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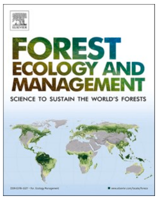

Disturbance and climate affect species richness and aboveground biomass relationship in a forest–savanna transition ecosystem

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ABSTRACT

The relationship between species richness and aboveground biomass (richness–biomass relationship) is a major facet of ecosystem functions and has stimulated debates over the past decades. However, we still lack basic knowledge on whether this relationship has consistent patterns across natural and human-impacted vegetation cover types. More importantly, the effects of disturbance and climatic conditions on species richness and aboveground biomass remain controversial. Using data from 197 0.5-ha plots established within a forest-savanna transition ecosystem, we determined three ecological vegetation covers via non-metric multidimensional scaling, obtained gridded climate data and calculated disturbance index from species succession guilds. We examined the

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consistency of the richness–biomass relationship across the vegetation covers using general linear models and further analysed the effects of disturbance and climatic conditions on this relationship using non-mixed and mixed linear models. We identified three vegetation cover types corresponding to Old-growth forests, Cocoa agroforests and Woodland savannas, suggesting a succession gradient from late-, mid-, and early-successions, respectively. Aboveground biomass consistently increased with species richness across the three vegetation cover types (i.e. positive relationship). Species richness interacts with climate humidity to increase aboveground biomass while interaction of species richness and disturbance rather decreases aboveground biomass consistently across the vegetation cover types. Our results provide insights into the relationship between diversity and ecosystem functions, having implications for ecosystem restoration and understanding ecological consequences of disturbance and climate change in the forest-savanna ecosystem.

1. Introduction

Tropical forests are extremely important to humanity. They contain about 50 – 80 % of the Earth's biodiversity (Rajpar, 2018; Raven, 1988), harbour over 95 % of the world's estimated 40,000 tree species (Slik et al., 2015), and store half of the world's biomass carbon in their terrestrial vegetation (Lewis et al., 2015). Despite the provision of these important ecosystem services, tropical forests are experiencing unprecedented human disturbance by land conversion (Foley et al., 2005) which is depleting biodiversity ecosystem functions (BEF) (Naeem et al., 2012). The BEF has attracted interests and debates in recent decades and the relationship between species richness and biomass has been at the core of this debates (Cardinale et al., 2007; Chisholm et al., 2013; Guo and Berry, 1998; Mittelbach et al., 2001; Roswell et al., 2023; Schuldt et al., 2023). Controversies range from the simple existent of the relationship (Adler et al., 2011), to its variation over time (Cardinale et al., 2007) and space (Chisholm et al., 2013), the magnitude and direction (Mittelbach et al., 2001), the shape (Guo and Berry, 1998; Mittelbach, 2010; Mittelbach et al., 2001) and the role of succession gradient (Lasky et al., 2014) on the relationship. Ongoing discussions focus on environmental determinants of this relationship; how does disturbance affect the richness–biomass relationship across vegetation cover types? This is important because long-term disturbance is expected to impose a successional shift in the diversity-biomass relationship (Lasky et al., 2014).

The relationship between species richness and aboveground biomass describes the effects that differing number of tree species may have on stand-level aboveground biomass (Rosenzweig, 1995). The prevalence of the relationship depends on the spatial scale considered (Chisholm et al., 2013; Day et al., 2014), is influenced by climate (Ammer, 2019), and by both climate and soil (Homeier and Leuschner, 2021; Li et al., 2020). Losses in productivity is linked to concomitant decline in species richness across global forest ecosystems (Liang et al., 2016).

Disturbance plays important roles in the richness–biomass relationship. It has been demonstrated that diversity–biomass relationships are dynamic across succession; correlations between species diversity and biomass change with succession in tropical forests (Lasky et al., 2014). Long-term disturbances may reduce biomass within the community while altering the species richness; from slow-growing shade-bearers to fast-growing pioneers. As a result, disturbance fosters the establishment and persistence of certain species successional guild, such as pioneers and non-pioneers light demanding (NPLD) trees, which increases the richness of species in the community (Hawthorne, 1996, 1995). It is thus speculated that species richness would peak along the disturbance gradient and then decline once disturbance intensities get too high to support the survival of shade-tolerant species in the system (Bongers et al., 2009). However, at extremely high levels of disturbance, dominated by pioneer tree species, the difference between old-growth and disturbed forests would be smaller as all communities are expected to have relatively few NPLD and pioneer species (Bongers et al., 2009).

The magnitude of the richness–biomass relationship is equally important. Studies have recorded a positive, or negative, or hump-shaped or even no relationship at all between richness and biomass. In the case of a positive relationship where higher species richness enhances biomass, niche complementary would likely be the underlying mechanism (Cardinale et al., 2007; Loreau and Hector, 2001). However, dominance by species with particular traits, (e.g. monodominant forest stands; Djuikouo et al., 2010) may impose a selection effect and result in a negative relationship, with subsequent effects on ecosystem processes (Loreau and Hector, 2001). A hump-shaped relationship is evident when large heterogenous environments are studied. As such a gradient involving the positive and negative conditions that make up the two sides of the of the hump-shaped curve with the possibility of a plateau are studied (Guo and Berry, 1998). Studies therefore need to sample wider gradient to cover wide environmental conditions influencing the relationship between species richness and biomass.

The forest-savanna transition (*sensu* Oliveras and Malhi, 2016) defines the ecosystem where both forests and open woodland savannas exist as discrete patches under a similar climate zone (Veenendaal et al., 2015). Elsewhere, forest-savanna transitions have often been referred to as savanna *sensu lato* (Bouvet et al., 2018), zones of (ecological) tension (Veenendaal et al., 2015) or more generally as vegetation transitions or ecotones (Gosz, 1993; Kark and van Rensburg, 2006). Although forest-savanna transitions occur across the tropics, the afro-tropical forest and savanna are probably the most remarkable, occupying presumably 50 % of continental area and therefore represent a large biomass carbon pool (Djiofack et al., 2024). Yet, studies examining the relationship between diversity and ecosystem function in the forest-savanna transitions are hard to find. The origin and development of these transitions in some African countries stems from human disturbance (Bouvet et al., 2018; Youta-Happi et al., 2003), although ecological niche construction may also account for the emergence of ecotones (Liautaud et al., 2020). Studying species richness–biomass within this sensitive ecosystem is key to estimating the impacts of climate change on ecosystem functions (Tilman et al., 2014).

The goal of this study was to evaluate the consistency of species richness–aboveground biomass relationship across vegetation cover types while exploring the influence of climate and disturbance mechanisms. To do this, we established 197 0.5-ha plots across sites in a forest–savanna transition ecosystem undergoing human pressure from agriculture (e.g. cocoa agroforests) and random fire events (e.g. for hunting). Our approach of using fixed, medium-sized plots permitted us to exclude the weak richness–biomass relationship reported with large sized plots (Day et al., 2014) or the influence of varying plot sizes (Chisholm et al., 2013). We investigated the following three questions: (1) Is the relationship between species richness and aboveground biomass consistent across vegetation cover types? (3) How does species succession guilds mediate the response of aboveground biomass to species richness? (3) How does other factors such as climate and human disturbance affect the species richness–biomass relationship?

2. Material and methods

2.1. Study area

This study focused on a forest-savanna transition ecosystem in central Cameroon between 4°39 and 4°49 N, and 11°4 and 11°19 E (Fig. 1). The forest-savanna transition covers about 35 % (14–17 million hectares) of the approximately 47.6 million hectares of Cameroon's national territory (Mayaux et al., 1999; Onana, 2018) and is characterized by transitional vegetation of the Guineo–Congolian and the Sudanian sectors (White, 1983). Different forest formations are known within the Guineo–Congolian sector, including the semi-deciduous forests dominated by Malvaceaes and Cannabaceaes, and the Atlantic forests characterized by rare Caesalpiniaceae (Letouzey, 1985). The Sudanian zone is characterised by saxicolous savannas with stunted Combretaceaes (Letouzey, 1985). Both vegetation formations occur at low to mid altitude (600–900 m). Co-existence of savannas, gallery forests and tall canopy forests are separated by moderately sharp boundaries (Mitchard and Flintrop, 2013). The mean annual temperature of the study area is between 21.5°C and 25.3°C with mean annal rainfall between 1513 mm and 2157 mm (Fick and Hijmans, 2017). Soils are sesquioxide and ferralitics on acid rocks. The indurated ferralitic soils are characterized by gravel outcrops and are especially frequent in savannas (Yerima and Ranst, 2005).

2.2. *Study design and field measurements*

We used a stratified random plot design (Gentry, 1988) for the establishment of small plots of 0.5 ha. Within each 0.5 ha small plot, all trees with diameter at 1.3 m breast height (DBH) ≥ 5 cm were measured and identified *in-situ*. Large trees with buttresses or deformations were measured at 30 cm below or above the deformation or buttress. Only woody non-liana species were sampled as sites were visibly scarce of lianas. Morpho-species codes were consistently assigned to unidentified species (e.g. Fabaceae 1, *Beilschmiedia* sp1, Unknown 1). Botanical specimens were collected for further confirmation of the *in-situ* identification at the mini-herbarium of the Plant Systematics and Ecology laboratory of the Higher Teachers' Training College of the University of Yaoundé I and the National Herbarium of Cameroon in Yaoundé. Among the 58,835 trees sampled from the 197 0.5-ha plots, 1261 trees were identified as morpho-species (e.g. *Drypetes* sp., *Uapaca* sp.) and were used for the biomass calculations. We homogenised the nomenclature for genera and families according to the APG IV (2016) classification and species names were corrected using the Plants of the World Online (POWO, 2023; http://www.plantsoftheworldonline.org).

2.3. *Vegetation cover types and succession*

Being unsure of which vegetation cover type to allot the sampled plots and consequently determined the succession state of the forest, we employed a non-metric multidimensional scaling with stable solution from random starts (NMDS) in combination with indicator species analyses to assign plots to different vegetation cover types. The NMDS was run on a species × plot matrix while specifying the Bray-Curtis dissimilarity as the optimal measure of ecological distance (Legendre and Legendre, 1998). We used the *metaMDS* function from the vegan *R*-package (Oksanen et al., 2012), allowing all the default commands but specifying the number of dimensions (i.e. $k = 3$), minimum and maximum numbers of random starts in search of stable solution (i.e. *trymax* = 500) and maximum number of iterations in the single NMDS run (i.e. *maxit* = 999). We used the $k = 3$ dimensions obtained from the NMDS, as separate ecological groups upon which indicator species or multi-level pattern analysis (De Cáceres and Legendre, 2009) was run. We tested whether there was a subset of species (or indicator species) showing a non-random association with each of the three ecological groups using the *multipatt* function in the *indicspecies R*-package (De Cáceres and Legendre, 2009). The *multipatt* function created combinations of the three predetermined ecological groups and compares each combination with the species matrix, chooses the combination with a highest association value and test the statistical significance of the best matching associations (De Cáceres and Legendre, 2009).

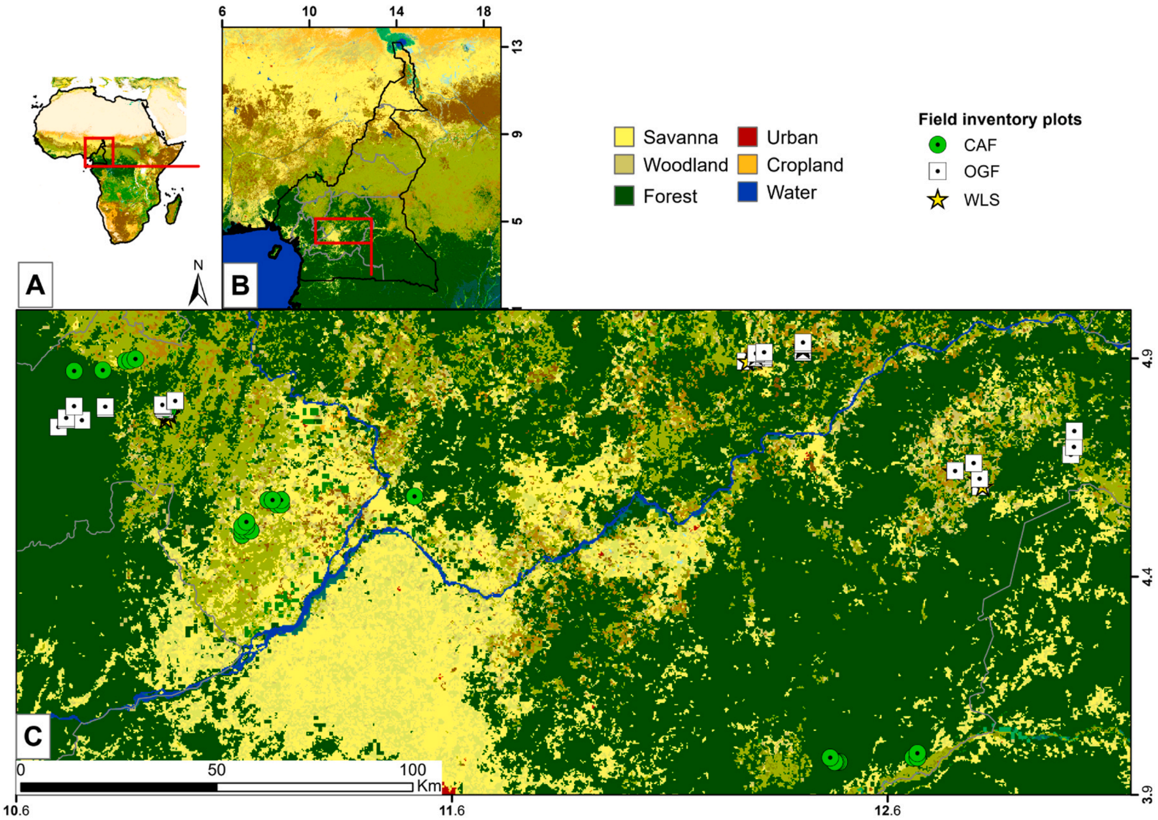

Fig. 1. Location of the study. Maps showing: (A) Africa with Cameroon inside red square; (B) Cameroon with study site inside red rectangle and (C) study site with different colours and symbols representing the plots and land use in the forest-savanna ecosystem in Cameroon.

2.4. Species richness and aboveground biomass

We considered the total number of species as the species richness and used the climate-based allometric equation 7 from Chave et al. (2014) which is similar to locally-derived allometric equations because of its dependence on the local climatic factors (see Eq.1). We supplied as covariates of the allometric equation, the tree diameter (DBH, cm), species mean wood density (WD, g cm^{-3}) and the environmental stress index (E) as the main predictors of AGB (Mg ha^{-1}). We obtained WD for tree species from the DRYAD global repository (Chave et al., 2009; Zanne et al., 2009) using the following steps described by Gourlet-Fleury et al. (2011): (i) for well identified tree species with corresponding WD in the DRYAD database, we attributed the mean WD from the different values, and (ii) for trees identified as morpho-species (7.3 % of trees in the data), we attributed the means of the genus, family, order or simply plot-level mean WD if the previous was not found. We used equation 6a of Chave et al. (2014) to calculate E (Eq. 2), which is based on temperature seasonality (TS) from the *Worldclim* dataset (bioclimatic variable 4, see Fick and Hijmans 2017), climatic water deficit (CWD, mm yr^{-1}) and precipitation seasonality (PS) as defined in the *Worldclim* dataset (bioclimatic variable 15, see Fick and Hijmans 2017). The above procedures for computing the E and AGB were conducted using the *computeE* and *computeAGB* functions in the BIOMASS R-package (Réjou-Méchain et al., 2017).

$$AGB = \exp(-2.024 - 0.896 \times E + 0.920 \times \ln(WD) + 2.795 \times \ln(D) - 0.0461 \times [\ln(D)^2]) \tag{1}$$

$$E = (0.178 \times TS - 0.938 \times CWD - 6.61 \times PS) \times 10^{-3} \tag{2}$$

The total plot-level AGB was calculated as the sum of AGB for all trees within a plot.

2.5. Disturbance and humidity indexes

We calculated a disturbance index (DI) or pioneer index (*sensu* Hawthorne 1996) for each plot (see Eq. 3) as the weighted number of species per succession guilds (pioneers, non-pioneer light-demanders, shade-bearers) over the total number of species (sum_{spp}) (Hawthorne, 1996, 1995). The DI integrates the effects of a wide range of disturbance including windthrow, logging, farming or fire (Hawthorne, 1996; Sheil and Burslem, 2003). The DI also highlights regeneration or succession of a forest, as judged from the proportion of pioneers species and other non-pioneer light-demanders in the community (Hawthorne, 1996) and has been used to predict disturbance in tropical vegetations (Bongers et al., 2009). Because our study involved agricultural crops, we added cultivated species to the calculation of DI. Assuming that pioneer species are the first colonizers and would be the strongest indicators of disturbance, we weighted the number of pioneers species (P_{spp}) by a factor of 3 and the number of non-pioneer light-demander species ($NPLD_{spp}$) by a factor of 2 and number of cultivated species ($Agric_{spp}$) by a factor of 1 (Hawthorne, 1996, 1995). Shade-bearer species can be indicator of undisturbed forest and were thus not weighted or simply weighted by a factor of 0. Data for species succession guilds were obtained from the *CoForTraits* database (Bénédet et al., 2019) and complemented with our expert knowledge of the local flora.

$$\mathrm{DI} = \frac{\left((P_{spp} \times 3) + (NPLD_{spp} \times 2) + (Agric_{spp} \times 1) \times 100\right) \times 100}{sum_{spp}} \tag{3}$$

Humidity index (HI) was calculated from the plot's mean annual precipitation (MAP, mm) and mean annual temperature (MAT, °C) based on Eq. 4 (Eq.4; Tuhkanen, 1980) below. MAP and MAT were obtained from the *WorldClim* database version 2.1 (https://www.worldclim.org/data/worldclim21.html) at a resolution of 30 arc sec, for the period from 1970 to 2000 (Fick and Hijmans, 2017). Higher HI values imply higher air humidity or lower aridity. It should be noted that the HI has been used as indicator of the degree of climate humidity (Tuhkanen, 1980) as well as a predictor of the relationship between species richness and biomass (Li et al., 2020).

$$\mathrm{HI} = \frac{MAP}{(MAT + 10)} \tag{4}$$

2.6. Statistical analysis

To explore the relationship between species richness and aboveground biomass (AGB) across vegetation cover types (VCT) and whether disturbance and/or climate affect the richness–biomass relationship, we fitted several non-mixed and mixed linear models involving additive and interactive terms. The linear non-mixed models were fitted using a generalised least square (*gls*) as this minimizes the total error and yields an unbiased and precise prediction. Because species richness was repeatedly measured in the different vegetation cover and that VCT could vary randomly in space, another set of linear mixed-effect (*lme*) models were fitted introducing the VCT as the random effect terms. Both the *gls* and *lme* models were fitted using the Maximum Likelihood method opposed to the Restricted Maximum Likelihood method because of its robustness in comparing models with different fixed effect terms (Pinheiro et al., 2022). In all the models, AGB was the response while species richness, climate and disturbance were the predictors, and these were fitted as the fixed effect term and VCT as the random effect term.

In a series of *gls* models, we examined whether prediction of AGB would be random, that is, none of species richness, disturbance or climate factors significantly predicts AGB (null model, Table 1; M1); whether species richness significantly predicts AGB (Table 1; M2). We presumed that, and examined whether, species richness would have a quadratic effect on AGB (Table 1; M3) but we discarded the quadratic or null model if it was not significant at $P \leq 0.05$. We equally examined whether AGB and species richness were related to disturbance index (DI) and/or humidity index (HI), as additive or interactive fixed-effect terms (Table 1; M1-M11). Because we expected that the vegetation cover types would have a random effect, we re-fitted M1 to M11 as *lme* models (Table 1; M12-M121) and used the VCT as the random effect terms. For each of the *gls* and *lme* models, we tested a specific hypothesis (Table 1). Finally, we compared the performances of the 21 *gls* and *lme* models using the following coefficients of determination; Bayesian Information Criterion (BIC), Akaike Information Criterion (AIC), log-likelihood (logLik), deviance and the variance explained (R^2). We used the *gls* function from the nlme *R*-package (Pinheiro et al., 2022), and the *lmer* function from the *lme4 R*-package (Bates et al., 2015).

We selected the most parsimonious model as the one with the lowest BIC, AIC, logLik, deviance and highest R^2. We calculated the marginal R^2 (R^2_m; variance explained only by the fixed effect terms) and conditional R^2 (R^2_c; variance explained by both the fixed effect and the random effect terms) for the mixed effect models using the *MuMIn R*-package (Bartoń, 2009).

To explore the effect of long-time disturbance on species diversity, hence the richness–biomass relationship, we used the *gls* model to determine the contributions of succession guilds on species richness. Succession guilds of each species was determined as the proportion of the number of species belonging to one of pioneer, NPLD, cultivated or shade-bearer species.

For each stage of the analyses, we explore the behaviour of the model or relationship when all plots were pooled together and across each vegetation cover type. We repeated the original analyses with the locally weighted polynomial (loess) regressions and specified the smoothing ($span = 1$) and degree of polynomials ($degree = 2$).

3. Results

A total of 197 0.5-ha plots comprising 58 835 trees having diameter

Table 1
Models structure for the species richness–biomass relationship including covariates and hypotheses. AGB; Aboveground biomass, DI; Disturbance index, HI; Humidity index, VCT; Vegetation cover type. Models M1 to M11 were fitted as non-mixed Generalised Least Square (*gls*) and refitted as models M12 to M21 using mixed-effects Mixed effect models. The three vegetation cover types (Old-growth forests, Wood land savannas and Cocoa-agroforests) as the random effect terms.

Models	Coded model structure	Hypotheses
M1	AGB ∼ 1	Prediction of AGB would be random
M2	AGB ∼ Diversity	Variation of AGB would be predicted by species richness (positive or negative relationship)
M3	AGB ∼ Diversity + I (Diversity^2)	Variation of AGB would be predicted by the quadratic effect of species richness
M4	AGB ∼ DI	Variation of AGB would be linearly (but negative) predicted by disturbance index
M5	AGB ∼ Diversity + DI	Disturbance index would directly affect the positive species richness–relationship; - succession guild curves for pioneers and cultivated species will be lower than those for non-pioneer light-demanding and shade-bearer species.
M6	AGB ∼ Diversity × DI	
M7	AGB ∼ HI	Variation of AGB would be linearly (but positive) predicted by humidity index
M8	AGB ∼ Diversity + HI	Humidity index would directly affect the positive richness–biomass relationship
M9	AGB ∼ Diversity × HI	
M10	AGB ∼ Diversity + DI + HI	Humidity and disturbance indexes would combine to directly affect the positive richness–biomass relationship
M11	AGB ∼ Diversity × DI × HI	
M12	AGB ∼ 1 + (1 | VCT)	M1 - M11 above is a function of the vegetation cover types
M13	AGB ∼ Diversity + (1 | VCT)	
M14	AGB ∼ DI + (1 | VCT)	
M15	AGB ∼ Diversity + DI + (1 | VCT)	
M16	AGB ∼ Diversity × DI + (1 | VCT)	
M17	AGB ∼ HI + (1 | VCT)	
M18	AGB ∼ Diversity + HI + (1 | VCT)	
M19	AGB ∼ Diversity × HI + (1 | VCT)	
M20	AGB ∼ Diversity + DI + HI + (1 | VCT)	
M21	AGB ∼ Diversity × DI × HI × (1 | VCT)	

Table 2
Summary of plot-level predictor and response variables for each vegetation cover types. CAF; cacao agroforests, OGF; old-growth forests, WLS; Woodland savanna. Mean and standard deviation are provided. AGB; Aboveground biomass; $Shad_{spp}$; number of shade bearer species; P_{spp}; number of pioneers species; $NPLD_{spp}$; number of non-pioneer light-demander species; $Agric_{spp}$; number of cultivated species.

	Vegetation cover types		
	CAF	OGF	WLS
Number of plots (x 0.5-ha)	140	37	20
Mean number of species	4.4 ± 4.19	19.68 ± 8.39	4.9 ± 3.13
Number of indicator species	4	106	19
AGB (Mg.ha^{-1})	115.02 ± 78.7	217.99 ± 119.1	103.23 ± 117.0
$Shad_{spp}$	43	123	14
P_{spp}	56	80	41
$NPLD_{spp}$	67	99	28
$Agric_{spp}$	15	7	0
Disturbance index	173.06 ± 28.60	166.71 ± 33.18	236.67 ± 29.92
Humidity index	49.06 ± 3.64	50.71 ± 6.82	49.72 ± 4.62
Total trees	39,791	11,107	7,937

of ≥ 5 at 1.3 m breat height were used for this study. The response and predictor variables were determined for each plot and are summarized in Table 2 in below.

Three groups of vegetation cover types each consisting of several plots were identified from the combination of NMDS analysis (Table 2; Fig. S1) and indicator species analysis (Table S1). The first vegetation cover was a group of 37 plots and was interpreted as old-growth forests (OGF; Fig. S1) because of the 106 indicator species (Table S1). The second vegetation cover was composed of 20 plots and because of the 19 indicator species (Table S1), this vegetation cover was interpreted as the Woodland savannas (WLS; Fig. S1). The third vegetation cover comprised 140 plots and four indicator species (Table S1) and was interpreted as the Cocoa agroforests (CAF; Fig. S1). *Posthoc* pair-wise comparisons of the three vegetation cover types showed significant differences between pairs of the vegetation cover types (Fig. S2).

The relationship between species richness and aboveground biomass was positive and significant both when all vegetation cover types were pooled together ($F = 3.09$, $R^2 = 0.46$, $P < 0.001$; Fig. 2a) and when vegetation cover types were considered independently (*gls* for OGF: $F = 4.26$, $R^2 = 0.57$, $P < 0.001$; WLS: $F = 7.32$, $R^2 = 0.46$, $P = 0.001$; CAF: $F = 5.97$, $R^2 = 0.42$, $P < 0.001$; Fig. 2c, e, g), signifying that aboveground biomass increases with species richness irrespective of the vegetation cover type. The strength of this relationship (expressed by R^2) decreases across the vegetation cover types from OGF, through WLS to CAF (Table 3) but a rapid increase in biomass with species richness was observed for the WLS (see inset of Fig. 2e). The curves of the species richness-biomass relationship were unimodal indicating that aboveground biomass increases with species richness for each vegetation cover type (Fig. 2c, e, g).

The proportion of species' succession guild mediated the effects of species richness on aboveground biomass (Fig. 2). With all the vegetation cover types pooled together, increase in species richness was matched by; a decrease in the proportion of cultivated species (Fig. 2b), an initial increase then later decrease towards the end of the relationship (monotonic curvilinear) of NPLD and pioneer species (Fig. 2b and Fig. S5) and an increase of shade-bearer species (Fig. 2b and Fig. S5). For each of the three vegetation cover types, increase in species richness was matched by different patterns of species succession guild: (i) a decrease in the proportions of cultivated, pioneer and NPLD species but an increase in proportion of shade-bearer for OGF (Fig. 2d; Fig. S6b); (ii) a decrease in the proportions of pioneer and shade-bearer nut an increase in the proportion of NPLD species for WLS (Fig. 2f; Fig. S6c) and (iii) a decrease in the proportions of cultivated species, and an increase in the proportions of NPLD, pioneer and shade-bearer species for CAF (Fig. 2h; Fig. S6a).

Best statistically significant models explaining variation of aboveground biomass, involved either one predictor only (e.g. richness or humidity index), two predictors (species richness and disturbance index or species richness and humidity index) or all the three predictors (richness, disturbance, and humidity) when fitted either with non-mixed effect model or with mixed effects model (Table 3). A total of 12 models were significantly different thus rejecting the null hypotheses that their variances or intercepts were different from zero. These models included five mixed effect models (M19, M18, M16, M21, M21; Table 3) and seven non-mixed effect models (M11, M9, M5, M8, M7, M4, M2; Table 3). The vegetation cover types were significant as the random effect terms across all the mixed effect models and the three predictors were equally significant as interaction or additive fixed effect terms in some models (Table 3). The most parsimonious model among the 12 selected models with the lowest BIC, AIC and logLik and highest R^2 involved the species richness and the humidity index (i.e. model M19; Table 3).

Disturbance index and humidity index had significant influence on species richness and on aboveground biomass (Fig. 3, Figs. S3 & S4; Table 3). The disturbance index had a significant negative influence on the aboveground biomass (*gls*: $F = -0.61$, $R^2 = 0.046$, $P = 0.002$) and on the species richness (*gls*: $F = -0.010$, $R^2 = 0.026$, $P = 0.023$) when all the

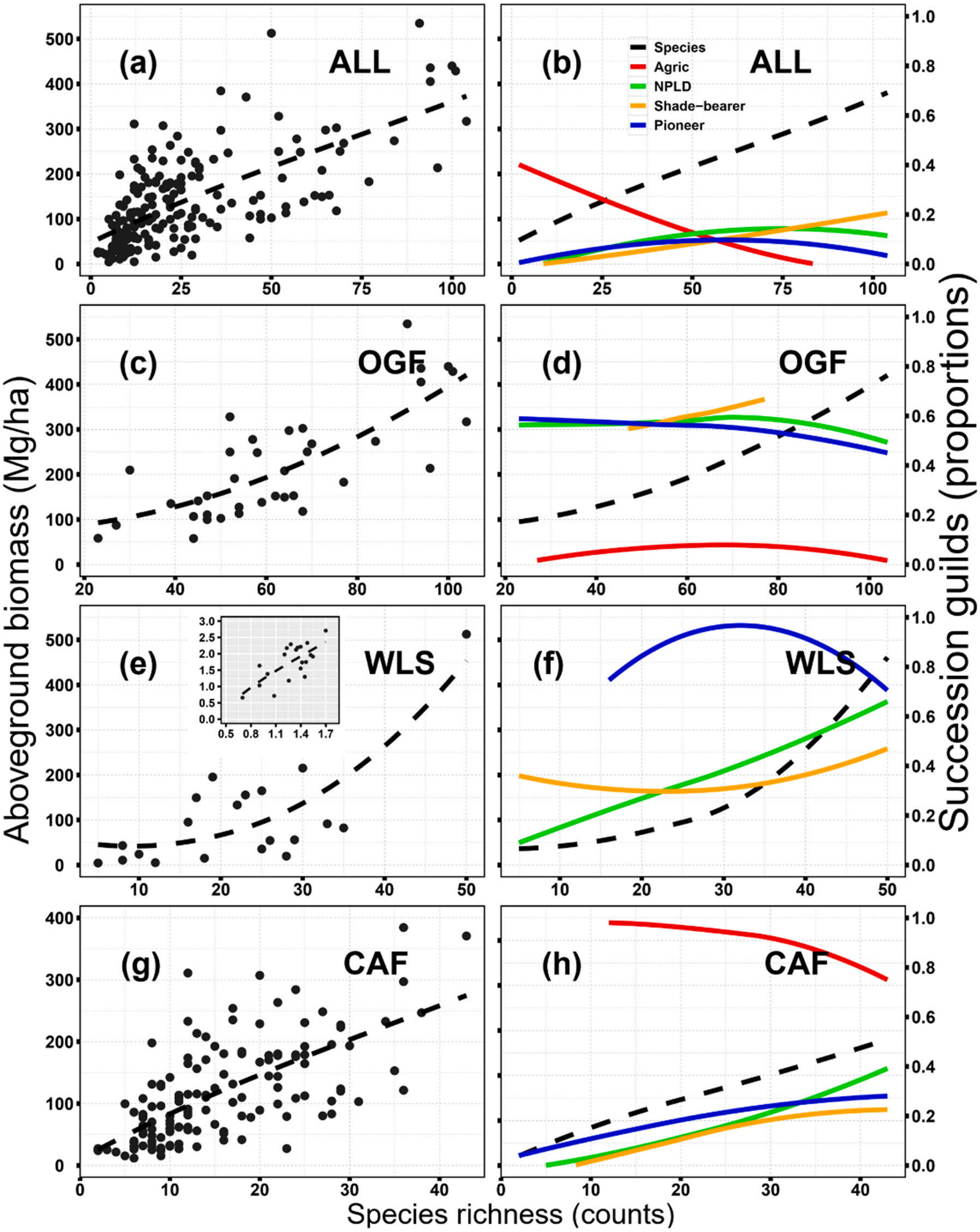

Fig. 2. Relationships between species richness and aboveground biomass mediated by species successional guilds. Left panel (a, c, e, g) with primary x-axis and y-axis represents the relationships between species richness and aboveground biomass. Right panel (b, d, f, h) with secondary y-axis represents proportion of species succession guilds. Coloured lines in right panel represent species succession guilds for cultivated (Agric), Non-pioneer light-demanding (NPLD), Shade-bearer and pioneer species. Black dashed lines in both panels represent the same species richness – biomass regression models. Models were fitted for; All vegetation cover types pooled (a, b); for Old-growth forests (OGF: c, d); for Wood land savanna (WLS: e, f) with inset showing log transformed scales and for Cocoa agroforest (CAF: g, h).

vegetation cover types were pooled (Fig. 3a; Table 3). Out of the three vegetation cover types, WLS had the highest average disturbance index but lowest average aboveground biomass and moderate species richness (Table 2) while the OGF had the lowest disturbance index but the highest species richness (Table 2; Fig. S3a) and highest average aboveground biomass (Fig. S3b). A slight increase in aboveground biomass matching a small increase in disturbance index was observed for the CAF (Fig. S3b) but this relationship was not statistically significant (*gls*: $F = 0.418$, $R^2 = -0.004$, $P = 0.519$). In contrast to disturbance index, the humidity index rather had a significant positive influence on the aboveground biomass (*gls*: $F = 4.50$, $R^2 = 0.041$, $P = 0.004$) and on the species richness (*gls*: $F = 0.72$, $R^2 = 0.022$, $P = 0.037$) considering all vegetation cover types pooled (Fig. S4; Table 3). Out of the three vegetation cover types, WLS and CAF had a similar lowest average

Table 3

Model results for the prediction of aboveground biomass from species diversity, climate and disturbance. AGB represents aboveground biomass, Diversity represents species richness, DI represents Disturbance index, HI represents Humidity index, (1 | VCT) defines the three vegetation cover types (old-growth forest, woodland savanna, and cocoa agroforest) as mixed-effect terms. Coefficients determination for each model included BIC; Bayesian Information Criterion, AIC; Akaike Information Criterion, logLik; Maximum Likelihood parameter, R_m^2; marginal coefficient of determination, R_c^2 conditional coefficient of determination; *P*; *P*-value significant at 0.005 for the fixed effect term (P_m) and mixed effect (P_c). Results are ordered beginning with the most parsimonious models.

Models	Coded model structure	BIC	AIC	logLik	R_m^2	R_c^2	P_m	P_c
M19	$\text{AGB} \sim \text{Diversity} \times \text{HI} + (1 \mid \text{VCT})$	2243.178	2223.479	−1105.739	0.634	0.771	<0.001	<0.001
M18	$\text{AGB} \sim \text{Diversity} + \text{HI} + (1 \mid \text{VCT})$	2249.438	2233.022	−1111.511	0.619	0.772	<0.001	<0.001
M13	$\text{AGB} \sim \text{Diversity} + (1 \mid \text{VCT})$	2249.859	2236.726	−1114.363	0.612	0.762	<0.001	<0.001
M16	$\text{AGB} \sim \text{Diversity} \times \text{DI} + (1 \mid \text{VCT})$	2252.196	2232.496	−1110.248	0.621	0.755	0.002	<0.001
M15	$\text{AGB} \sim \text{Diversity} + \text{DI} + (1 \mid \text{VCT})$	2253.918	2237.502	−1113.751	0.611	0.762	1	<0.001
M20	$\text{AGB} \sim \text{Diversity} + \text{DI} + \text{HI} + (1 \mid \text{VCT})$	2254.338	2234.638	−1111.319	0.618	0.771		<0.001
M21	$\text{AGB} \sim \text{Diversity} \times \text{DI} \times \text{HI} \times (1 \mid \text{VCT})$	2256.592	2223.760	−1101.880	0.642	0.766	0.252	<0.001
M9	$\text{AGB} \sim \text{Diversity} \times \text{HI}$	2260.118	2243.702	−1116.851	0.506		<0.001	-
M6	$\text{AGB} \sim \text{Diversity} \times \text{DI}$	2264.092	2247.676	−1118.838	0.496			-
M11	$\text{AGB} \sim \text{Diversity} \times \text{DI} \times \text{HI}$	2267.124	2237.575	−1109.788	0.541		0.001	-
M2	$\text{AGB} \sim \text{Diversity}$	2267.881	2258.031	−1126.016	0.458		<0.001	-
M5	$\text{AGB} \sim \text{Diversity} + \text{DI}$	2268.949	2255.816	−1123.908	0.470		<0.001	-
M8	$\text{AGB} \sim \text{Diversity} + \text{HI}$	2269.195	2256.062	−1124.031	0.469		<0.001	-
M10	$\text{AGB} \sim \text{Diversity} + \text{DI} + \text{HI}$	2271.351	2254.935	−1122.467	0.477		0.090	-
M3	$\text{AGB} \sim \text{Diversity} + \text{I(Diversity\^{}2)}$	2272.833	2259.701	−1125.850	0.459		0.565	-
M14	$\text{AGB} \sim \text{DI} + (1 \mid \text{VCT})$	2361.682	2348.549	−1170.275	0.040	0.202		<0.001
M17	$\text{AGB} \sim \text{HI} + (1 \mid \text{VCT})$	2363.102	2349.969	−1170.984	0.023	0.229		<0.001
M12	$\text{AGB} \sim 1 + (1 \mid \text{VCT})$	2363.449	2353.600	−1173.800	0.000	0.221		<0.001
M4	$\text{AGB} \sim \text{DI}$	2379.315	2369.466	−1181.733	0.046		<0.001	-
M7	$\text{AGB} \sim \text{HI}$	2380.334	2370.484	−1182.242	0.041		0.004	-
M1	$\text{AGB} \sim 1$	2383.360	2376.794	−1186.397	0.000			-

humidity index and lowest average species richness while the highest average humidity index was recorded for the OGF with a corresponding highest average species richness (Table 2; Fig. S4a).and highest average aboveground biomass (Table 2; Fig. S4b).

4. Discussion

Understanding the relationship between species diversity and aboveground biomass across vegetation cover types is imperative for devising strategies for managing biodiversity ecosystem functions (Lasky et al., 2014; Naeem et al., 2012). We found that aboveground biomass increases with species richness consistently across three vegetation cover types in a forest-savanna transition zone in Cameroon. Moreover, we found that the effect of species richness on aboveground biomass weakens across these vegetation cover types with old-growth forest having the tightest and cocoa-agroforest having the weakest relationship. Lastly, we found that among others, species richness interacts with climate humidity to increase aboveground biomass while interaction between species richness and disturbance decreases aboveground biomass across the vegetation cover types. We discuss these results in the light of ecological succession and environmental determinism and anthropization.

Our results from the non-metric multidimensional scaling (NMDS) analysis revealed three distinct groups of vegetation cover types notably Old-growth forests, Woodland savannas, and Cocoa agroforests (Fig. S.1), each of these are clearly identifiable by the specific indicator species that characterized them (Table S1). These vegetation cover types may be therefore indicative of an exceptional blend between ecological succession and human activities operating within this forest-savanna transition ecosystem. The Old-growth forest with the highest diversity of 106 indicator species may indicate a mature forest in the late successional stage. As has been reported elsewhere and in this study (Table 2), Old-growth forests are usually characterised by high proportions of shade-bearer species (Vleminckx et al., 2020). In contrast, Cocoa agroforests, which has the lowest diversity of only four indicator species, is an example of a human-impacted vegetation cover type. The Cocoa agroforests may be thought as a vegetation cover type in which the succession process is regulated to balance agricultural productivity with ecological concerns. As a result, high-value timber and other tree species of economic importance are conspicuous in Cocoa agroforests (Sonwa et al., 2014). Considered as a vegetation cover type at the intermediate succession stage, the Woodland savannas with a diversity of 19 indicator species reflects a mix of grassland and scattered trees, regaining its initial state after human disturbance such as fire and grazing. A similar observation had rather interpreted these changes as forest encroaching into savanna (Mitchard et al., 2009; Mitchard and Flintrop, 2013; Youta-Happi et al., 2003). Our results equally showed that both species richness and aboveground biomass decrease with the intensity of disturbance (Fig. 3;Fig. S3a) and thus suggest that land use can have opposing effects on the recovery of vegetation quality and structure, as also reported for neotropical forests (Marcano-Vega et al., 2002; Pascarella et al., 2000). We recorded substantial shift in species succession guilds, from shade-bearer species (which are usually dominant in intact old-growths), to pioneer species (which are prominent in disturbed young vegetation). Indeed, the proportion of pioneers (low quality) species was highest in the most disturbed woodland savannas than any other vegetation cover types in this study. However, the proportion of pioneers was negatively related to species richness while the proportion of shade-bearer species were rather positively related to species richness (Fig. S5), suggesting that a gradual succession from pioneers to shade-bearers is matched by an increase in species richness from woodland savanna to old-growth forests.

The relationship between species richness and ecosystem function (as measured by biomass) have been reported be positive, negative, or curvilinear (Guo and Berry, 1998; Mittelbach et al., 2001). In this study, we found aboveground biomass to increase with species richness (positive relationship) and this was consistent for the three vegetation cover types (Fig. 2a, c, e, g). This result corroborates those from other tropical ecosystems (Chisholm et al., 2013; Day et al., 2014; Homeier and Leuschner, 2021; Steur et al., 2022). We postulate that this positive relationships are consistent with niche complementarity hypothesis, where higher species richness implies that species develop different niches and are therefore able to access more variable resources, thus enhancing the overall biomass (Poorter et al., 2015). This relationship has been observed for smaller plots of 0.04-ha and becomes inconsistent for larger plots of 0.25-ha and 1-ha, suggesting that the species richness–biomass relationship is highly scale-dependent (Chisholm et al., 2013; Day et al., 2014; Sullivan et al., 2017). Succession niche effect

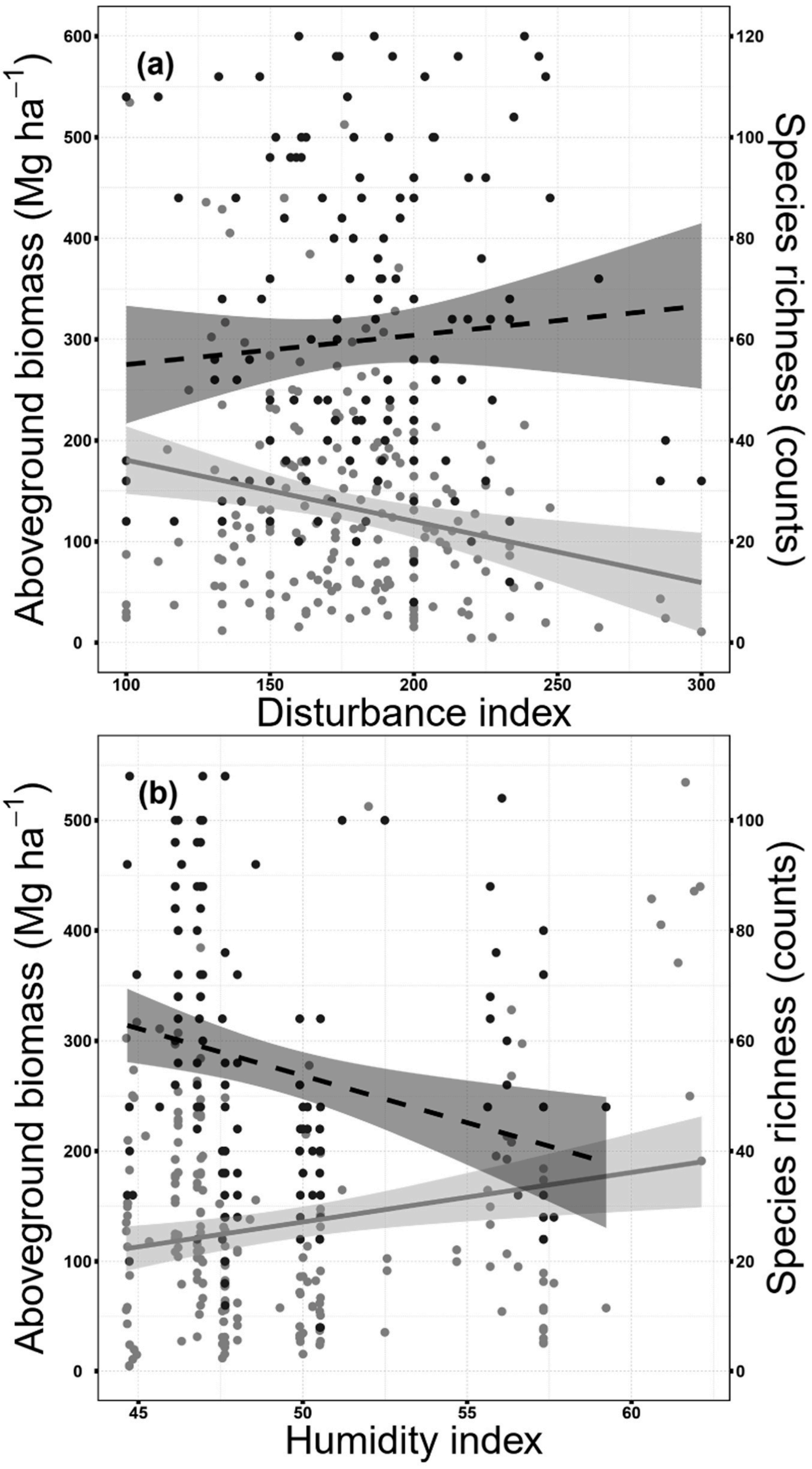

Fig. 3. Relationships between aboveground biomass and species richness with disturbance index and with humidity index. (a) Disturbance index (x-axis) versus aboveground biomass (y-axis) in grey and disturbance index versus species richness (secondary y-axis) in black symbols. (b) Humidity index (x-axis) versus aboveground biomass (y-axis) in grey and humidity index versus species richness (secondary y-axis) in black symbols.

occurs when stands dominated by early-successional fast-growing species are more productive than those with more diverse communities which are usually composed of both early-successional and less productive late-successional species (Lasky et al. 2014 & references therein). We noticed that the proportion of pioneers early-succession species declined from plots with low species richness to plots with high-species richness (Fig. S5). This pattern is consistent with increasing aboveground biomass, which we observed for the woodland savannas (Fig. S.4).

Our results equally showed that species richness–biomass relationship weakens across the three vegetation cover types, suggesting that environmental determinants mediate the relationship, consistent with a recent global experimental analysis (Duffy et al., 2017). Specifically, the effect of species richness on biomass was weakest for Cocoa agroforest and strongest for Old-growth forests. A potential explanation of this result is that the influence of species richness on biomass is a response to environmental factors related to climate and disturbance. Indeed, our analysis indicated that climate humidity index (a derivative of mean annual precipitation and temperature expressing climatic humidity) had a strong positive effect on the richness and biomass. The vegetation cover types with higher humidity index (higher humidity) also had more species and higher biomass. Thus, climate humidity may be the most important determinant of the species richness–biomass relationship for this forest-savanna transition, as also reported for Mongolian steppe communities (Li et al., 2020). Earlier, rainfall has been known to be a critical determinant of woody cover in mixed woodland savannas (Sankaran et al., 2005).

Considered as an independent determinant or a covariate of climate humidity, our results showed that disturbance also mediated the effect of species richness on biomass in this forest-savanna landscape. This is important because disturbance is expected to affect species diversity over long time scales (Molino and Sabatier, 2001). As measured from the plant perspective in this study, disturbance may entail a complex interaction of human activities at play: for example, fire that partially or completely consumes the forest cover can favour establishment of many previously non-existent species (Bond et al., 2005; Gentry 1988; Legendre, Legendre 1998), logging and windthrow open the forest canopy in favour of the establishment of fast-growing species (Chazdon, 2014).

The positive relationship between species richness and biomass has important co-benefits for biodiversity conservation and climate change mitigation (Pan et al., 2011). Species-rich ecosystems can sequester substantial amount of carbon; a major consideration for conservation policies (Anderson-Teixeira, 2018; Gibbs et al., 2007). Old-growth forests with the high aboveground biomass also have high species richness, with substantially more biomass than other vegetation cover with high disturbance. Nevertheless, Woodland savanna and other less species-rich vegetation cover types with low biomass provide other important ecosystem services, including but not limited to belowground biomass storage, habitat for faunal diversity, water regulation, and nutrient cycling (Egoh et al., 2009). Woodland savannas and other similar ecosystems with less species and biomass can benefit from restoration activities but must integrate ecological, economic and social dimensions in both research and management policies (Bai et al., 2007).

5. Conclusion

We found a consistent pattern in the relationship between species richness and aboveground biomass across three ecologically determined vegetation cover types. The relationship is positive linear for Old-growth forests, Woodland savanna and Cocoa agroforests, indicating that species richness consistently increases aboveground biomass in this forest-savanna ecosystem. We noted that climate humidity greatly promotes the establishment of species and sequestration of biomass, but disturbance tends to alter the quality and quantity of species richness and biomass. Thus, we recommend that both field and airborne models developed to predict biomass from species richness for this landscape should directly incorporate measures of climate humidity and disturbance to increase their applicability. REDD policies that prioritize species-rich vegetation cover types could incorporate ecological restoration of less species-rich vegetation to regain initial diversity and productivity functions.

Authors contributions statement

M.C.N, M.B.L. and R.L.P.B.K. designed the research; M.C.N, M.B.L., R.L.P.B.K., M.G.B., C.K.D., A.B.T.F., L.B.F., A.M., S.M., M.C.S.M., G.N., N.E.N.N., S.T.M. and L.T.S., participated in data collection; M.B.L analysed the data; M.C.N, M.B.L. and R.L.P.B.K. wrote the first draft, S.T.M., N.G., M.R.M.E., B.S., and L.Z read the draft and provided useful feedback.

CRediT authorship contribution statement

Nicole M. Guedje: Writing – review & editing, Supervision, Methodology. **Louis Zapfack:** Writing – review & editing, Supervision, Methodology. **Laure B. Fabo:** Writing – review & editing, Methodology. **Alex B.T. Fomekong:** Writing – review & editing, Methodology. **Lise Zemagho:** Writing – review & editing, Supervision, Methodology. **Cyntia K. Djouking:** Writing – review & editing, Methodology. **Bonaventure Sonké:** Writing – review & editing, Supervision, Methodology. **Marius R.M. Ekué:** Writing – review & editing, Methodology, Funding acquisition. **Narcisse E.N. Njila:** Writing – review & editing, Methodology, Data curation. **Stephane T. Momo:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **Le Bienfaiteur T. Sagang:** Writing – review & editing, Methodology. **Marius G. Babonguen:** Writing – review & editing, Methodology. **Marie C.S. Momo:** Writing – review & editing, Supervision, Methodology. **Moses B. Libalah:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Géraldine D. Nguemo:** Writing – review & editing, Methodology, Data curation. **Louis-Paul-Roger B. Kabelong:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Data curation, Conceptualization. **Tagnang N. Madountsap:** Writing – review & editing, Methodology. **Adrian Medou:** Writing – review & editing, Methodology. **Melanie C. Nyako:** Writing – review & editing, Writing – original draft, Methodology, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122196.

References

Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Stanley Harpole, W., O'Halloran, L.R., Grace, J.B., Michael Anderson, T., Bakker, J.D., Biederman, L.A., Brown, C.S., Buckley, Y.M., Calabrese, L.B., Chu, C.J., Cleland, E.E., Collins, S.L., Cottingham, K.L., Crawley, M.J., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Fay, P.A., Firn, J., Frater, P., Gasarch, E.I., Gruner, D.S., Hagenah, N., Lambers, J.H.R., Humphries, H., Jin, V.L., Kay, A.D., Kirkman, K.P., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Lambrinos, J.G., Li, W., MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W., Mortensen, B., Orrock, J.L., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D., Stevens, C.J., Sullivan, L.L., Wang, G., Wragg, P.D., Wright, J.P., Yang, L.H., 2011. Productivity is a poor predictor of plant species richness. Science 80 (333), 1750–1753. https://doi.org/10.1126/science.1204498.

Ammer, C., 2019. Diversity and forest productivity in a changing climate. N. Phytol. 221, 50–66. https://doi.org/10.1111/nph.15263.

Anderson-Teixeira, K.J., 2018. Prioritizing biodiversity and carbon. Nat. Clim. Chang. https://doi.org/10.1038/s41558-018-0242-6.

APG IV, 2016. An update of the Angiosperm Phylogeny group classification for the orders and families of flowering plants: APG IV. Bot. J. Linn. Soc. 181, 1–20. https://doi.org/10.1111/boj.12385.

Bai, Y., Wu, J., Pan, Q., Huang, J., Wang, Q., Li, F., Buyantuyev, A., Han, X., 2007. Positive linear relationship between productivity and diversity: Evidence from the Eurasian Steppe. J. Appl. Ecol. 44, 1023–1034. https://doi.org/10.1111/j.1365-2664.2007.01351.x.

Bartoń, K., 2009. MuMIn: Multi-model inference. CRAN 〈https//cran.r-project.org/web/packages/MuMIn/index.html〉.

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Bénédet, F., Doucet, J.-L., Fayolle, A., Gillet, J.-F., Gourlet-Fleury, S., Vincke, D., 2019. CoForTraits, African plant traits information database. version 1.0. [WWW Document].

Bond, W.J., Woodward, F.I., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. N. Phytol. 165, 525–538. https://doi.org/10.1111/j.1469-8137.2004.01252.x.

Bongers, F., Poorter, L., Hawthorne, W.D., Sheil, D., 2009. The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. Ecol. Lett. 12, 798–805. https://doi.org/10.1111/j.1461-0248.2009.01329.x.

Bouvet, A., Mermoz, S., Le Toan, T., Villard, L., Mathieu, R., Naidoo, L., Asner, G.P., 2018. An above-ground biomass map of African savannahs and woodlands at 25 m resolution derived from ALOS PALSAR. Remote Sens. Environ. 206, 156–173. https://doi.org/10.1016/j.rse.2017.12.030.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., Weis, J.J., 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proc. Natl. Acad. Sci. U. S. A. 104, 18123–18128. https://doi.org/10.1073/pnas.0709069104.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Chang. Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629.

Chazdon, R.L., 2014. Forest Regeneration following Selective Logging and Land-Use Synergisms. In: Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation. Chicago. University of Chicago Press, Chicago, pp. 146–166. https://doi.org/10.7208/9780226118109-012.

Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K., Bebber, D.P., Bin, Y., Bohlman, S.A., Bourg, N.A., Brinks, J., Bunyavejchewin, S., Butt, N., Cao, H., Cao, M., Cárdenas, D., Chang, L.W., Chiang, J.M., Chuyong, G., Condit, R., Dattaraja, H.S., Davies, S., Duque, A., Fletcher, C., Gunatilleke, N., Gunatilleke, S., Hao, Z., Harrison, R.D., Howe, R., Hsieh, C.F., Hubbell, S.P., Itoh, A., Kenfack, D., Kiratiprayoon, S., Larson, A.J., Lian, J., Lin, D., Liu, H., Lutz, J.A., Ma, K., Malhi, Y., Mcmahon, S., Mcshea, W., Meegaskumbura, M., Mohd. Razman, S., Morecroft, M.D., Nytch, C.J., Oliveira, A., Parker, G.G., Pulla, S., Punchi-Manage, R., Romero-Saltos, H., Sang, W., Schurman, J., Su, S.H., Sukumar, R., Sun, I.F., Suresh, H.S., Tan, S., Thomas, D., Thomas, S., Thompson, J., Valencia, R., Wolf, A., Yap, S., Ye, W., Yuan, Z., Zimmerman, J.K., 2013. Scale-dependent relationships between tree species richness and ecosystem function in forests. J. Ecol. 101, 1214–1224. https://doi.org/10.1111/1365-2745.12132.

Day, M., Baldauf, C., Rutishauser, E., Sunderland, T.C.H., 2014. Relationships between tree species diversity and above-ground biomass in Central African rainforests: implications for REDD. Environ. Conserv. 41, 64–72. https://doi.org/10.1017/S0376892913000295.

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574. https://doi.org/10.1890/08-1823.1.

Djiofack, B.Y., Beeckman, H., Bourland, N., Belanganayi, B.L., Laurent, F., Ilondea, B.A., Nsenga, L., Huart, A., Longwwango, M.M., Deklerck, V., Lejeune, G., Verbiest, W.W. M., Van den Bulcke, J., Van Acker, J., De Mil, T., Hubau, W., 2024. Protecting an artificial savanna as a nature-based solution to restore carbon and biodiversity in the Democratic Republic of the Congo. Glob. Chang. Biol. 30, 1–18. https://doi.org/10.1111/gcb.17154.

Djuikouo, M.N.K., Doucet, J.L., Nguembou, C.K., Lewis, S.L., Sonké, B., 2010. Diversity and aboveground biomass in three tropical forest types in the Dja Biosphere Reserve, Cameroon. Afr. J. Ecol. 48, 1053–1063. https://doi.org/10.1111/j.1365-2028.2010.01212.x.

Duffy, J.E., Godwin, C.M., Cardinale, B.J., 2017. Biodiversity effects in the wild are common and as strong as key drivers of productivity. Nature 549, 261–264. https://doi.org/10.1038/nature23886.

Egoh, B., Reyers, B., Rouget, M., Bode, M., Richardson, D.M., 2009. Spatial congruence between biodiversity and ecosystem services in South Africa. Biol. Conserv. 142, 553–562. https://doi.org/10.1016/j.biocon.2008.11.009.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 80 (309), 570–574. https://doi.org/10.1126/science.1111772.

Gentry, A.H., 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Ann. Missouri Bot. Gard. 75, 1–34. https://doi.org/10.5205/reuol.592-5661-1-LE.0401201019.

Gibbs, H.K., Brown, S., Niles, J.O., Foley, J.A., 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. Environ. Res. Lett. https://doi.org/10.1088/1748-9326/2/4/045023.

Gosz, J.R., 1993. Ecotone hierarchies. Ecol. Appl. 3, 369–376. https://doi.org/10.2307/1941905.

Gourlet-Fleury, S., Rossi, V., Rejou-Mechain, M., Freycon, V., Fayolle, A., Saint-Andre, L., Cornu, G., Gerard, J., Sarrailh, J.M., Flores, O., Baya, F., Billand, A., Fauvet, N., Gally, M., Henry, M., Hubert, D., Pasquier, A., Picard, N., 2011. Environmental filtering of dense-wooded species controls above-ground biomass stored in African moist forests. J. Ecol. 99, 981–990. https://doi.org/10.1111/j.1365-2745.2011.01829.x.

Guo, Q., Berry, W.L., 1998. Species richness and biomass: Dissection of the hump-shaped relationships. Ecology 79, 2555–2559 https://doi.org/10.1890/0012-9658(1998)079[2555:SRABDO]2.0.CO;2.

Hawthorne, W.D., 1995. Ecological profiles of Ghanaian forest trees. Trop. For. Pap. No. 29, vi, vi.

Hawthorne, W.D., 1996. Holes and the sums of parts in Ghanaian forest: regeneration, scale and sustainable use. Proc. R. Soc. Edinb. Sect. B Biol. Sci. 104, 75–176. https://doi.org/10.1017/S0269727000006126.

Homeier, J., Leuschner, C., 2021. Factors controlling the productivity of tropical Andean forests: climate and soil are more important than tree diversity. Biogeosciences 18, 1525–1541. https://doi.org/10.5194/bg-18-1525-2021.

Kark, S., van Rensburg, B.J., 2006. Ecotones: marginal or central areas of transition? Isr. J. Ecol. Evol. 52, 29–53. https://doi.org/10.1560/IJEE.52.1.29.

Lasky, J.R., Uriarte, M., Boukili, V.K., Erickson, D.L., John Kress, W., Chazdon, R.L., 2014. The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. Ecol. Lett. 17, 1158–1167. https://doi.org/10.1111/ele.12322.

Legendre, P., Legendre, L., 1998. Numerical Ecology, Numerical Ecology Second English Edition. https://doi.org/10.1021/ic050220j.

Letouzey, R., 1985. Carte phytogéographique du Cameroun, 1:500 000, 8 feuillets + 5 notices. Institut de la Carte Internationale de la Végétation, Toulouse, France.

Lewis, S.L., Edwards, D.P., Galbraith, D., 2015. Increasing human dominance of tropical forests. Science 80 (349), 827–832. https://doi.org/10.1126/science.aaa9932.

Li, Zijing, Li, Zhiyong, Tong, X., Zhang, J., Dong, L., Zheng, Y., Ma, W., Zhao, L., Wang, L., Wen, L., Dang, Z., Tuvshintogtokh, I., Liang, C., Li, F.Y., 2020. Climatic humidity mediates the strength of the species richness–biomass relationship on the Mongolian Plateau steppe. Sci. Total Environ. 718, 137252 https://doi.org/10.1016/j.scitotenv.2020.137252.

Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.D., McGuire, A.D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J.V., Chen, H.Y.H., Lei, X., Schelhaas, M.J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R., Oleksyn, J., Zawiła-Niedźwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L.V., Odeke, D.E., Vasquez, R. M., Lewis, S.L., Reich, P.B., 2016. Positive biodiversity-productivity relationship predominant in global forests. Science 80 (354). https://doi.org/10.1126/science.aaf8957.

Liautaud, K., Barbier, M., Loreau, M., 2020. Ecotone formation through ecological niche construction: the role of biodiversity and species interactions. Ecography 714–723. https://doi.org/10.1111/ecog.04902.

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412, 72–76. https://doi.org/10.1038/35083573.

Marcano-Vega, H., Aide, T.M., Báez, D., 2002. Forest regeneration in abandoned coffee plantations and pastures in the Cordillera Central of Puerto Rico. Plant Ecol. 161, 75–87. https://doi.org/10.1023/A:1020365507324.

Mayaux, P., Richards, T., Janodet, E., 1999. A vegetation map of Central Africa derived from satellite imagery. J. Biogeogr. 26, 353–366.

Mitchard, E.T.A., Flintrop, C.M., 2013. Woody encroachment and forest degradation in sub-Saharan Africa's woodlands and savannas 1982-2006. Philos. Trans. R. Soc. B Biol. Sci. 368, 1–7. https://doi.org/10.1098/rstb.2012.0406.

Mitchard, E.T.A., Saatchi, S.S., Gerard, F., Lewis, S.L., Meir, P., 2009. Measuring Woody Encroachment along a Forest – Savanna Boundary in Central Africa. Earth inter. 13, 1–29. https://doi.org/10.1175/2009EI278.1.

Mittelbach, G.G., 2010. Understanding species richness-productivity relationships: the importance of meta-analyses. Ecology 91, 2540–2544. https://doi.org/10.1890/09-1029.1.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? Ecology 82, 2381–2396 https://doi.org/10.1890/0012-9658(2001)082[2381:WITORB]2.0.CO;2.

Molino, J., Sabatier, D., 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. Science 294 (80), 1702–1704. https://doi.org/10.1126/science.1060284.

Naeem, S., Duffy, J.E., Zavaleta, E., 2012. The functions of biological diversity in an age of extinction. Science 336 (80), 1401–1406. https://doi.org/10.1126/science.1215855.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2012. vegan: Community Ecology Package. https://doi.org/https://github.com/vegandevs/vegan.

Oliveras, I., Malhi, Y., 2016. Many shades of green: The dynamic tropical forest–savannah transition zones. Philos. Trans. R. Soc. B Biol. Sci. https://doi.org/10.1098/rstb.2015.0308.

Onana, J.M., 2018. Mapping the ecosystems of Cameroon. Int. J. Biol. Chem. Sci. 12, 940–957.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333 (80), 988–993. https://doi.org/10.1126/science.1201609.

Pascarella, J.B., Aide, T.M., Serrano, M.I., Zimmerman, J.K., 2000. Land-use history and forest regeneration in the Cayey Mountains, Puerto Rico. Ecosystems 3, 217–228. https://doi.org/10.1007/s100210000021.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R. Core Team, 2022. "nlme" Title Linear and Nonlinear Mixed Effects Models. R Packag. version 3.1-164, ⟨https//CRAN.R-project.org/package=nlme⟩.

Poorter, L., van der Sande, M.T., Thompson, J., Arets, E.J.M.M., Alarcón, A., Álvarez-Sánchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G., Boit, A., Bongers, F., Carvalho, F. a, Casanoves, F., Cornejo-Tenorio, G., Costa, F.R.C., de Castilho, C.V., Duivenvoorden, J.F., Dutrieux, L.P., Enquist, B.J., Fernández-Méndez, F., Finegan, B., Gormley, L.H.L., Healey, J.R., Hoosbeek, M.R., Ibarra-Manríquez, G., Junqueira, a B., Levis, C., Licona, J.C., Lisboa, L.S., Magnusson, W.E., Martínez-Ramos, M., Martínez-Yrizar, A., Martorano, L.G., Maskell, L.C., Mazzei, L., Meave, J. a, Mora, F., Muñoz, R., Nytch, C., Pansonato, M.P., Parr, T.W., Paz, H., Pérez-García, E. a, Rentería, L.Y., Rodríguez-Velazquez, J., Rozendaal, D.M. a, Ruschel, a R., Sakschewski, B., Salgado-Negret, B., Schietti, J., Simões, M., Sinclair, F.L., Souza, P.F., Souza, F.C., Stropp, J., ter Steege, H., Swenson, N.G., Thonicke, K., Toledo, M., Uriarte, M., van der Hout, P., Walker, P., Zamora, N., Peña-Claros, M., 2015. Diversity enhances carbon storage in tropical forests. Glob. Ecol. Biogeogr. 24, 1314–1328. https://doi.org/10.1111/geb.12364.

POWO, 2023. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew [WWW Document]. R. Bot. Gard. Kew. URL https://powo.science.kew.org/ (accessed 3.9.23).

Rajpar, M.N., 2018. Tropical Forests Are An Ideal Habitat for Wide Array of Wildlife Species, in: Tropical Forests - New Edition. https://doi.org/10.5772/intechopen.73315.

Raven, P., 1988. Our Diminishing Tropical Forests in Biodiversity, in: Biodiversity. p. 504.

Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., Hérault, B., 2017. Biomass: an R package for estimating above-ground biomass and its uncertainty in tropical forests. Methods Ecol. Evol. 8, 1163–1167. https://doi.org/10.1111/2041-210X.12753.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time, Species Diversity in Space and Time. Cambridge University Press, UK. https://doi.org/10.1017/cbo9780511623387.

Roswell, M., Harrison, T., Genung, M.A., 2023. Biodiversity-ecosystem function relationships change in sign and magnitude across the Hill diversity spectrum. Philos. Trans. R. Soc. B Biol. Sci. 378 https://doi.org/10.1098/rstb.2022.0186.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Roux, X., Le, Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Worden, J., Zambatis, N., 2005. Determinants of woody cover in African savannas. Nature 438, 8–11. https://doi.org/10.1038/nature04070.

Schuldt, A., Liu, X., Buscot, F., Bruelheide, H., Erfmeier, A., He, J.S., Klein, A.M., Ma, K., Scherer-Lorenzen, M., Schmid, B., Scholten, T., Tang, Z., Trogisch, S., Wirth, C., Wubet, T., Staab, M., 2023. Carbon–biodiversity relationships in a highly diverse subtropical forest. Glob. Chang. Biol. 29, 5321–5333. https://doi.org/10.1111/gcb.16697.

Sheil, D., Burslem, D.F.R.P., 2003. Disturbing hypotheses in tropical forests. Trends Ecol. Evol. 18, 18–26. https://doi.org/10.1016/S0169-5347(02)00005-8.

Slik, J.W.F., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P., Alves, L.F., Ashton, P., Balvanera, P., Bastian, M.L., Bellingham, P.J., van den Berg, E., Bernacci, L., da Conceição Bispo, P., Blanc, L., Böhning-Gaese, K., Boeckx, P., Bongers, F., Boyle, B., Bradford, M., Brearley, F.Q., Breuer-Ndoundou Hockemba, M., Bunyavejchewin, S., Calderado Leal Matos, D., Castillo-Santiago, M., Catharino, E.L.M., Chai, S.-L., Chen, Y., Colwell, R.K., Chazdon, R.L., Robin, C.L., Clark, C., Clark, D.B., Clark, D.A., Culmsee, H., Damas, K., Dattaraja, H.S., Dauby, G., Davidar, P., DeWalt, S.J., Doucet, J.-L., Duque, A., Durigan, G., Eichhorn, K.A.O., Eisenlohr, P.V., Eler, E., Ewango, C., Farwig, N., Feeley, K.J., Ferreira, L., Field, R., de Oliveira Filho, A.T., Fletcher, C., Forshed, O., Franco, G., Fredriksson, G., Gillespie, T., Gillet, J.-F., Amarnath, G., Griffith, D.M., Grogan, J., Gunatilleke, N., Harris, D., Harrison, R., Hector, A., Homeier, J., Imai, N., Itoh, A., Jansen, P.A., Joly, C.A., de Jong, B.H.J., Kartawinata, K., Kearsley, E., Kelly, D.L., Kenfack, D., Kessler, M., Kitayama, K., Kooyman, R., Larney, E., Laumonier, Y., Laurance, S., Laurance, W.F., Lawes, M.J., Amaral, I.L., do, Letcher, S.G., Lindsell, J., Lu, X., Mansor, A., Marjokorpi, A., Martin, E.H., Meilby, H., Melo, F.P.L., Metcalfe, D.J., Medjibe, V.P., Metzger, J.P., Millet, J., Mohandass, D., Montero, J.C., de Morisson Valeriano, M., Mugerwa, B., Nagamasu, H., Nilus, R., Ochoa-Gaona, S., Onrizal, Page, N., Parolin, P., Parren, M., Parthasarathy, N., Paudel, E., Permana, A., Piedade, M.T.F., Pitman, N.C.A., Poorter, L., Poulsen, A.D., Poulsen, J., Powers, J., Prasad, R.C., Puyravaud, J.-P., Razafimahaimodison, J.-C., Reitsma, J., Dos Santos, J.R., Roberto Spironello, W., Romero-Saltos, H., Rovero, F., Rozak, A.H., Ruokolainen, K., Rutishauser, E., Saiter, F., Saner, P., Santos, B.A., Santos, F., Sarker, S.K., Satdichanh, M., Schmitt, C. B., Schöngart, J., Schulze, M., Suganuma, M.S., Sheil, D., da Silva Pinheiro, E., Sist, P., Stevart, T., Sukumar, R., Sun, I.-F., Sunderland, T., Sunderand, T., Suresh, H. S., Suzuki, E., Tabarelli, M., Tang, J., Targhetta, N., Theilade, I., Thomas, D.W., Tchouto, P., Hurtado, J., Valencia, R., van Valkenburg, J.L.C.H., Van Do, T., Vasquez, R., Verbeeck, H., Adekunle, V., Vieira, S.A., Webb, C.O., Whitfeld, T., Wich, S.A., Williams, J., Wittmann, F., Wöll, H., Yang, X., Adou Yao, C.Y., Yap, S.L., Yoneda, T., Zahawi, R.A., Zakaria, R., Zang, R., de Assis, R.L., Garcia Luize, B., Venticinque, E.M., 2015. An estimate of the number of tropical tree species. Proc. Natl. Acad. Sci. U. S. A 112. https://doi.org/10.1073/pnas.1423147112.

Sonwa, D.J., Weise, S.F., Schroth, G., Janssens, M.J.J., Howard-Yana Shapiro, 2014. Plant diversity management in cocoa agroforestry systems in West and Central Africa-effects of markets and household needs. Agrofor. Syst. 88, 1021–1034. https://doi.org/10.1007/s10457-014-9714-5.

Steur, G., ter Steege, H., Verburg, R.W., Sabatier, D., Molino, J.F., Bánki, O.S., Castellanos, H., Stropp, J., Fonty, É., Ruysschaert, S., Galbraith, D., Kalamandeen, M., van Andel, T.R., Brienen, R., Phillips, O.L., Feeley, K.J., Terborgh, J., Verweij, P.A., 2022. Relationships between species richness and ecosystem services in Amazonian forests strongly influenced by biogeographical strata and forest types. Sci. Rep. 12, 1–11. https://doi.org/10.1038/s41598-022-09786-6.

Sullivan, M.J.P., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., Chave, J., Cuni-Sanchez, A., Hubau, W., Lopez-Gonzalez, G., Miles, L., Monteagudo-Mendoza, A., Sonké, B., Sunderland, T., Ter Steege, H., White, L.J.T., Affum-Baffoe, K., Aiba, S.I., De Almeida, E.C., De Oliveira, E.A., Alvarez-Loayza, P., Dávila, E.Á., Andrade, A., Aragão, L.E.O.C., Ashton, P., Aymard, G.A., Baker, T.R., Balinga, M., Banin, L.F., Baraloto, C., Bastin, J.F., Berry, N., Bogaert, J., Bonal, D., Bongers, F., Brienen, R., Camargo, J.L.C., Cerón, C., Moscoso, V.C., Chezeaux, E., Clark, C.J., Pacheco, Á.C., Comiskey, J.A., Valverde, F.C., Coronado, E.N.H., Dargie, G., Davies, S.J., De Canniere, C., Djuikouo, M.N., Doucet, J.L., Erwin, T.L., Espejo, J.S., Ewango, C.E.N., Fauset, S., Feldpausch, T.R., Herrera, R., Gilpin, M., Gloor, E., Hall, J.S., Harris, D.J., Hart, T.B., Kartawinata, K., Kho, L.K., Kitayama, K., Laurance, S.G.W., Laurance, W. F., Leal, M.E., Lovejoy, T., Lovett, J.C., Lukasu, F.M., Makana, J.R., Malhi, Y., Maracahipes, L., Marimon, B.S., Junior, B.H.M., Marshall, A.R., Morandi, P.S., Mukendi, J.T., Mukinzi, J., Nilus, R., Vargas, P.N., Camacho, N.C.P., Pardo, G., Peña-Claros, M., Pétronelli, P., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Primack, R. B., Priyadi, H., Quesada, C.A., Reitsma, J., Réjou-Méchain, M., Restrepo, Z., Rutishauser, E., Salim, K.A., Salomão, R.P., Samsoedin, I., Sheil, D., Sierra, R., Silveira, M., Slik, J.W.F., Steel, L., Taedoumg, H., Tan, S., Terborgh, J.W., Thomas, S. C., Toledo, M., Umunay, P.M., Gamarra, L.V., Vieira, I.C.G., Vos, V.A., Wang, O., Willcock, S., Zemagho, L., 2017. Diversity and carbon storage across the tropical forest biome. Sci. Rep. 7, 1–12. https://doi.org/10.1038/srep39102.

Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. Annu. Rev. Ecol. Evol. Syst. 45, 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917.

Tuhkanen, S., 1980. Climatic parameters and indices in plant geography, Acta Phytogeographica Suecica. Almqvist & Wiksell International, Stockolm.

Veenendaal, E.M., Torello-Raventos, M., Feldpausch, T.R., Domingues, T.F., Gerard, F., Schrodt, F., Saiz, G., Quesada, C.A., Djagbletey, G., Ford, A., Kemp, J., Marimon, B. S., Marimon-Junior, B.H., Lenza, E., Ratter, J.A., Maracahipes, L., Sasaki, D., Sonké, B., Zapfack, L., Villarroel, D., Schwarz, M., Yoko Ishida, F., Gilpin, M., Nardoto, G.B., Affum-Baffoe, K., Arroyo, L., Bloomfield, K., Ceca, G., Compaore, H., Davies, K., Diallo, A., Fyllas, N.M., Gignoux, J., Hien, F., Johnson, M., Mougin, E., Hiernaux, P., Killeen, T., Metcalfe, D., Miranda, H.S., Steininger, M., Sykora, K., Bird, M.I., Grace, J., Lewis, S., Phillips, O.L., Lloyd, J., 2015. Structural, physiognomic and above-ground biomass variation in savanna-forest transition zones on three continents - How different are co-occurring savanna and forest formations? Biogeosciences 12, 2927–2951. https://doi.org/10.5194/bg-12-2927-2015.

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. J. Veg. Sci. 31, 440–453. https://doi.org/10.1111/jvs.12861.

White, F., 1983. The Vegetation of Africa, A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa, UNESCO. https://doi.org/10.2307/2260340.

Yerima, B.P.U.K., Ranst, V.E., 2005. Major soil classification systems used in the tropics: soils of Cameroon. Trafford Publishing.

Youta-Happi, J., Bonvallot, J., Hotyat, M., Guillet, B., Peltre, P., Schwartz, D., Servant, M., Simonneaux, V., 2003. Bilan de la dynamique du contact forêt-savane en quarante ans (1950-1990) Dans la région du confluent du Mbam et du Kim, Centre-Cameroun, in: Peuplements Anciens et Actuels Des Forêts Tropicales. p. 380 p.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A.A., Ilic, J., Jansen, S., Lewis, S.L.S.L., Miller, R.B.B., Swenson, N.G.G., Wiemann, M.C.C., Chave, J., 2009. Global wood density database. Dryad 235, 33. https://doi.org/10.5061/dryad.234.