, previous studies failed to demonstrate a significant link between soil charcoal abundance and guild abundances (Vleminckx et al. 2014). This may have partly resulted from an inadequacy between the spatial resolution of their sampling design and the spatial structures of soil charcoal abundance across their study area. Indeed, the authors noticed that charcoal abundance was spatially autocorrelated at very fine spatial scales, mostly inferior to 50 m (although spatial autocorrelation remained significant at larger scales), suggesting that past forest fires may have occurred more locally than expected when designing the sampling. These observations oriented us to re-investigate the hypothesis stated in Vleminckx et al. (2014), which suggested that the present-day forest stand composition in the forests of south-eastern Cameroon is the result of past human disturbances that occurred 100 to 300 years ago, and to better estimate the relative effects of these disturbances compared to edaphic conditions. To do so, we carried out a finer-scale sampling design, potentially more appropriate to test a relationship between soil charcoal abundance and the abundance of LD and SB species.

Here, we develop an original approach in a tropical forest of south-eastern Cameroon, consisting in directly searching for individual trees belonging to seven selected species, abundant and characterised by contrasted light-demanding requirements, inventorying surrounding trees and determining soil charcoal abundance and other soil variables. Using this approach, the objective of the present research is to evaluate the relative impacts of past human disturbances compared to the influence of key soil properties on the relative abundance of different tree guilds and trees' wood specific gravity. More

specifically, we aim at confronting the following hypotheses: (1) the present-day abundance of light-demanding trees in the forest canopy of south-eastern Cameroon has been explained by the opening of the landscape caused by past slash-and-burn activities, independently from any edaphic influence. We expect this hypothesis to be supported by soil charcoal being positively correlated to the abundance of light-demanding trees, especially the LLP and NPLD (considering the age of the last major human disturbances), and negatively correlated to the abundance of shade-bearer trees and to species wood specific gravity. (2) LD species establish preferentially, because of their fast-growing strategy, in relatively fertile conditions compared to shade-bearer trees, independently from any human influence. We expect this hypothesis to be supported by soil fertility indicators being positively correlated to the abundance of light-demanding trees and negatively correlated to the abundance of shade-bearer trees and to species wood specific gravity. (3) Past slash-and-burn activities determined both the quantity of soil charcoals and soil properties, and so that we cannot disentangle the soil and human effects on LD species distribution.

Methods

Study area

The study area (389,000 ha), hereafter “*Mindourou*” (name of the nearest main village), is a forest logging concession located in South-East Cameroon, at an elevation ranging from ca. 550 to 950 m asl (3°000-3°450 N, 13°370-14°300 E; Fig. 1). The area is homogeneously covered by a transition formation between evergreen and semi-evergreen tropical forest (Fayolle et al. 2016). The upper canopy of the region is dominated by long-lived light-demanding species like *Pericopsis elata* (Fabaceae) and *Triplochiton scleroxylon* (Malvaceae) (Vleminckx et al. 2014; Morin-Rivat et al. 2017; Ligot et al. 2019). Mean annual temperature oscillates around 23 °C and mean annual precipitations reach ca. 1625 mm, with no substantial variation across our sampling points (www.worldclim.org). Rainfall is unequally distributed over the year, with a dry season stretching from December to January (climatedata.eu). Topography presents a network of half-orange-shaped hills with swamp areas on their base. The geology consists of Precambrian metamorphic rocks (gneiss, granite and greenstone belts) of the Ntem complex (Iglesias-Martínez et al. 2018) and metasedimentary rocks or migmatite of the Yaounde group (Toteu et al. 2001). Soils are dominated by haplic Ferralsols (FAO-WRB classification), strongly weathered with low nutrient content, and locally Plinthosols where drainage is poorer down in the valleys (IUSS Working Group WRB 2015; Jones et al. 2013).

Sampling locations and target species

Our study focused on seven target tree species, well-represented in the study area, easily identifiable and well-known for their light requirements (Hawthorne 1995; Bénédet et al. 2013; Meunier et al. 2015, Table 1). Four of these taxa were strict shade-bearers (hereafter, SB): *Desbordesia glaucescens* (Irvingiaceae), *Dialium pachyphyllum* (Fabaceae), *Diospyros crassiflora* (Ebenaceae), and *Staudtia kamerunensis* (Myristicaceae). The three others were long-living pioneer light-demanders (LLP): *Milicia excelsa* (Moraceae), *Pericopsis elata* (Fabaceae) and *Triplochiton scleroxylon* (Malvaceae). The three LLP species displayed a bell-shaped demographic structure (DBH-frequency curve) in the region, suggesting that they grew up following past canopy disturbance while their saplings are now facing regeneration issues (Morin-Rivat et al. 2017, Nature Plus & Pallisco 2012; Pallisco, pers. comm.).

A total of 60 individuals (21 LLP and 39 SB), hereafter “*target trees*”, displaying a DBH (Diameter at Breast Height, i.e. at 1.3 m above the soil surface) ≥ 20 cm, and belonging to the seven target species, were inventoried over a large portion of the logging concession (the largest distance between two target trees was of 113 km), with each species represented by three to 14 individuals (Table 1). For practical reasons, trees were located nearby recent roadsides, explaining their directional-like and clumped-shaped distribution (Fig. 1). As far as possible, the sampling aimed at avoiding excessive disparity in the spatial distribution of SB and LLP trees. Nevertheless, clumped patterns of guilds were observed in the western and south-eastern parts of the sampling (Fig. 1). We overcame this issue in our analyses by using constrained spatial randomisation procedures designed to address this type of sampling (see the *Data Analysis* section below). All trees were inventoried on flat hilltops to avoid any risk associated to colluvium processes on slope or downhill, which could have potentially biased soil charcoal abundance estimations (Vleminckx et al. 2014).

We identified all surrounding individuals (DBH ≥ 20 cm) in a radius of 15 m around each of the 60 target trees, which allowed reaching a minimum of eight stems. This resulted in a dataset comprising 676 individuals belonging to 117 species (including the seven target species). To facilitate the reading, we will use the terms “plots” to designate the 60 locations corresponding to the target trees and the surrounding inventoried individuals. The number of species represented in each plot ranged between 6 and 13. Within each plot, we recorded the abundance of the SB and LLP, but also of the non-pioneer light demanders, hereafter NPLD, to obtain an additional response variable potentially reflecting an influence or past human disturbances. Cryptic pioneers were not found in our inventories. Short-living pioneers (SLP) should not be taken into account as this guild is replaced after 30 years by long-living pioneers during forest succession, while the youngest charcoals recorded in the study region were around 100 year-old (Vleminckx et al. 2014). Nevertheless, to further verify this, the latter guild was integrated into our analyses as a negative control. The overall community of trees in our dataset represented about 65% of the whole richness of canopy tree species (ca. 200 species, Vleminckx et al. 2014) encountered in the logging concession area.

Soil sampling and analyses

Composite soil samples were prepared by mixing equivalent volumes of three bulked soil cores collected at 0-10 cm below the litter, at each corner of a virtual triangle centred on each target tree (each corner distant of ca. one metre from the trunk). The following properties were characterised: soil texture (percentage of sand, silt, and clay), pH in water, soil organic matter content (in %), and the concentration in five plant-available elements (Ca, K, Mg, Al, and P; in mg/kg). Soil analyses were performed following standard protocols (Pansu & Gautheyrou 2006). Samples were air-dried and sieved through a 2-mm screen. Soil textural fractions (percentages of clay, silt, and sand) were determined by wet sieving and pipetting methods after H₂O₂ pre-treatment to remove aggregation followed by clay dispersion with Na-citrate. pH in water (pH-H₂O) was measured in a 1:5 (v/v) soil-water suspension after 5 min stirring and 2 h of contact using a combination glass electrode. Major cations (Ca, Mg, K, Al) and available phosphorus (P) were extracted with 0.5 M CH₃COONH₄ 0.02 M EDTA at pH 4.65 and determined by atomic emission spectrometry (ICP-OES, Vista-MPX, Varian, Australia). Soil organic matter (SOM) was determined by loss on ignition at 550 °C. Topographical information was not included among our explanatory variables as all plots were inventoried on a flat plateau surface to avoid the influence of colluvium process or any other effects related to a steep slope (soil stability) or seasonally flooded conditions (downhill).

Charcoal abundance data

Next to the three points where bulked soil samples were collected for soil property analyses, soil volumes were excavated (using a hand auger of 20 cm-long × 5 cm-diameter screw blade) at three different depths, 0-10, 10-20 and 20-40 cm (140 cm³ per 10 cm of vertical soil profile). For each collected soil volume, we estimated soil charcoal abundance using the charcoal abundance index (CAI) used in Vleminckx et al. (2014), which takes the following values: 0 = absence of charcoal, 1 = charcoal traces (scattered fragments or coal powder) and/or at least 5 pieces with a length < 5 mm or 1 piece with a length ≥ 5 mm; 2 = more than 5 pieces with a length < 5 mm and/or more than 1 piece ≥ 5 mm. We then calculated the mean CAI over the three excavation points for each soil layer. The two most superficial layers (0-10 and 10-20 cm) were thinner than the deepest one (20-40 cm). This is because we suspected that charcoal reflecting the most recent Human disturbances, which have potentially influenced the present-day forest stand composition, are mostly located near the soil surface, based on a previously observed relationship between charcoal age and soil depth in the same area (Vleminckx et al. 2014).

Data analysis

Soil charcoal abundance and edaphic heterogeneity among plots

We performed a Principal Component Analysis (PCA) to decompose the variation of soil conditions and charcoal abundance and search for orthogonal dimensions reflecting variables that vary independently. Target trees and variables were projected on PCA biplots, on axes 1-2 and 3-4 (the first three components explained more variation than expected under a broken stick model). We tested Pearson correlations between plots scores on each of these three axes and each variable.

Differences between LLP and SB plots for soil variables and charcoal abundance were tested using a Wilcoxon test. To account for spatial autocorrelation, the observed Wilcoxon statistic was compared to 4999 values of this statistic obtained by using Moran Spectral Randomizations (MSR, Wagner & Dray 2015). The MSR is a spatially-constrained permutation procedure allowing an explicit consideration of the multiscale spatial autocorrelation structures in any quantitative variable. The MSR uses information on the spatial connectivity among sampling points obtained when selecting Moran's Eigenvector Maps (MEMs, Dray et al. 2006) which are commonly used to model multi-scale spatial structures in ecological data. Connections among plots were defined using a Gabriel's graph which has been shown appropriate in the case of highly irregular sampling design (Bauman et al. 2018a). The MEMs selection was optimised following a forward selection procedure (Blanchet et al. 2008) that has been shown to provide correct type I error rate for the selection of spatial eigenvectors (Bauman et al. 2018b). In the MSR, the connectivity information is then used in a constrained randomisation algorithm to reproduce variables that accurately mimic the observed spatial structures of the randomised variable(s). The observed Wilcoxon test statistic was considered significant (bilateral test) if lying outside of the 2.5 to 97.5% quantiles of null values.

To further examine whether charcoal abundance was associated to any soil properties, we tested (i) the correlation between charcoal abundance and soil physico-chemical properties (comparison of the observed Pearson correlation with 4999 null values obtained with the MSR method), and (ii) the difference of soil variables between plots where charcoal fragments were found (n = 51) and charcoal-free plots (n = 9), using the MSR test of the Wilcoxon statistic described above.

Response and explanatory variables used in multiple regression analyses

We used five response variables potentially reflecting past human disturbance effects on the forest stand composition: the abundance of SLP, LLP, NPLD and SB, and the mean wood specific gravity (WSG; g/cm^3) of the community of trees in each plot. WSG values were obtained from a Global wood density database (Zanne et al. 2009). Thirteen out of the 117 (11.1%) species had missing values for WSG. The latter were replaced by values obtained using *Bayesian Hierarchical Matrix Factorization* (BHMF, Schrodte et al. 2015) to impute missing trait data, based on taxonomy (species, genus, and family). These imputations were justified by the fact that WSG is well phylogenetically conserved (Slik, 2006; Chave et al. 2006). Indeed, the inter-specific variation of this trait has been shown to be greater than its intra-specific variation (Chave et al. 2006), with substantial differences reported between light-demanding and shade-bearer species (King et al. 2005). We further tested the difference of WSG between SLP, LLP, NPLD and SB among the 117 species of our dataset (one-way ANOVA and Tukey test of pairwise comparisons), with the hypothesis that WSG decreases with light requirement.

To evaluate whether the central tree was a reliable representative of the functional variability of its surrounding community, we also: (1) verified whether the WSG was, on average, more similar between trees within a same plot than among trees sampled from different plots. To do so, we used the TAU_{st} statistic which was designed to quantify functional trait clustering (Hardy & Senterre 2007). The latter statistic was tested by comparing its observed value with 4999 values obtained after random permutation of species in the plots by species table; (2) tested the Pearson correlation between the WSG of the central tree and the mean WSG of its surrounding community (using a Pearson's product moment correlation test).

Explanatory variables comprised the ten measured soil variables described in the "*Soil sampling and analyses*" section and mean CAI in the 0-10 and 10-20 cm soil layer. The mean CAI in the 20-40 cm soil layer was not used as Vleminckx et al. (2014) have demonstrated that all charcoals collected at this depth dated more than 1500 years and therefore do not reflect disturbances that have impacted the present-day species composition. As a further check, we tested the effect of this variable on each response variable as a negative control in multiple regression analyses.

Prior to performing data analysis (see next sections), response and explanatory variables were normalized using a Box-Cox transformation, then standardised (z-score transformation). Abundance data were not normalised, following recommendations of O'Hara & Kotze (2010) not to transform occurrence data. CAI was not normalised neither as the Box-Cox transformation did not allow improving the normality of CAI values' distribution. A table containing, for each plot, the spatial coordinates (UTM; zone N33), the WSG of the target tree, the mean WSG of the plot community, the abundance of each species inventoried around the target tree, and soil variables' measurements is provided in supplementary material (Appendix S1). The list of 117 species inventoried among plots and their corresponding guild and WSG is available in Appendix S2.

Partitioning the relative effects of past human disturbances and soil properties

We first tested the adjusted coefficient of determination (adjusted R^2) of a multiple regression model of each response variable against the set of explanatory variables obtained after excluding overly collinear variables (i.e. displaying a variance inflation factor ≥ 5 , Rogerson 2001). The adjusted R^2 value was tested using the MSR, following Bauman et al. (2019). If, and only if the adjusted R^2 was significant (i.e. higher or equal to the 95% of null values obtained after performing 4999 MSR randomisations of the response variable), a variation partitioning analysis was performed to calculate the proportion of the variation (adjusted R^2 values) of the response variable explained (i) purely by charcoal abundance

in the 0-10 and 10-20 cm soil layers, (ii) purely by soil conditions, and (iii) by the effect of charcoals and soil combined. The significance of each of the three fractions was also tested using the MSR method.

Multiple regression and model averaging analyses

If, and only if the adjusted R^2 of a response variable against the set of non-collinear charcoal and soil variables was significant (see previous section), we calculated the model-averaged coefficients quantifying the relative effect of each explanatory variable. The latter consisted in the following steps: Multiple regression models were performed to explain the response variable with all combinations ($n = 109$) of explanatory variables in which collinearity was limited (max. VIF < 5). The collinearity limitation is a required step to avoid underestimating model-averaged coefficients (Freckleton et al. 2011). We calculated the expected predictive accuracy (weight) of each regression model using the corrected Akaike Information Criterion (AIC_c). An averaging analysis of the models' coefficient estimates weighted by the AIC_c of the models was performed to quantify the relative importance of each explanatory variable. The 95% confidence envelope of the averaged coefficient estimates was used to determine whether the latter estimates were significantly lower or higher than zero. The latter envelope was calculated using the MSR procedure to produce 4999 null values of each coefficient estimate.

All statistical analyses were performed in the R statistical environment (R Development Core Team 2018), using an R code provided in Appendix S3 (references for the R packages used for our analyses are detailed in this appendix).

Results

Difference of WSG among ecological guilds and plots

Highly significant differences of WSG were found among guilds ($P \leq 0.001$), with increasing WSG values from SLP to SB (Fig. S1). Differences were not significant between two consecutive guilds (SLP-LLP, LLP-NPLD, NPLD-SB) (Tukey test for multiple pairwise comparisons). We detected a significant clustering of WSG values within plots ($TAU_{st} = 0.202$; $P = 0.046$), as well as a highly significant correlation (test of Pearson's product moment correlation) between the WSG of the target trees and the mean WSG of their neighbours (r -Pearson = 0.34; $P = 0.008$), showing that the wood density of the target tree reflected well the one of its surrounding trees.

Soil and charcoal abundance heterogeneity

The first PC axis (explaining 30.6% of the whole soil and charcoal abundance inertia combined) corresponded to an acidity gradient (pH-H₂O) opposing plots with relatively high soil fertility (r -Pearson correlation of plot scores with pH, Mg, Ca ≥ 0.70 ; $P \leq 0.001$; see Table S1) to more nutrient-depleted plots displaying relatively higher soil Al content ($r = -0.75$; $P \leq 0.001$). This axis separated LLP from SB target trees (Fig. 2), with a significant difference of axis 1 scores between the two guilds ($P \leq 0.001$; t -test of mean comparison).

Differences between the two guilds were significant for soil pH, Ca, and Mg ($P < 0.05$; Table S2) but not for Al. The second PC axis explained a portion of the total inertia (27.4%) comparable to axis 1, and was mostly explained by soil texture variables (clay and sand, $r = 0.74$ and -0.87 , respectively; $P \leq 0.001$), OM, K and P ($r = 0.75$, 0.66 and -0.45 , respectively; $P \leq 0.001$). This axis did not separate well LLP from SB trees, and none of the five variables associated the most with the axis were significantly different between the two groups (Table S2). The third axis (explaining 12.8% of the inertia) was mostly

explained by the abundance of soil charcoal in the 0-10 and 10-20-cm soil layers ($r = 0.76$ and 0.64 , respectively; $P \leq 0.001$). Although this third component did not clearly separate LLP from SB trees, charcoal abundance in the most superficial soil layer (0-10 cm) was significantly higher around LLP trees than around SB trees ($P = 0.02$; Table S2).

Tests of Pearson's product moment correlations between plots scores on the first three axes of the PCA and each explanatory variable are presented in Table S1. No significant correlation was found between soil charcoal abundance in any soil layer and soil variables when correcting for spatial autocorrelation (MSR test), except for a positive correlation between K and CAI in the 0-10 cm soil layer ($r = 0.176$) although the latter might correspond to a false positive considering the number of tests and the P -value ($P = 0.043$). Accordingly, soil K content was also the only soil variable displaying nearly significantly higher values in plots where charcoal fragments were observed (66.13 mg/kg) compared to charcoal-free plots (51.12 mg/kg) ($P = 0.045$; Table S3). Nevertheless, even if significant, the difference of values only reached 23% of the highest K content, which could not be considered very marked from an ecological point of view.

Relative effects of charcoal and soil properties on tree community composition

Among all response variables (i.e. the abundance of SLP, LLP, NPLD and SB, and the mean WSG), only the mean WSG was significantly explained by soil charcoal abundance (in the 0-10 and 10-20 cm layers) and soil variables (adjusted R^2 of the multiple regression model = 0.243; $P = 0.027$; MSR test; adjusted R^2 values and P -values of the multiple regressions tests for guilds abundances are available in Appendix S4). The fraction of the mean WSG variation "purely" explained by the abundance of charcoals in the 0-10 and 10-20 cm soil layers reached a nearly similar value (adjusted $R^2 = 8.61\%$) as for the fraction explained by the VIF-selected soil variables (9.54%), the first value being marginally significant while the second was significant ($P = 0.054$ and 0.047 , respectively, MSR test) (Fig. 3a). The soil-charcoal fraction (6.10%) was not significant ($P = 0.112$) (Fig. 3a). The mean WSG was significantly and negatively associated to (in decreasing order of importance) Mg, Ca and CAI in the most superficial soil layer (0-10 cm) (averaged coefficient estimates = -0.023, -0.026 and -0.029, with $P = 0.004$, 0.001 and 0.001, respectively; MSR test with 4999 randomisations; Fig. 4). A second set of variation partitioning analyses was therefore conducted to partition the fractions of the mean WSG variation explained by CAI in the 0-10 cm soil layer, and by Ca and Mg separately (Fig. 3b). The latter analysis showed that charcoal abundance and Ca significantly explained independent fractions (adjusted R^2) of the mean WSG variation, respectively 9.31% ($P = 0.049$) and 12.27% ($P = 0.023$), while the charcoal-Ca fraction reached 6.39% and was not tested significant (Fig. 3b). When using Mg instead of Ca, only the fraction corresponding to the "pure" Mg effect (10.61%) was significant ($P = 0.030$), while the pure charcoal effect (8.47%) and the Mg-charcoal effect (7.23%) were marginally significant ($P = 0.055$ and 0.076 , respectively).

The model averaged coefficient estimates and P -values obtained for the other explanatory variables (CAI in the 10-20 and 20-40 cm soil layers, pH-H₂O, organic matter content, soil texture, K and P) are detailed in Appendix S4. We then plotted the fitted values of the mean WSG against the untransformed values of CAI in the 0-10 cm soil layer, Ca and Mg. This allowed providing further information regarding the range of values of the latter variable that induce most of its effect on the response variable. This is presented in Fig. 5 which shows that the mean WSG values mostly vary within a range of Ca and Mg content values lower than 250 and 50 mg/kg, respectively.

Discussion

Our study shed light on the role exerted by past Human disturbances, estimated via the abundance of soil charcoal, on tree community assembly in Central African forests. Our results suggest that these disturbances have favoured the establishment of fast-growing light-demanding species with relatively low wood density, to the detriment of shade-bearer species displaying denser wood. Our results also support the idea that the positive impact of disturbances on light-wooded species has been amplified by soil nutrient availability, with both soil and charcoal abundance explaining independent fractions of the mean WSG variation.

Past Human disturbances partly explain the present-day dominance of light-wooded species

Charcoal remains present in the 0-10 cm soil layer are assumed to reflect the most recent episode of intense slash-and-burn activities, which occurred ca. one to three centuries ago across the whole central African region as attested by ^{14}C measurements (Vleminckx et al. 2014). It has been suggested that forest clearings resulting from these disturbances have likely favoured the establishment of fast-growing, light-demanding species, explaining their dominance in the region nowadays (Morin-Rivat et al. 2017). This was in agreement with our results, as we first demonstrated that charcoals in the superficial soil layer were significantly more abundant around LLP species than around SB ones (Table S2). The model averaging of the multiple regression coefficients then showed that the mean wood species gravity of species was negatively associated to the abundance of the same charcoals (Fig. 4), hence providing support for the role of past human disturbances on community assembly. No significant signal was found for the guild abundances, which may be the result of low statistical power due to the limited size of our plots comprising eight to ten stems only.

Charcoals collected in the 10-20 and the 20-40 cm soil layers did not show any significant association with guild abundances or mean WSG (Appendix S4), presumably because it has been demonstrated that these charcoals reflected older disturbances (> 300 years), which are not imprinted in the present-day forest composition anymore (Vleminckx et al. 2014).

The PCA suggested that soil charcoal abundance varied independently from the variation of soil properties across plots (Fig. 2). Nevertheless, correlation values reaching 0.26, 0.22, 0.21 and 0.18 were found between charcoal abundance in the 0-10 cm soil layer reached and Mg, Ca, P, and K respectively (Table S4). However, these correlations were not significant, except a nearly significant value found between K and CAI in the 0-10 cm soil layer ($r = 0.176$, $P = 0.043$). Soil K content was also the only variable showing a (nearly) significant difference ($P = 0.045$; Table S3) between plots where charcoal remains were found and charcoal-free plots. These weak soil-charcoal association signals do not allow providing strong support to the hypothesis that past human disturbances have partly modified soil properties (or that soil properties have influence the choice of slash-and-burn fields) in the study region, at least not as substantially as in Neotropical forest (Quintero-Vallejo et al. 2015). Additionally, the common effect of soil properties and charcoal abundance on the mean WSG was lower compared to the pure soil and charcoal effects (Fig. 3a and 3b) and was not tested significant, except marginally for the Mg-charcoal effect (Fig. 3b). These results suggest that soil and charcoal abundance have independently influenced species distribution, although a larger sampling size may have allowed detecting significant soil-charcoal fractions.

High Ca and Mg content favours the establishment of fast-growing species

We found that soil pH-H₂O, Ca and Mg contents were significantly higher in LLP plots than in SB ones (Table S2), while Ca and Mg were significantly negatively associated to the mean WSG of tree

communities (Figs. 3, 4, 5). These results were in agreement with the hypothesis that light-demanding species preferentially establish on relatively fertile and less acidic soils, and provide support for previous similar evidence (Ashton et Hall 1992; Lawrence 2003). The effects of Ca and Mg suggest the presence of limiting availability for these nutrients. More precisely, we showed that the mean WSG mostly varied within a range of Ca and Mg content < 250 mg/kg and < 50 mg/kg, respectively, which may suggest that beyond these values, the availability of these nutrients provides a selective advantage among the LD species (characterised by lower WSG) compared to the SB ones. Conversely, on soils with lower Ca and Mg contents, the resource acquisitive strategies of LD species may not be competitive compared to the more resource conservation traits characterising SB species.

Although Ca and Mg were significantly and positively correlated to pH-H₂O, K and P (Table S4), the latter three variables did not show any significant effect in the multiple regressions. No significant signal was found for organic matter neither, which was not significantly correlated to Ca and Mg (Table S4). Aluminium content was not significantly different between LLP and SB plots and did not explain the variation in the mean WSG of tree communities, although we expected the most acidic soils which are nutrient-depleted and displaying higher Al toxicity to select for resource conservation strategies and thus favour SB species. The absence of soil textural effect could be explained by the relatively low variation of these variables across our plots (Table S2). The non-significant coefficients observed for organic matter, Al and K may be due to a lack of statistical power as the *P*-values of their coefficients were close to 0.10 (Appendix S4). The absence of signal for the coefficients associated to pH-H₂O and P effects (*P* > 0.25) may indicate that P was not limiting and that soil pH did not only reflect soil properties that significantly explained the mean WSG of tree communities (Ca and Mg) but also several properties (acidity, Al content) that did not seem to influence the distribution of LD species.

Our study provides new statistical evidence regarding the link between past forest fires and the composition of tropical forest tree communities in south-eastern Cameroon, and therefore sheds light on the processes shaping plant community assembly in these ecosystems. This is of paramount importance considering the present-day dominance of LLP species in the upper canopy in vast areas of central African forests, but also because these forests have remained poorly investigated compared to those of other continents. Our study paves the way for additional similar studies, investigating other target species or even entire tree communities, to better evaluate the relative impact of past human disturbances compared to other environmental factors over the whole Central African region.

Acknowledgments

This study is part of the FRFC project (F.R.S./FNRS, No. 2.4577.10) entitled “Dynamics of light-demanding tree species and grasses in the humid forests of Central Africa in relationship with past anthropogenic and climate disturbances”, the CoForChange project (ANR/NERC) predicting the effects of global change on forest biodiversity in the Congo Basin, www.coforchange.eu and the TROPDIV-Project (GxABT-ULg, PPR 10.000). J. Vleminckx was funded by the Belgian Training Fund for Research in Industry and Agriculture (FRIA – F.R.S. /FNRS) and the “Fonds Van Buuren” (ULB). D. Bauman was funded by the Belgian National Fund for Scientific Research (F.R.S.-FNRS) and the Fondation Wiener-Anspach. We are grateful to NGO Nature+ (Belgium) and the forest company Pallisco (Douala, Cameroon; M. Rougeron, L. Douaud, P. Lagoute, R. Feteke) for granting permission to access inventory

sites and providing all necessary facilities. We also thank the reviewers for their comments that helped us improving the quality of our article.

References

- Ashton, P. S., & Hall, P. (1992). Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *Journal of Ecology*, *80*, 459–481.
- Baldeck, C. A., Tupayachi, R., Sinca, F., Jaramillo, N., & Asner, G. P. (2016). Environmental drivers of tree community turnover in western Amazonian forests. *Ecography*, *39*, 1089–1099. doi:10.1111/ecog.01575.
- Bauman, D., Drouet, T., Fortin, M.-J., & Dray, S. (2018a). Optimising the choice of a spatial weighting matrix in eigenvector-based methods. *Ecology*, *99*(10), 2159–2166.
- Bauman, D., Drouet, T., Dray, S., & Vleminckx, J. (2018b). Disentangling good from bad practices in the selection of spatial or phylogenetic eigenvectors. *Ecography*, *41*, 1638–1649.
- Bauman, D., Vleminckx, J., Hardy, O., & Drouet, T. (2019). Testing and interpreting the shared space-environment fraction in variation partitioning analyses of ecological data. *Oikos*, *128*, 274–285. doi: 10.1111/oik.05496
- Bénédet, F., Doucet, J.-L., Fayolle, A., Gourlet-Fleury, S., & Vincke, D. (2013). CoForTraits, base de données d'information sur les traits des espèces d'arbres africaines. Version 1.0. http://coforchange.cirad.fr/african_plant_trait.
- Biwolé, A.B., Morin-Rivat, J., Fayolle, A., Bitondo, D., Dedry, L., Dainou, K., ... Doucet, J.-L. (2015). New data on the recent history of the littoral forests of southern Cameroon: an insight into the role of historical human disturbances on the current forest composition. *Plant Ecology and Evolution*, *148*(1), 19–28.
- Bourland, N., Cerisier, F., Dainou, K., Livingstone Smith, A., Hubau, W., Beeckman, H., ... Doucet, J.-L. (2015). How tightly linked are *Pericopsis elata* (Fabaceae) patches to anthropogenic disturbances in Southeastern Cameroon? *Forests*, *6*, 293–310.
- Brcic, T. M., Willis, K. J., Harris, D. J., & Washington, R. (2007). Culture or climate? The relative influences of past processes on the composition of the lowland Congo rainforest. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1478), 229–242.
- Chave J., Muller-Landau H. C., Baker T. R., Easdale T., ter Steege H., & Webb C. O. (2006). Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. *Ecological Applications*, *16*, 2356–2367.
- Chuyong, G. B., Kenfack, D., Harms, K. E., Thomas, D. W., Condit, R., & Comita, L. S. (2011). Habitat specificity and diversity of tree species in an African wet tropical forest. *Plant Ecology*, *212*, 1363–1374.
- Clist, B. (2005). Des premiers villages aux premiers Européens autour de l'estuaire du Gabon : Quatre millénaires d'interactions entre l'homme et son milieu. PhD thesis, Université Libre de Bruxelles, Brussels. 938 pp.
- Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., ... Zhu, Y. (2014). Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology*, *102*, 845–856. doi: 10.1111/1365-2745.12232

- Condit, R., Engelbrecht, B. M. J., Pino, D., Perez, R., & Turner, B. L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 5064–5068.
- Da Costa, M. L., & Kern, D. C. (1999). Geochemical signatures of tropical soils with archaeological black earth in the Amazon. *Journal of Geochemical Exploration*, *66*(1/2), 369–385.
- Denham, T. P., Haberle, S. G., Lentfer, C., Fullagar, R., Field, J., Therin, M., ... Winsborough, B. (2003). Origins of Agriculture at Kuk Swamp in the Highlands of New Guinea. *Science*, *301*, 189–193.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46.
- Doucet, J.-L. (2003). L'alliance délicate de la gestion forestière et de la biodiversité dans les forêts du centre du Gabon. PhD thesis, Faculté Universitaire des Gembloux.
- Dray, S., Legendre, P., & Peres-Neto, P. R. (2006). Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, *196*, 483–493.
- Fayolle, A., Engelbrecht, B., Freycon, V., Mortier, F., Swaine, M., Réjou-Méchain, M., ... Gourlet-Fleury, S. (2012). Geological substrates shape tree species and trait distributions in African moist forests. *PLoS One*, *7*(8), e42381.
- Fayolle, A., Picard, N., Doucet, J.-L., Swaine, M., Bayol, N., Bénédet, F., ... Gourlet-Fleury, S. (2014). A new insight in the structure, composition and functioning of central African moist forests. *Forest Ecology and Management*, *329*, 195–205.
- Fayolle, A., Loubota Panzou, G. J., Drouet, T., Swaine, M. D., Bauwens, S., Vleminckx, J., ... Doucet, J.-L. (2016). Taller trees, denser stands and greater biomass in semi-deciduous than in evergreen lowland central African forests. *Forest Ecology and Management*, *374*, 42–50.
- Freckleton, R. P. (2011). Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. *Behavioral Ecology and Sociobiology*, *65*(1), 91–101.
- Glaser, B., & Birk, J. J. (2012). State of the scientific knowledge on properties and genesis of Anthropogenic Dark Earths in Central Amazonia (terra preta de Indio). *Geochimica et Cosmochimica Acta*, *82*, 39–51.
- Hardy, O. J., & Senterre, B. (2007). Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. *Journal of Ecology*, *95*, 493–506. doi: 10.1111/j.1365-2745.2007.01222.x
- Hawthorne, W. D. (1995). Ecological profiles of Ghanaian forest trees. *Tropical Forestry Papers No. 29*, 345 pp.
- Hubau, W. D. (2013). Exploring charcoal as a natural archive for palaeofire and vegetation history of the Mayumbe, Democratic Republic of the Congo. PhD thesis, Ghent University.
- Hubbell, S. P. (2001). The Unified Neutral Theory of Biodiversity and Biogeography. Princeton, NJ: Princeton University Press, 375.
- Iglesias-Martínez, M., Espí, J. A., & Edou-Minko, A. (2018). Geological setting of gold mineralisation of the Minvoul greenstone belt (Ntem complex, northern Gabon). *Journal of African Earth Sciences* *147*, 1–10. doi: 10.1016/j.jafrearsci.2018.06.011
- IUSS Working Group WRB (2015). World reference base for soil resources 2014 – International soil classification system for naming soils and creating legends for soil maps. Update 2015. World Soil Resources Reports No. 106. FAO, Rome.

- John, R., Dalling, J. W., Harms, K. E., Yavitt, J. B., Stallard R. F., Mirabello, M., ... Vallejo, M. (2007). Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences*, *104*(3), 864–869.
- Jones, A., Breuning-Madsen, H., Brossard, M., Dampha, A., Deckers, J., Dewitte, O., ... Zougmore, R., (eds.) (2013). Soil Atlas of Africa. European Commission, Publications Office of the European Union, Luxembourg. 176 pp.
- Kealhofer, L. (2003). Looking into the gap: land use and the tropical forests of Southern Thailand. *Asian Perspectives*, *42*(1), 72–95.
- Keller, A. B., Reed, S. C., Townsend, A. R., & Cleveland, C. C. (2013). Effects of canopy tree species on belowground biogeochemistry in a lowland wet tropical forest. *Soil Biology and Biochemistry*, *58*, 61–69.
- King, D. A., Davies, S. J., Supardi, M. N. N., & Tan, S. (2005). Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Functional Ecology*, *19*, 445–453.
- Lawrence, D. (2003). The response of tropical tree seedlings to nutrient supply: Meta-analysis for understanding a changing tropical landscape. *Journal of Tropical Ecology*, *19*, 239–250.
- Lehmann, J., Kern, D. C., Glaser, B., & Woods, W. I. (2003). Amazonian Dark Earths: Origin, Properties and Management. Kluwer, Dordrecht, The Netherlands, 523 pp.
- Ligot, G., Fayolle, A., Gourlet-Fleury, S., Dainou, K., Gillet, J.-F., De Ridder, M., ... Doucet, J.-L. (2019). Growth determinants of timber species *Triplochiton scleroxylon* and implications for forest management in central Africa. *Forest Ecology and Management*, *437*, 211–221.
- Lima, H. N., Schaefer, C. E. R., Mello, J. W. V., Gilkes, R. J., & Ker, J. C. (2002). Pedogenesis and pre-Colombian land use of Terra Preta Anthrosols (Indian black earth) of Western Amazonia. *Geoderma*, *110*, 1-17.
- Maire, V., Gross, N., Borger, L., Proulx, R., Wirth, C., Pontes, L. D., ... Louault, F. (2012). Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist*, *196*, 497–509. doi: 10.1111/j.1469-8137.2012.04287.x
- Meunier, Q., Moumbogou, C., & Doucet, J.-L. (2015). Les arbres utiles du Gabon. Presses Agronomiques de Gembloux. 340 pp.
- Morin-Rivat, J., Biwolé, A., Gorel, A.-P., Vleminckx, J., Gillet, J.-F., Bourland, N., ... Doucet, J.-L. (2016). High spatial resolution of late-Holocene human activities in the moist forests of central Africa using soil charcoal and charred botanical remains. *The Holocene* *26*(12), 1954–1967.
- Morin-Rivat, J., Fayolle, A., Favier, C., Bremond, L., Gourlet-Fleury, S., Bayol, N., ... Doucet, J.-L. (2017). Present-day central African forest is a legacy of the 19th century human history. *ELife*, *6*, e20343.
- Muledi, J. I., Bauman, D., Drouet, T., Vleminckx, J., Jacobs, A., Lejoly, J., ... Shutcha, M. N. (2017) Fine-scale habitats influence tree species assemblage in a miombo forest. *Journal of Plant Ecology*, *10*(6), 958–969.
- Nature Plus, & Pallisco, 2012. Evaluation de l'état des populations des essences exploitées par la société Pallisco et des décisions prises en matière d'aménagement. Pallisco, Cameroun.
- Odonne, G., Van den Bel, M., Burst, M., Brunaux, O., Bruno, M., Dambrine, E., ... Freycon, V. (2019). Long-term influence of early human occupations on current forests of the Guiana Shield. *Ecology*, *100*(10), e02806.
- O'Hara, R. B., & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, *1*, 118–122.

- Oslisly, R., White, L., Bentaleb, I., Favier, C., Fontugne, M., Gillet, J. F., & Sebag, D. (2013). Climatic and cultural changes in the west Congo Basin forests over the past 5000 years. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 368(1625), 20120304.
- Ouédraogo D.-Y., Fayolle A., Gourlet-Fleury S., Mortier F., Freycon V., Fauvet N., ... Favier C. (2016). The determinants of tropical forest deciduousness: Disentangling the effects of rainfall and geology in central Africa. *Journal of Ecology*, 104, 924–935.
- Pansu, M., & Gautheyrou, J. (2006). Handbook of soil analysis: mineralogical, organic and inorganic methods. Springer. 969 pp.
- Plourde, B. T., Boukili, V. K., & Chazdon, R. L. (2015). Radial changes in wood specific gravity of tropical trees: interand intraspecific variation during secondary succession. Anten N, editor. *Functional Ecology*, 29, 111–120.
- Poorter, L., Bongers, L., & Bongers, F. (2006). Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. *Ecology*, 87, 1289–1301.
- Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manriquez, G., ... Wright, I. J. (2008). Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*, 89, 1908–1920.
- Quesada, C.A., Phillips, O.L., Schwarz, Czimczik, C. I., Baker, T. R., Patiño, S. ... Lloyd, J. (2012). Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, 9, 2203–2246.
- Quintero-Vallejo, E., Klomberg, Y., Bongers, F., Poorter, L., Toledo, M., & Peña-Claros, M. (2015). Amazonian dark earth shapes the understory plant community in a Bolivian forest. *Biotropica*, 47(2), 152–161.
- R Development Core Team (2018). R: A language and environment for statistical computing, version 3. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Rogerson, P. A. (2001). Statistical methods for geography. London: Sage.
- Rollet, B. (1983). La régénération naturelle dans les trouées. *Bois et Forêts des Tropiques*, 202, 19–33.
- Russo, S. E., Davies, S. J., King, D. A., & Tan, S. (2005). Soil-related performance variation and distributions of tree species in a Bornean Rain Forest. *Journal of Ecology*, 93, 879–889.
- Schrodt, F., Kattge, J., Shan, H., Fazayeli, F., Karpatne, A., Banerjee, A., ..., Reich, P. B. (2015). BHPMF - a hierarchical Bayesian approach to gap-filling and trait prediction for macroecology and functional biogeography. *Global Ecology and Biogeography* 24, 1510–1521.
- Senterre, B. (2005). Recherches méthodologiques pour la typologie de la végétation et la Phytogéographie des forêts denses d’Afrique Tropicale, pp. 343. PhD dissertation, Université Libre de Bruxelles, Brussels, BE.
- Slik, J. W. F. (2006). Estimating species-specific wood density from the genus average in Indonesian trees. *Journal of Tropical Ecology*, 22, 481–482.
- Swaine, M. D., & Hall, J. B. (1988). The mosaic theory of forest regeneration and the determination of forest composition in Ghana. *Journal of Tropical Ecology*, 4, 253–269.
- Toteu, S. F., Van Schmus, W. R., Penaye, J., & Michard, A. (2001). New U–Pb and Sm–Nd data from north-central Cameroon and its bearing on the pre-Pan African history of central Africa. *Precambrian Research*, 108, 45–73.
- Van Gernerden, B. S., Olff, H., Parren, M. P. E., & Bongers, F. (2003). The pristine rain forest? Remnants of historical Human impacts on current tree species composition and diversity. *Journal of Biogeography*, 30, 1381–1390.

- Vitousek, P.M. (2004). *Nutrient Cycling and Limitation: Hawai'i as a Model System*. Princeton University Press, Princeton, NJ, USA.
- Vleminckx, J., Morin-Rivat, J., Biwolé, A. B., Daïnou, K., Gillet, J.-F., Doucet, J.-L., ... Hardy, O. J. (2014). Soil charcoal to assess the impacts of past Human disturbances on tropical forests. *Plos One*, *9*(11), e108–121.
- Vleminckx, J., Doucet, J.-L., Bauman, D., Hardy, O. J., Morin-Rivat, J., Biwolé, A. B., ... Drouet, T. (2017). The influence of spatially structured soil properties on tree community assemblages at a landscape scale in the tropical forests of southern Cameroon. *Journal of Ecology*, *105*, 354–366.
- Vleminckx, J., Salazar, D., Fortunel, C., Mesones, I., Davila, N., Lokvam, J., ... Fine, P.V.A. (2018). Divergent secondary metabolites and habitat filtering both contribute to tree species coexistence in the Peruvian Amazon. *Frontiers in Plant Science*, *9*, 836. doi: 10.3389/fpls.2018.00836.
- Wagner, H. H., & Dray, S. (2015). Generating spatially constrained null models for irregularly spaced data using Moran spectral randomization methods. *Methods in Ecology and Evolution*, *6*, 1169–1178.
- Willis, K. J., Gillson, L., & Brncic, T. M. (2004). How “virgin” is virgin rainforest? *Science*, *304*, 402–403.
- Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E., ... Zanne, A. E. (2010). Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, *91*, 3664–3674.
- Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S. L., ... Chave, J. (2009). Global wood density database. Dryad. Identifier: <http://hdl.handle.net/10255/dryad.235>.

Tables

Table 1. Guild (LLP = Long-living pioneer; SB = shade-bearer), wood-specific gravity (WSG, g/cm³), and occurrence of the seven targeted tree species in our sampling. The last column indicates the mean diameter at breast height (DBH) for each species (\pm standard deviation).

Species	Guild	WSG	Occurrence	DBH (cm)
<i>Milicia excelsa</i> (Moraceae)	LLP	0.574	8	76.7 (\pm 15.5)
<i>Pericopsis elata</i> (Fabaceae)	LLP	0.639	10	71.6 (\pm 13.7)
<i>Triplochiton scleroxylon</i> (Malvaceae)	LLP	0.335	3	84.9 (\pm 15.7)
<i>Desbordesia glaucescens</i> (Irvingiaceae)	SB	0.915	14	80.2 (\pm 17.4)
<i>Dialium pachyphyllum</i> (Fabaceae)	SB	0.922	8	52.8 (\pm 5.1)
<i>Diospyros crassiflora</i> (Ebenaceae)	SB	0.858	7	64.2 (\pm 22.1)
<i>Staudtia kamerunensis</i> (Myristicaceae)	SB	0.797	10	54.6 (\pm 20.4)

Figures

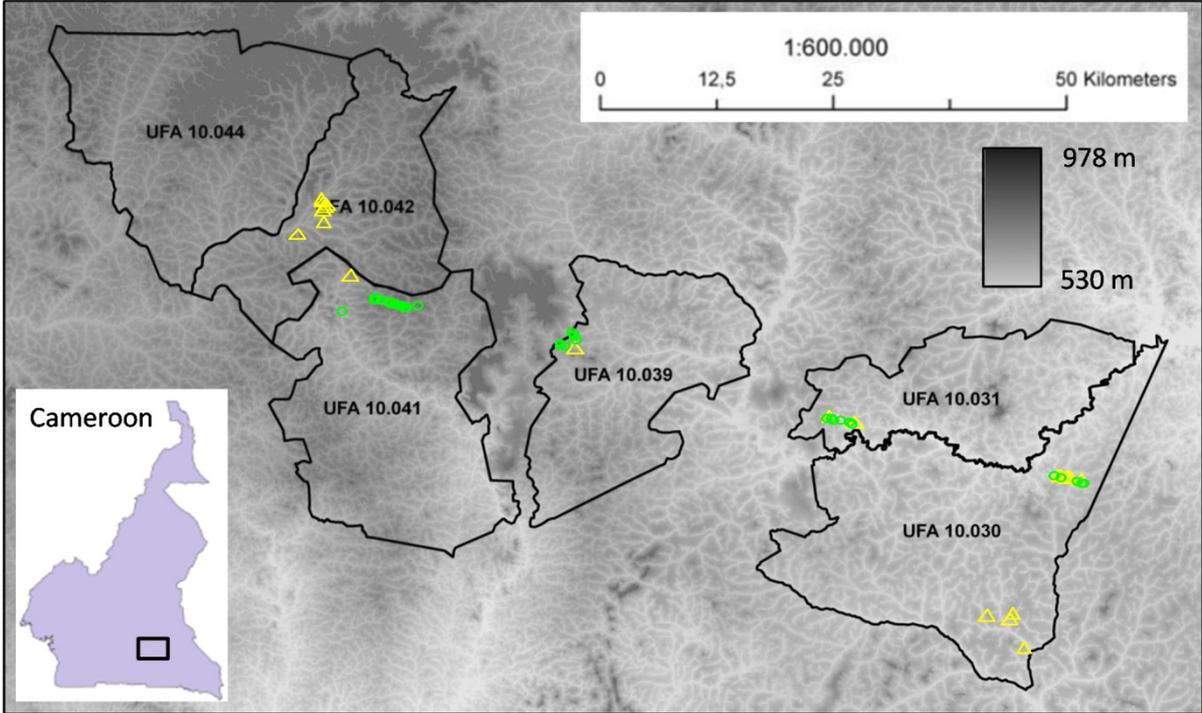


Fig.1. Distribution of the 60 target trees (black dots) over the study area. Green circles and yellow triangles correspond to shade-bearer and long-living pioneer target trees, respectively. The grey scale corresponds to an elevation gradient (in meters). UFA = “Unité Forestière d’Aménagement” (= “Management Forest Unit”).

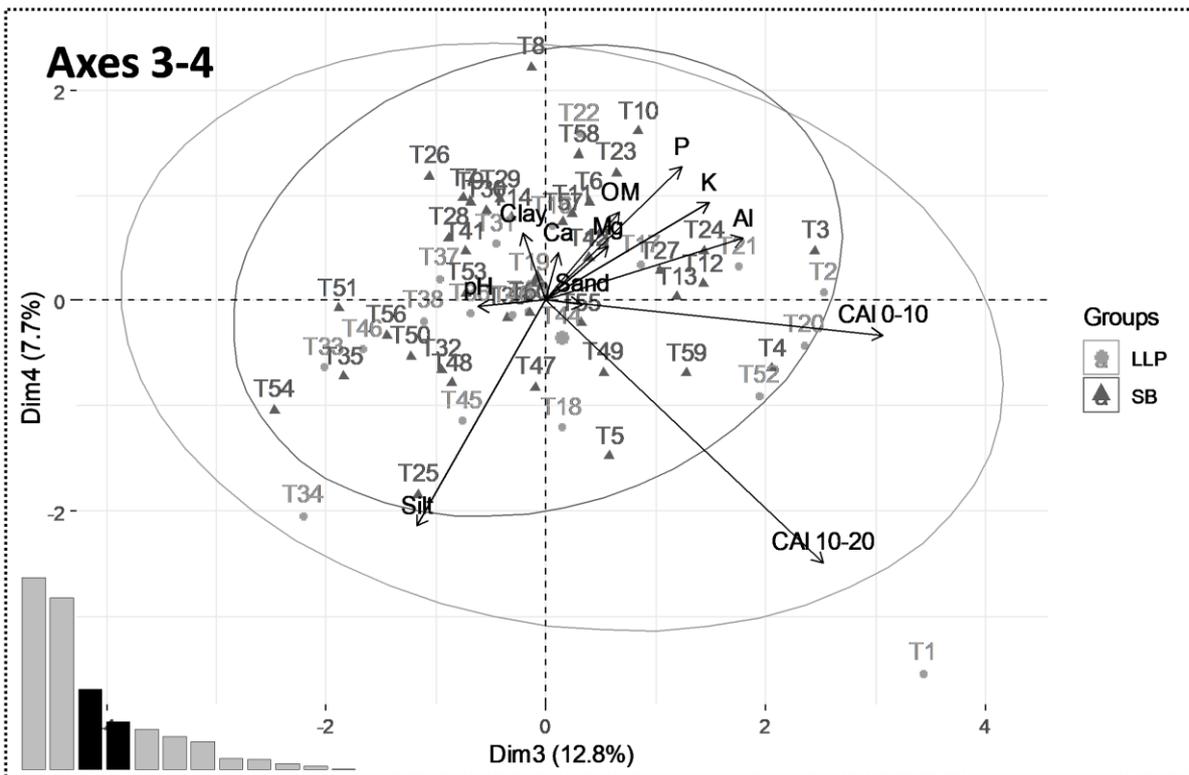
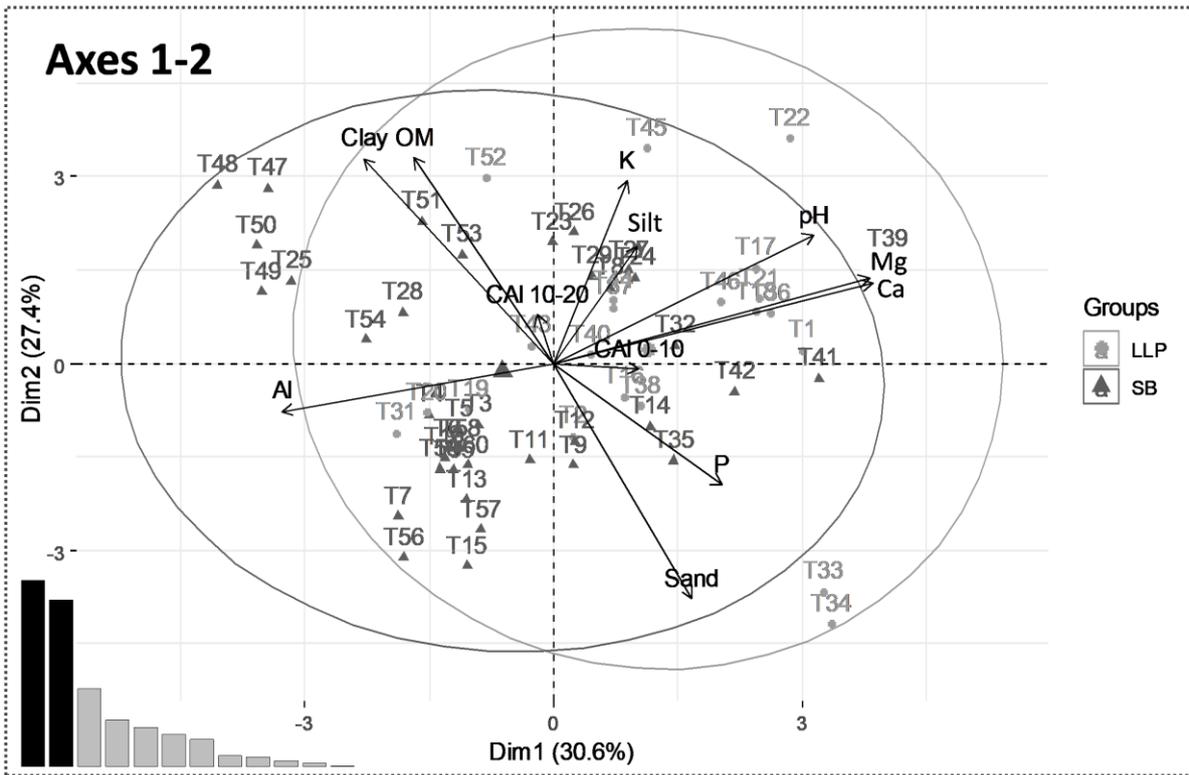


Fig. 2. PCA biplot showing plot scores and the projection of soil and charcoal abundance variables on axes 1-2 and 3-4. Only axes 1 to 3 represented higher variation than expected under a broken stick model. LLP/SB = Long-Living Pioneer/Shade-Bearer target trees.

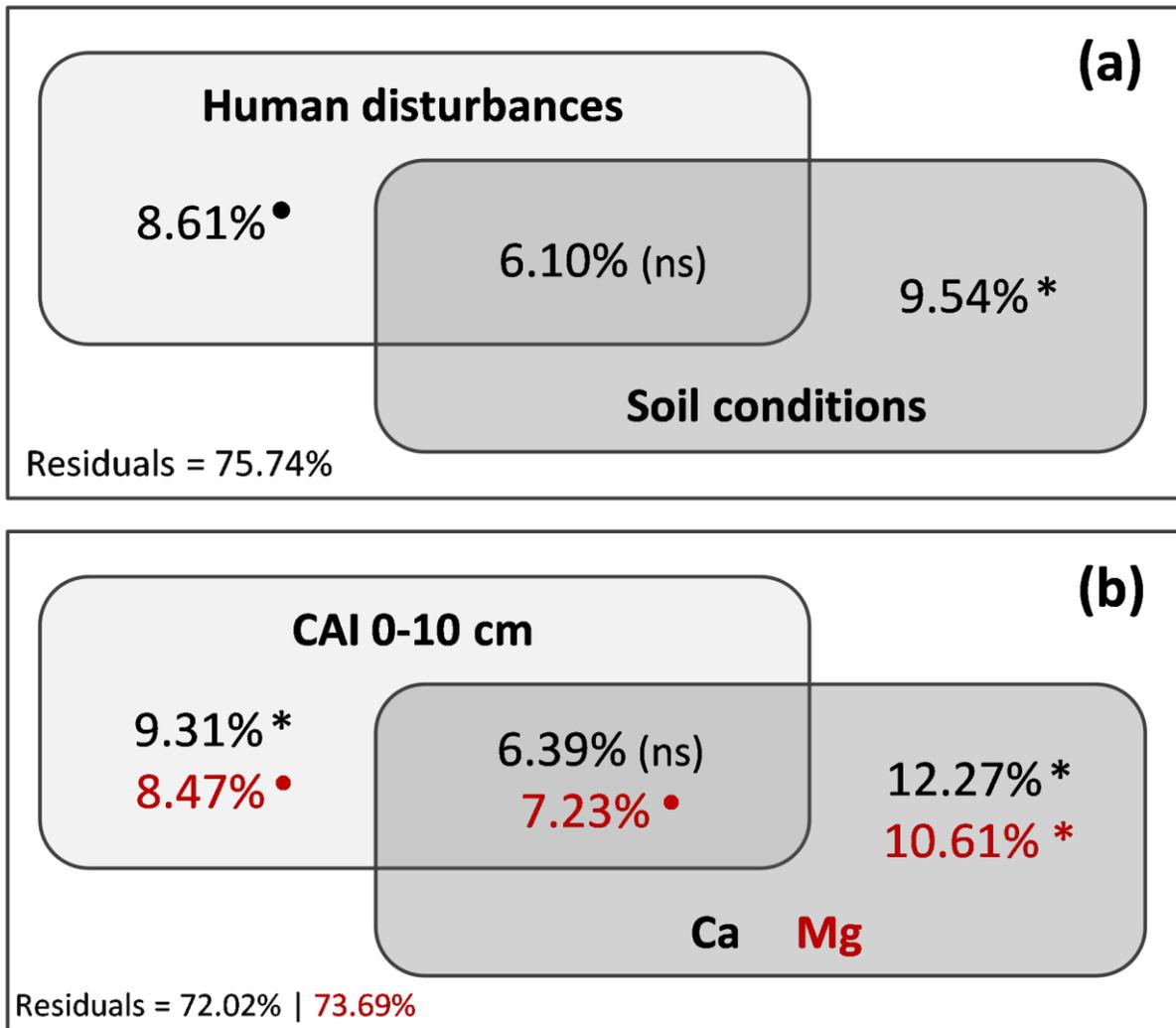


Fig. 3. (a) Venn diagram showing the proportions (adjusted R^2) of mean WSG variation explained purely by past human disturbances (assessed through charcoal abundance in the 0-10 and 10-20 cm soil layer), soil conditions (all VIF-selected soil variables) the co-variation of charcoal and soil variables. (b) Same diagram showing the proportions obtained by using the explanatory variables displaying a significant model-averaged coefficient (see Figure 4), i.e. charcoal abundance in the 0-10 cm soil layer (CAI 0-10 cm), Ca and Mg (values in red correspond to fractions obtained with Mg). $*P \leq 0.05$; $0.05 \leq P < 0.1$; *ns* = not significant.

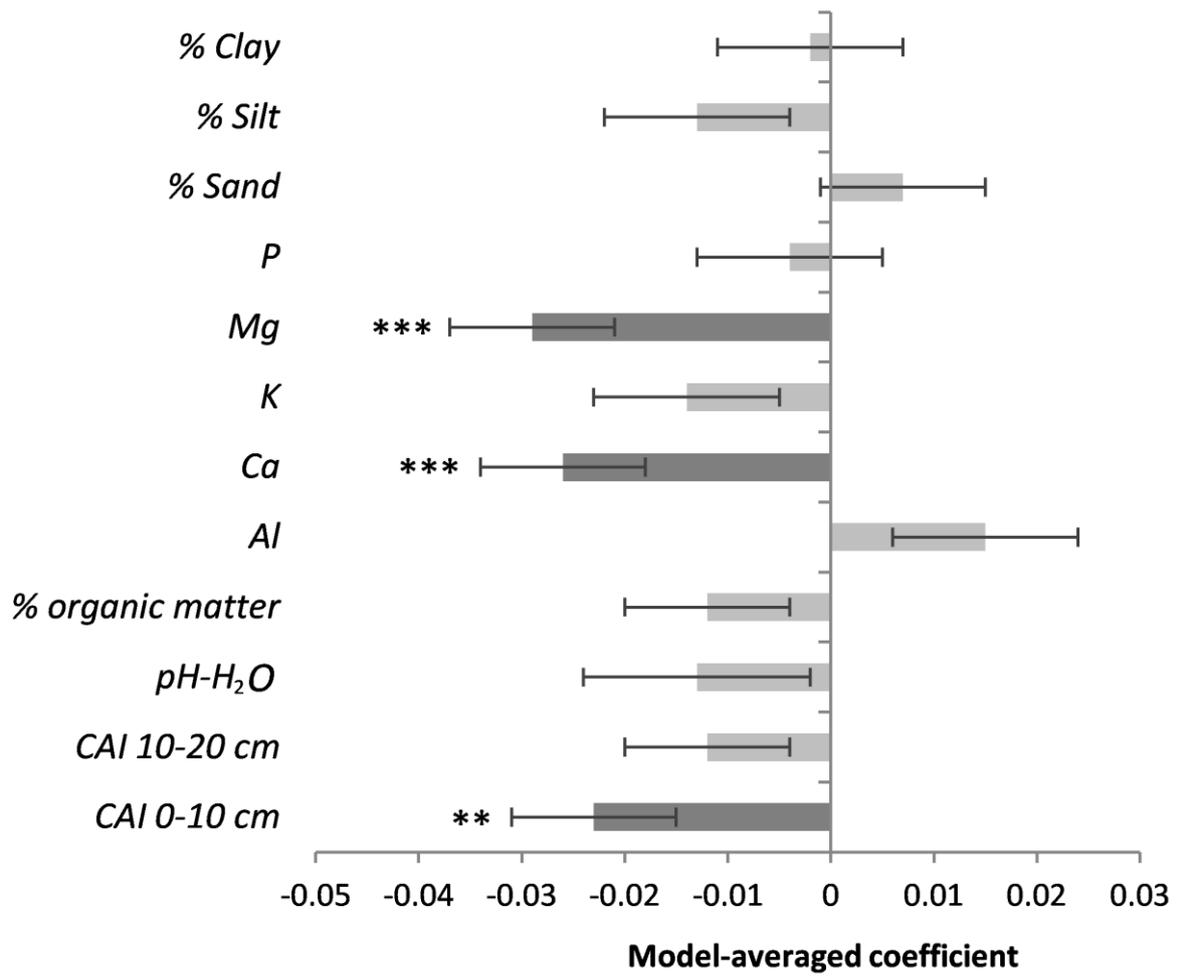


Fig. 4. Model average coefficients estimates quantifying the effect of seven explanatory variables on the mean wood-specific gravity variation, tested using the MSR procedure (** $P \leq 0.01$; *** $P \leq 0.001$). Error bars represent the standard deviations of the coefficient estimates.

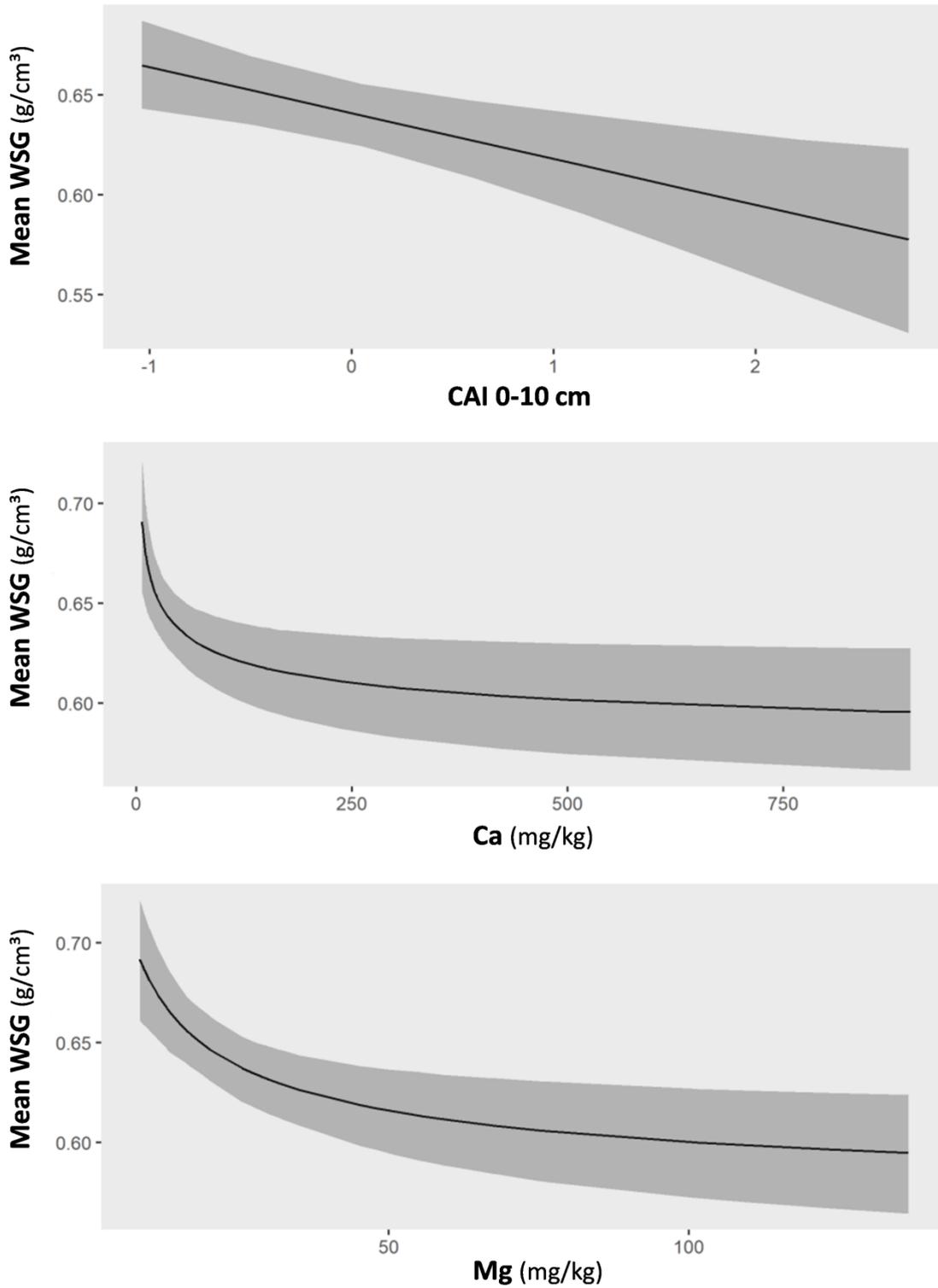


Fig. 5. Regression models illustrating the negative association between the mean wood specific gravity (Y axis) and: the mean CAI in the 0-10 cm soil layer, Ca and Mg (all variables were untransformed). The grey area corresponds to the 95% confidence envelope.

List of supplementary material

(available at <https://onlinelibrary.wiley.com/doi/full/10.1111/jvs.12861>)

Appendix 1 Main dataset used in our model averaging analyses, comprising the spatial coordinates of the target trees and all the response and explanatory variables.

Appendix S2. List of the 117 species recorded in our inventories, with their wood-specific gravity and corresponding light requirement guild.

Appendix S3. R code used to perform our analyses.

Appendix S4. Result details from the model averaging analysis.

Table S1. Pearson correlations between response variables and axis scores from a principal component analyses performed on soil and charcoal abundance variables.

Table S2. Mean values of each explanatory variable within the two groups of target trees (LLP and SB) and *P*-value of the MSR test of comparison between groups.

Table S3. Mean values of each explanatory and response variables within plots where charcoal remains were detected in the 0-10 cm soil layer and plots where no charcoals were found in the same layer.

Table S4. Pearson correlations among all pairs of explanatory variables.

Figure S1. Boxplots representing the distribution of wood-specific gravity values for each guild, showing the *p*-values of the one-way ANOVA (top left) and the Tukey test (red dotted horizontal lines). Black dotted lines correspond to median values, boxes are interquartile ranges and whiskers are minimum and maximum values.