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Structural complexity and large-sized trees explain shifting species richness and carbon relationship across vegetation types

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Abstract

1. It is prominently claimed that enhancing forest diversity would play a dual role of nature conservation and climate regulation. While the idea is intuitively appealing, studies show that species richness effects on above-ground carbon (AGC) are not always positive, but instead unpredictable especially across scales and complex terrestrial systems having large-diameter and tall-stature trees. Previous studies have further considered structural complexity and larger trees as determinants of AGC. Yet it remains unclear what drives differential diversity–AGC relationships across vegetation types.
2. Here we test whether structural complexity and large-sized trees play an influential role in explaining shifting diversity–AGC relationships across vegetation types, using a 22.3-ha sampled dataset of 124 inventory plots in woodlands, gallery forests, tree/shrub savannas and mixed plantations in West Africa.
3. Natural vegetation had greater species richness and structural complexity than mixed plantations, as expected. In addition, AGC was highest in gallery forests and mixed plantations, which is consistent with favourable environmental conditions in the former and high stocking densities and presence of fast-growing species in the latter. Significant interaction effects of species richness and vegetation on AGC revealed a vegetation-dependent species richness–AGC relationship: consistently, we found positive species richness–AGC relationship in both mixed plantations and woodlands, and nonsignificant patterns in gallery forests and tree/shrub savanna. Furthermore, there was a vegetation-dependent mediation of structural complexity in linking species richness to AGC, with stronger positive structural complexity effects where species richness–AGC relationships were positive, and stronger positive large-sized trees' effect where species richness–AGC relationships were neutral.
4. Our study provides strong evidence of vegetation-dependent species richness–AGC relationships, which operated through differential mediation by structural complexity of the species richness and large trees' effects. We conclude that even higher species richness in diversified ecosystems may not always relate positively with AGC, and that neutral pattern may arise possibly as a result of larger

dominant individual trees imposing a slow stand dynamic flux and overruling species richness effects.

KEYWORDS
larger trees, niche complementarity, species diversity, stand structures, structural equation model

1 | INTRODUCTION

The relationship between diversity and the capacity of ecosystems to store carbon in biomass has been a core research topic for the last two decades. World-wide, there is an increased number of studies on how species diversity influences biomass carbon stock in various ecosystems (An-ning, Tian Zhen, & Jian Ping, 2008; Aryal, Shrestha, Maraseni, Wagle, & Gaire, 2018; Carol Adair, Hooper, Paquette, & Hungate, 2018; Con et al., 2013; Forrester & Bauhus, 2016; Lasky et al., 2014; Liu et al., 2018; McNicol, Ryan, Dexter, Ball, & Williams, 2018; Rawat, Arunachalam, Arunachalam, Alatalo, & Pandey, 2019). These studies are particularly central in understanding climate change-related biodiversity losses, and have important implications in current political talks and efforts to reduce greenhouse gas emission through strengthening preservation and sustainable use of forest biodiversity.

Although it is prominently claimed that conserving and enhancing stand diversity could play a dual role of nature conservation and regulation of global climate, conclusions from many studies reveal that tree diversity effects on biomass and carbon stocks are unpredictable, especially across complex terrestrial systems such as forests. For instance, positive relationships were reported in the following studies (Barrufol et al., 2013; Cheng, Zhang, Zhao, & von Gadow, 2018; Huang, Su, Li, Liu, & Lang, 2019; Liang et al., 2016; Liu et al., 2018; Mensah, Veldtman, du Toit, Glèlè Kakaï, & Seifert, 2016; Paquette & Messier, 2011; Ruiz-Benito et al., 2014; Vilà et al., 2007), although being mostly carried out in temperate or boreal forests characterized by rather low tree diversity (Carol Adair et al., 2018; Cheng et al., 2018; Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011; Paquette & Messier, 2011; Vilà et al., 2013). On the other hand, species diversity–productivity relationships have been shown to take various forms in empirical studies (Díaz & Cabido, 2001; Dormann, Schneider, & Gorges, 2019; Forrester & Bauhus, 2016; Whittaker, 2010). For instance, there are also reports of negative relationship between species diversity and biomass production in natural forests of Barro Colorado Island in Central Panama (Ruiz-Jaen & Potvin, 2011), central Europe (Szwagrzyk & Gazda, 2007) and Northwest China (An-ning et al., 2008). The inconsistency of the findings across regions and biogeographical areas (Dormann et al., 2019; Forrester & Bauhus, 2016; Liang et al., 2016; Sullivan et al., 2017), suggests that the mechanisms that drive the diversity–biomass carbon relationship may depend on vegetation type and structure, habitat heterogeneity (environmental conditions), temporal and successional change, study scale and diversity measures. While it is increasingly recognized that more research studies on biodiversity–carbon relationships are still needed, especially across other ecosystems, it is equally important that we advance our understanding of how (and why) these relationships shift across vegetation types. What has remained particularly unclear is how vegetation stand properties and structure can explain shifting diversity–carbon relationships across vegetation types.

Forest stand structure influences ecosystem functions, including biodiversity (Lindenmayer, Margules, & Botkin, 2000), stand productivity and biomass carbon (Lutz et al., 2018; McNicol et al., 2018; Mensah, Veldtman, du Toit, et al., 2016; Yoshida et al., 2017). Across vegetation types, structural variability or complexity may influence ecosystem processes and functioning. Stand structural complexity, as commonly predicted from a combination of measures that relate to the horizontal and vertical extent as well as to the internal branching pattern of the trees, is known to account for variability in both vertical and horizontal tree size and crown (Seidel et al., 2019; Wang, Lei, Ma, Kneeshaw, & Peng, 2011). Structural complexity is therefore expected to define how species capture and use resource (Van Pelt, Sillett, Kruse, Freund, & Kramer, 2016; Yachi & Loreau, 2007). Because the mechanisms by which diversity influences carbon stock may vary according to the vegetation, one could ask whether incorporating stand structural complexity, as a measure accounting for differential structuring among vegetation types and analysing the relationship between diversity and above-ground carbon (AGC) from a structural perspective would help to provide insights into why (and how) this relationship would vary across different vegetation types.

Shifts in species richness–AGC relationships can be attributed to different correlation patterns between species richness, tree stock density and AGC (Chisholm et al., 2013; Ruiz-Benito et al., 2014). For some vegetation types, species richness may promote stocking density, which in turn increases stand AGC, while for others, species richness may increase without much change in total stem/tree density. Thus, stocking density may play a role in shifting species richness and AGC relationships, although such a density effect may be of less biological interest when compared to species sampling effects, and niche complementarity/facilitation effects (Chisholm et al., 2013). Because AGC is intrinsically related to tree size, the apparent effect of tree density may be operating through the relative density of particular size classes such as large-diameter trees, which are well known to dominate the structure, dynamics and function of tropical forests (Fayolle et al., 2016; Lutz, Larson, Freund, Swanson, & Bible, 2013; Lutz, Larson, Swanson, & Freund, 2012; Lutz et al., 2018). Therefore, it will provide insightful information to

clarify the additional role of the relative density of larger trees (e.g. the 1% of trees with the largest diameter in the stand) in affecting stand AGC, either directly or indirectly via stand structural complexity. This is especially important as large-diameter trees may be functionally different from smaller trees (Engone Obiang et al., 2019).

Large-diameter trees are known to be of ecological importance in forest habitats (Lutz et al., 2012), as they define resource use by remaining individuals through reduction of resources and competitive exclusion (Carroll, Cardinale, & Nisbet, 2011; Mason, de Bello, Dolezal, & Leps, 2011; Mensah, du Toit, & Seifert, 2018). Studies at both global and regional scales have shown that large-diameter trees comprise a large fraction of the biomass in many forests (Bastin et al., 2015; Fayolle et al., 2016; Lutz et al., 2012, 2018; Slik et al., 2013). In a recent global-scale study, Lutz et al. (2018) analysed 48 plots across primary and secondary forests covering 1,278 ha, and including 9,298 species and 210 plant families; they found a strong positive relationship between overall forest biomass and large-diameter threshold (diameter such that trees greater than or equal to that diameter constituted half of the above-ground live biomass of the plot). More generally, they found that the largest 1% of trees contributed to 50% of the overall forest biomass and that plots with high biomass had large-diameter trees and high large-diameter thresholds but relatively low species richness within the large-diameter structural class (Lutz et al., 2018). At regional and local scales, larger trees have also been reported to contain large portion of the stand basal area and above-ground biomass (AGB; Bastin et al., 2015; Lutz et al., 2012, 2013; Mensah, Veldtman, & Seifert, 2017), and further predict stand-level AGB and carbon (Lung & Espira, 2015; Mensah, Veldtman, du Toit, et al., 2016). Despite being of such importance for forest biomass carbon, relatively little is known about how large-diameter trees modulate community species richness–AGC relationship. In a previous study in a mistbelt forest type in Southern Africa, it was found that, whereas individuals that can potentially reach the canopy stratum contribute strongly to the total stand biomass, their species richness effect on total AGB was weaker than that of sub-canopy layer (Mensah, du Toit, et al., 2018). The authors argued that the weaker positive relationship between the emergent layer richness and its AGB resulted from the abundance of larger diameter trees within a reduced species pool, as also shown across primary and secondary forests (Lutz et al., 2018), where the number of species that reached the local large-diameter threshold further varied greatly among and within regions (table 1 in Lutz et al., 2018). To the extent that different vegetation types are structurally divergent (e.g. assemblage of species with different maximum diameter, total height and branching patterns), our ability to model shifting richness–AGC relationship across different habitats may be improved by also focusing on larger diameter trees.

The vegetation in West Africa is characterized by several ecosystems from the Guinean littoral forests to the southern Sahel, which are separated mainly by the amount of rainfall they receive. The most common forms are rainforests (1,500–3,000 mm annual rainfall), forest-savanna mosaic (1,200–1,500 mm), woodland-savannas (800–1,200 mm), the Sahel (200–500 mm) and desert (<200 mm; Atsri, Konko, Cuni-Sanchez, Abotsi, & Kokou, 2018; White, 1983). Deciduous forests, woodlands, gallery forests and savannas (tree/shrub) harbour a considerable pool of species with a high level of structure and complexity owing to different sets of trophic groups and environmental gradients (Adomou, 2005). These ecosystems are also habitat for several large mammals including elephants, primates and birds, and support local livelihoods through provision of a wide range of vital ecosystem services (Atsri et al., 2018; Gnonlonfoun et al., 2019). They contribute to regulate regional climate through storing large amount of carbon in different pools including plant and soil. In spite of their high diversity and complexity, these vegetation types are under-represented in local and regional studies on biodiversity and carbon relationship (Asase, Asitoakor, & Ekpe, 2012; Jucker et al., 2016). As a result, little is known about how diversity would affect biomass and carbon in West African vegetation types. Observational studies are therefore needed to improve our general understanding of diversity effects on carbon storage. Such understanding is vital if we are to improve both biodiversity conservation and carbon storage.

In this study, we used data from 124 forest inventory plots in a semi-arid zone in Benin Republic, to examine diversity–AGC relationships in four dominant vegetation types. In particular, we (1) investigated how species richness, structures and AGC stock varied among woodlands, gallery forests, tree/shrub savannas and mixed plantations; we tested the hypothesis that tree species diversity and structural complexity would be higher in natural vegetation types. We also (2) determined how AGC was related to species richness across vegetation types; we expected that tree species richness would positively affect AGC, but we did not know the magnitude of the effects, and especially whether a particular ecosystem would favour stronger positive diversity–carbon relationship than other ecosystems; we tested for interaction effects of species richness and vegetation types specifically; we also hypothesized that species richness would positively influence AGC, but the effects may vary with vegetation type, possibly, as a result of different structuring. Finally, we investigated (3a) whether structural complexity would explain differential diversity–AGC patterns across vegetation types, and (3b) whether large-sized trees also played an additional role in mediating diversity–AGC patterns.

2 | MATERIALS AND METHODS

2.1 | Study area and forest plots

The present study was conducted in the Bellefoungou Forest Reserve (9°46′40″–9°49′00″N and 1°42′00″–1°45′00″E)—BFR in Djougou district in Republic of Benin (see Figure S1). BFR, with a current estimated area of 709 ha, is characterized by the Sudano-Guinean transition zone climate in northern Benin (White, 1983). The average daily temperature is 28°C, and annual rainfall 1,200 mm. There is one rainy season from April to October and one dry season from November to March. The wet season is unimodal, with one peak

occurring between July and August at about 200–250 mm per month (Adomou, 2005). BFR is a mosaic of gallery forests, woodlands, tree/shrub savannas and mixed plantations, occurring at a low elevation of 405 m a.s.l., and playing an important role in biological conservation.

Dominant species varied with vegetation types. In the gallery forests, *Vitellaria paradoxa* C.F.Gaertn., *Anogeissus leiocarpa* (DC) Guill. & Perr., *Daniellia oliveri* (Rolfe) Hutch. & Dalziel, *Isoberlinia tomentosa* (Harms) Craib & Stapf and *Pavetta crassipes* K.Schum are the most dominant species. Woodlands and tree/shrub savannas are characterized by a high dominance of *Isoberlinia doka* Craib & Stapf, *I. tomentosa*, and *V. paradoxa*, but can be distinguished by the presence of *D. oliveri* and *Burkea africana* Hook. (for tree/shrub savannas) and *A. leiocarpa* and *Detarium microcarpum* Guill. & Perr. for woodlands. In the mixed plantations, dominant species are *Tectona grandis* L.f., *V. paradoxa*, *I. doka*, *Khaya senegalensis* (Desv.) A. Juss. and *Parinari curatellifolia* Planch. ex Benth.

In the 1980s, some margin areas of the BFR were occupied by local communities who had established farmlands for subsistence agriculture. However, in 1995, with the implementation of the national forestry plan, these local populations were displaced as part of the national efforts to reduce the pressure on pristine forest resources (FAO, 2001), and exotic and native species (e.g. *T. grandis*, *Gmelina arborea* Roxb, *K. senegalensis*) plantations were established in 1998 to restore the farmlands and other degraded areas. These plantations did not receive silvicultural and management interventions, hence, they evolved into multispecies stands with the occurrence of other native species including *V. paradoxa*, *I. doka*, *Diospyros mespiliformis* Hochst. ex A. Rich. and *A. leiocarpus* (V.K. Salako, E.E. Ago, S. Mensah, J. Bogaert, P. Akouété, I.I. Toko, R. Glèlè Kakaï, unpublished data). Like most tropical sudanian vegetation, these stands exhibit a well-structured, multi-storey woody vegetation, consisting of sub-canopy, canopy and emergent tree species.

The dataset used in the analyses consisted of floristic information (tree species names, tree density and diameter at breast height—DBH and tree height) from 124 plots. These plots were established using a stratified random sampling scheme: 30 in the mixed plantations, 24 in the gallery forests, 30 in tree\shrub savannas and 40 in woodlands (see Table S1). These plots were homogenous in terms of climate, topography and soil type within each vegetation type. Plot size and shape were 60 m × 30 m in gallery forest and 42 m × 42 m (approximately 1,800 m^2) for the other vegetation types, as recommended by previous studies (Salako et al., 2013). With an average plot size of 0.18 ha, the total sampled area was 22.3 ha across the 124 plots. In each plot, all individuals of DBH ≥5 cm were measured for their DBH and total height, and identified at species and family levels. The number of primary branches at crown base level was also recorded for each individual to account for the crown structure.

2.2 | AGC storage

Overall, 54 species were enumerated in the four vegetation types. However, there was no regional biomass equation for West Africa, and species-specific local biomass equations have been documented for 13 of the 54 species (see Table S2). We further identified two multispecies biomass equations that could be used for tree biomass and carbon quantification in our study area: (a) the land use/cover biomass equations developed in Benin (Chabi, Lautenbach, Orekan, & Kyei-Baffour, 2016) and (b) the multispecies allometric biomass equation developed by Chave et al. (2014). However, among the documented Chabi et al. (2016) models, we only used that of DBH as single predictor, to avoid collinearity issues with the use of remaining models. On the other hand, Chave et al. (2014) used destructive dataset of trees >5 cm DBH at 58 sites across a wide range of environmental and vegetation types in Africa, South America, South Asia and Australia. They concluded that when tree diameter, total height and wood density are simultaneously used, a single model could hold across tropical vegetation types, with no detectable effect of region or environmental factors. Based on the AGB estimated for the 13 species using the species-specific biomass equations (see Table S2), we then compared the deviations in these species' biomass estimates when using the 'forest land' biomass equation developed by Chabi et al. (2016) [AGB = exp (2.39 + (0.11 × DBH))] and the multispecies allometric biomass equation developed by Chave et al. (2014) [$AGB = 0.0673 \times (\rho \times DBH^2 \times H)^{0.976}$], where AGB is the above-ground biomass in kg, ρ is the species-specific wood density (g/cm^3), DBH the diameter at breast height (cm) and H the total height (m). Unlike Chave et al. (2014), the deviations associated with Chabi et al. (2016) 'forest land' model were found to be comparatively large and increased with increasing tree diameter (see Figure S2). Next, we compared the plot level AGB estimates from Chave et al. (2014) with those from a hybrid approach consisting of using species-specific data when available and Chave et al. (2014) when species (or genus) data are not available. The hybrid method and Chave et al. (2014) estimates of plot AGB were highly correlated ($r^2 > 0.97$; see Figure S3). Across vegetation types, the estimated plot AGB using the hybrid approach was on average 1.03 times the estimated AGB using the Chave et al. (2014) equation. Hence, the Chave et al. (2014) equation was applied to estimate the AGB for all individual trees present in the plots, not only for consistency, but also because it incorporates wood density and height (which account for species-specific growth and variation in height for trees with the same DBH). Data on species-specific wood density were obtained from local studies in West Africa (Amahowe et al., 2018; Chabi et al., 2016; Nygård & Elfving, 2000) and from the Global Wood Density Database (Zanne et al., 2009) when species (or genus) data are not available. Above-ground tree carbon (AGC) was then quantified by applying a carbon fraction of 0.5. Tree carbon data was afterwards scaled up from tree to plot level.

2.3 | Species diversity and structural complexity metrics

Here we computed plot-level species diversity and structural complexity metrics. In particular, we used species richness (taxonomic diversity) at plot level, defined as the number of distinct species enumerated inside each plot.

As pointed out by Seidel et al. (2019), structural complexity can be predicted from a combination of conventional measures that relate to the horizontal and vertical extent as well as to the internal branching pattern of the trees. For the quantification of structural complexity, we focused on both vertical (tree height), and horizontal (tree diameter) differentiation across individual trees inside each plot. To account for the internal branching pattern as suggested (Seidel et al., 2019), we used information on the number of primary branches at crown base level. The number of primary branches at crown base height was recorded for each individual tree during data collection. Hence, structural complexity was quantified by computing at plot level, three coefficients of variation (CV; i.e. standard deviation to mean ratio): CV for the individual tree diameter (CV-DBH), CV for the individual tree height (CV-Ht) and CV for the number of primary branches (CV-Npb).

2.4 | Data analyses

All statistical analyses were performed in the R statistical software package, version 4.0.0 (R Core Team, 2020). We used boxplots to explore the variation in plot-level species diversity (species richness), structures (tree diameter, tree height and branching patterns) and AGC among the four vegetation types (see Figure S4). We then tested for significant effects of vegetation types on species richness, structures and AGC using separate GLMM, in which vegetation type effects were considered as fixed, and plot as a random factor to account for unknown heterogeneity effects (Mensah, du Toit, et al., 2018; Mensah, Pienaar, et al., 2018). Above-ground carbon, CV of tree height, diameter and branching pattern, were modelled as continuous response variables, by applying GLMM with Gaussian distribution after log-transformation. Species richness was analysed as count data using Poisson GLMM. The parameters of the mixed-effects models were estimated using the LME4 package with a restricted maximum likelihood estimator (Bates, Mächler, Bolker, & Walker, 2015). The reported probability values were computed using the Satterthwaite approximations to the degrees of freedom in the LMERTEST package (Kuznetsova, Brockhoff, & Christensen, 2016). Conditional (variance explained by fixed and random factors) and marginal (variance explained by fixed effects only) R^2 values were calculated following Nakagawa, Johnson, and Schielzeth (2017).

With a pooled dataset for all the four vegetation types, we next tested for significant individual and interaction effects of species richness and vegetation types on AGC using simple and multiple linear models. We did not deny the potential effects of tree density on AGC, since AGC was computed at plot level as sum of the individual tree carbon inside each plot. To control for the possible confounding effects of tree density, we first standardized the plot level densities for each vegetation type, and removed their potential effect on AGC with a simple linear regression. We then repeated the initial models with the residuals of the linear regressions replacing AGC as the dependent variable. For both regression stages, that is, whether or not tree density was controlled, we found significant interactions between species richness and vegetation type (see Table S3), which suggests a vegetation-dependent relationship between species richness and AGC. Hence, we examined the relationship between species richness and AGC for each vegetation type, first separately, and second by including plot level tree density (see Table S4), and we used scatterplot and regression lines for easier interpretation.

Because of the assumption that the between-vegetation variation of structural complexity would drive the differential patterns of species richness–carbon relationship, we (a) explored the bivariate relationships of AGC with structural complexity metrics for each vegetation type using scatter plot; and (b) tested for the significant role of structural complexity in mediating species richness effects on AGC for each vegetation using structural equation models (SEMs). The advantage in using SEM here is that it offers possibilities for testing simultaneously direct and indirect relationships among a set of observed (measured) and unobserved (latent) variables; and also provides a path analysis of the relative importance of the different variables in affecting the main response variable (Grace & Bollen, 2005; Mensah, du Toit, et al., 2018). We quantified structural complexity as a latent variable, using coefficient of variation of tree diameter, tree height and number of primary branches, thereby taking into account both vertical and horizontal differentiation in tree size and branching patterns. Unlike structural complexity which was a composite variable, species richness was based on a single indicator variable. We tested the a priori model that AGC increased with increasing species diversity (i.e. positive diversity effects on AGC), as result of positive mediation of structural complexity (Figure 1a).

Because AGB is related to tree size, the apparent effect of tree density on AGB is assumed to operate through relative density of particular size classes such as large-diameter trees. Also, previous studies have suggested that large-sized trees contribute significantly to stand biomass carbon (Bastin et al., 2015; Lutz et al., 2018; Slik et al., 2013), and because of their competitive abilities for above- and below-ground resource uptake, impose competitive constraints on

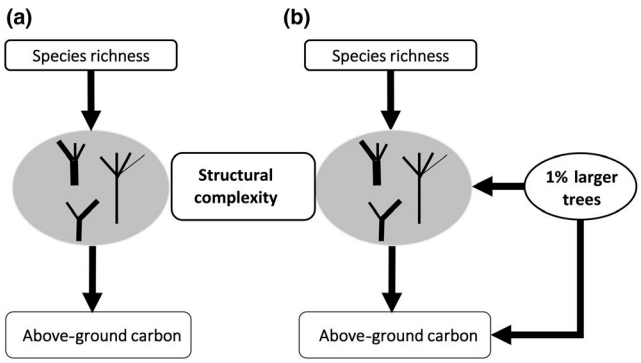

FIGURE 1 Conceptual models for testing if structural complexity and large-sized trees explain differential diversity–carbon patterns across vegetation types. For (a) we tested the a priori model that AGC increased with increasing species diversity (i.e. positive diversity effects on AGC), as result of positive mediation of structural complexity. For (b) we hypothesized that large-sized trees also played a stronger influencing role in vegetation types with weaker species richness–biomass carbon relationship. AGC, above-ground carbon

small- and medium-sized trees (Mensah, du Toit, et al., 2018). Hence, we were particularly interested in testing whether large-sized trees also played a stronger influencing role in vegetation types with weaker species richness–biomass carbon relationship. Therefore we also constructed a second SEM incorporating additional direct and indirect paths between AGC and the top 1% largest trees relative density and AGC (Figure 1b). The top 1% large-sized trees were identified for each vegetation type separately using the 99th percentile scores for tree diameter, and applied to each plot. Their relative density was calculated within each plot by computing the ratio of their absolute density over total tree density per plot, thereby accounting for tree density effect. The goodness of fit of the models was assessed using the chi-square (χ^2), the comparative fit index (CFI) and the root mean square error of approximation (RMSEA) statistics (Grace & Bollen, 2005; Mensah, Veldtman, Assogbadjo, Glèlè Kakaï, & Seifert, 2016). Because the SEM, null hypothesis assumes no discrepancy between the observed data and the model, lower χ^2 values and higher probability values ($p > 0.05$) are indicative of better fitting models (Grace & Bollen, 2005; Mensah, du Toit, et al., 2018). Similarly, higher values of CFI (close to 1) and lower values of RMSEA (close to 0) indicate acceptable model. The SEMs were fitted in the R platform using the 'sem' function from 'LAVAAN' package (Rosseel, 2012).

3 | RESULTS

3.1 | Variation of diversity, structure and AGC across the four vegetation types

Species richness and AGC varied significantly among vegetation types, with respectively 70% and 47% of variance explained (Table 1; see Figure S4). For species richness, mixed plantations,

TABLE 1 Results of GLMMs testing the effects of vegetation type on (a) species richness, (b) above-ground carbon (AGC), (c) coefficient of variation of diameter at breast height (CV-DBH), (d) coefficient of variation of height (CV-Ht) and (e) coefficient of variation of number of primary branches (CV-Npb). σ^2, variance; Cond, conditional; Est, coefficient estimates; Marg, marginal; Rsd, residual. Gallery forest is used here as baseline

	Fixed effects				Random effects		R^2 (%)	
	Est	*SE*	*z*/*t*	*p*	σ^2_{Plot}	σ^2_{Rsd}	Marg	Cond
(a) Species richness								
(Intercept)	2.92	0.05	63.42	<0.001	0.000	—	0.70	0.70
Mixed plantations	−1.32	0.09	−14.08	<0.001				
Tree/shrub savanna	−0.55	0.07	−7.72	<0.001				
Woodland	−0.40	0.06	−6.37	<0.001				
(b) log (AGC)								
(Intercept)	8.88	0.05	176.59	<0.001	0.005^{ns}	0.066	46.53	50.29
Mixed plantations	0.03	0.07	0.42	0.676				
Tree/shrub savanna	−0.59	0.07	−8.34	<0.001				
Woodland	−0.34	0.07	−5.08	<0.001				
(c) log (CV-DBH)								
(Intercept)	3.68	0.04	95.21	<0.001	0.006^{ns}	0.031	69.31	74.31
Mixed plantations	−0.54	0.048	−11.19	<0.001				
Tree/shrub savanna	0.17	0.05	3.52	<0.001				
Woodland	0.14	0.05	3.06	0.003				
(d) log (CV-Ht)								
(Intercept)	3.46	0.05	73.86	<0.001	0.011^{**}	0.043	73.90	79.35
Mixed plantations	−1.10	0.06	−19.30	<0.001				
Tree/shrub savanna	−0.39	0.06	−6.93	<0.001				
Woodland	−0.28	0.05	−5.18	<0.001				
(e) log (CV-Npb)								
(Intercept)	3.69	0.08	45.28	<0.001	0.000^{ns}	0.159	42.33	42.33
Mixed plantations	−0.71	0.11	−6.46	<0.001				
Tree/shrub savanna	0.11	0.11	1.05	0.298				
Woodland	0.11	0.10	1.06	0.291				

$^{**}p < 0.01$.

$^{ns}p > 0.05$.

tree/shrub savanna and woodlands had regression coefficients which were respectively 1.32 ± 0.09, 0.55 ± 0.07 and 0.40 ± 0.06 significantly lower than that of gallery forest (the baseline; Table 1).

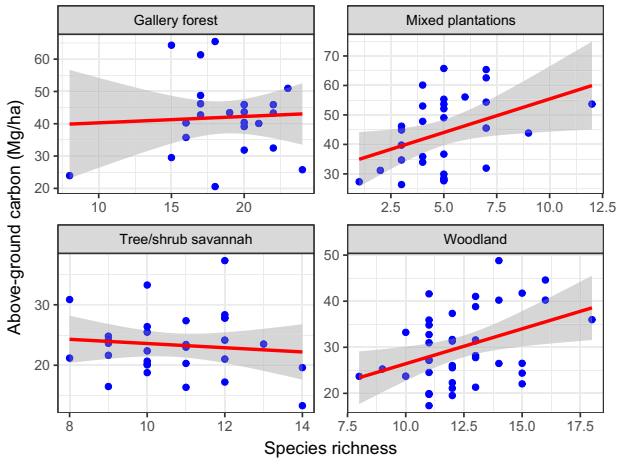

FIGURE 2 Scatter plot of species richness and above-ground carbon for each vegetation type. The red lines represent the fitted values and the shaded regions the pointwise 95% confidence interval on the fitted values

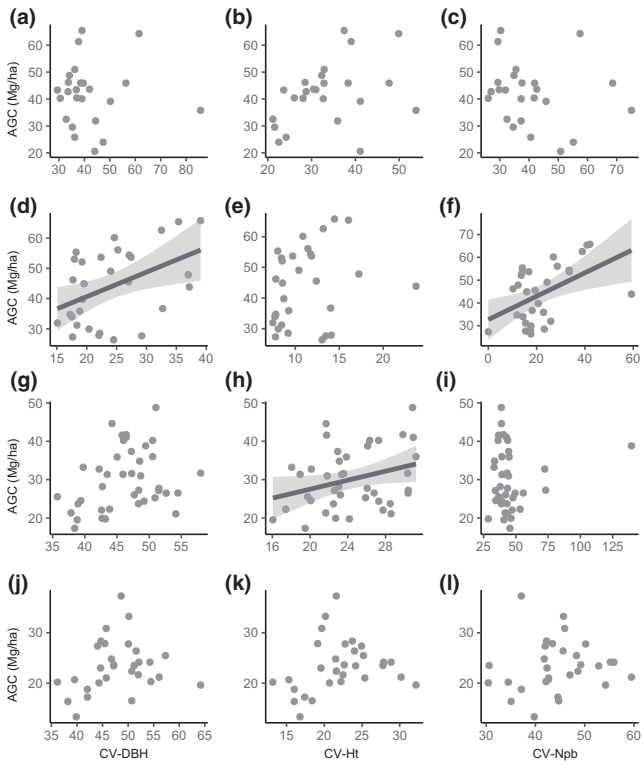

FIGURE 3 Bivariate relationships between above-ground carbon (AGC) and structural complexity metrics for each vegetation type: gallery forest (a–c); mixed plantations (d–f); woodland (g–i) and tree/shrub savanna (j–l). Linear regression lines are shown only for significant bivariate relationships ($p < 0.05$). The structural complexity metrics were: coefficient of variation of diameter at breast height (CV-DBH), coefficient of variation of height (CV-Ht) and coefficient of variation of number of primary branches (CV-Npb)

This indicates that species richness was highest in the gallery forest and lowest in the mixed plantations (see Figure S4). Nevertheless, both mixed plantations and gallery forests had significantly higher AGC stocks, as compared to tree/shrub savanna and woodlands (Table 1). As for tree structure and branching patterns, we also found significant variations between the four vegetation types (see Figure S4; Table 1), with mixed plantations exhibiting significantly lower mean diameter and crown branches, as compared to gallery forests and woodlands.

3.2 | Relationship between species richness and AGC across vegetation types

We found no significant influence ($p = 0.757$) of species richness when assessing diversity effects on AGC pooled data for all vegetation types (see Figure S5). However, when we controlled for tree

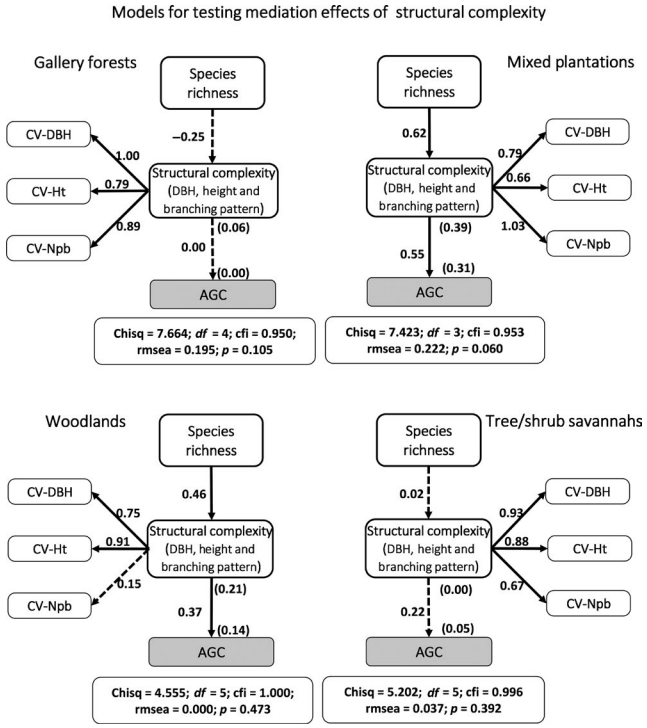

FIGURE 4 Structural equation model-fit statistics and path summary relating species richness to above-ground carbon (AGC) via structural complexity. The single-pointed arrows are the causal paths. The values without parentheses are the standardized path coefficients. Significant paths ($p < 0.05$) are represented with solid arrows and non-significant paths ($p > 0.05$) by dashed arrows. The values with parentheses are the coefficients of determination, indicating the total variation in a dependent variable that is explained by the combined independent variables. cfi: comparative fit index; Chisq: chi-square test ($p > 0.05$ indicates absence of significant discrepancy between the data and the model); CV-DBH: coefficient of variation of DBH; CV-Ht: coefficient of variation of height; CV-Npb: coefficient of variation of number of primary branches; detailed statistics and significance of paths are shown in Table 2; rmsea: root mean square error of approximation

density across vegetation types, we found significant positive effects of species richness on AGC, with 22% of variation explained across vegetation types (see Table S3). Furthermore, whether or not tree density effects were accounted for, there were significant interaction effects of species richness and vegetation type ($F = 29.65$; $p < 0.001$ for the interaction model with AGC as the dependent variable; and $F = 20.81$; $p < 0.001$ for the interaction model with the residuals as the dependent variable; see Table S3), suggesting that species richness effects on AGC varied with vegetation type. Consistently, we found that species richness–AGC relationship was positive in both mixed plantations and woodland, and nonsignificant in gallery forests and tree/shrub savannas (Figure 2; Table S4).

3.3 | Species richness and large-sized trees effects on AGC via structural complexity across vegetation types

We hypothesized that differential structural complexity would explain the different patterns of richness–carbon relationship across

TABLE 2 Results of the separate structural equation models testing species richness effects, large-sized trees and structural complexity effects on AGC. Fit statistics are presented in Figures 4 and 5

Paths	Est	*SE*	*Z*	*p*
Models testing for structural complexity effects				
Gallery forest				
Path from species richness to structural complexity	−0.25	0.19	−1.33	0.183
Path from structural complexity to AGC	0.00	0.20	0.01	0.991
Mixed plantations				
Path from species richness to structural complexity	0.62	0.11	5.81	<0.001
Path from structural complexity to AGC	0.55	0.13	4.36	<0.001
Woodlands				
Path from species richness to structural complexity	0.46	0.14	3.38	0.001
Path from structural complexity to AGC	0.37	0.15	2.45	0.014
Tree & shrub savanna				
Path from species richness to structural complexity	0.02	0.19	0.13	0.898
Path from structural complexity to AGC	0.22	0.18	1.23	0.219
Models testing for structural complexity effects and 1% large-sized trees' effects				
Gallery forest				
From species richness to structural complexity	−0.15	0.16	−0.97	0.333
From large-sized trees relative density to structural complexity	0.51	0.13	3.97	<0.001
From structural complexity to AGC	−0.42	0.18	−2.35	0.019
From large-sized trees relative density to AGC	0.72	0.12	5.79	<0.001
Mixed plantations				
From species richness to structural complexity	0.62	0.11	5.82	<0.001
From large-sized trees relative density to structural complexity	0.04	0.13	0.37	0.711
From structural complexity to AGC	0.55	0.13	4.33	<0.001
From large-sized trees relative density to AGC	0.05	0.15	0.34	0.731
Woodlands				
From species richness to structural complexity	0.26	0.15	1.73	0.083
From large-sized trees relative density to structural complexity	0.49	0.13	3.67	<0.001
From structural complexity to AGC	0.08	0.19	0.44	0.662
From large-sized trees relative density to AGC	0.50	0.15	3.31	0.001
Tree & shrub savanna				
From species richness to structural complexity	0.03	0.16	0.22	0.828
From large-sized trees relative density to structural complexity	0.48	0.14	3.48	0.001
From structural complexity to AGC	−0.07	0.17	−0.42	0.678
From large-sized trees relative density to AGC	0.57	0.14	4.03	<0.001

Abbreviations: AGC, above-ground carbon; Est, path standardized coefficients.

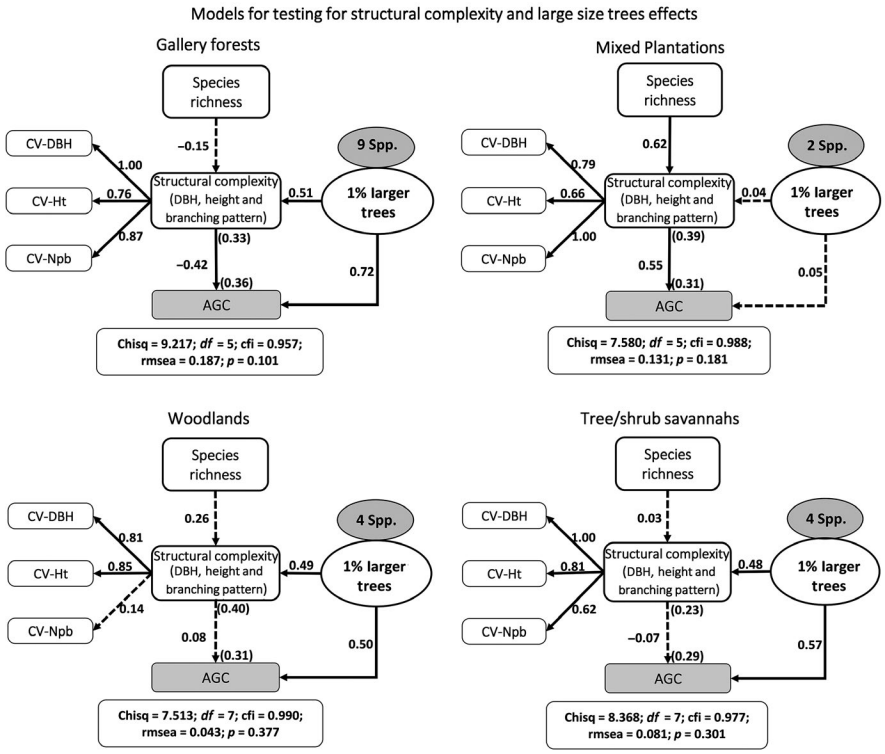

FIGURE 5 Structural equation model-fit statistics and path summary relating species richness, structural complexity and the top 1% larger trees' relative density to above-ground carbon (AGC). 1% larger trees: top 1% larger trees' relative density. Spp.: number of species. See Figure 4 for the remaining legend; detailed statistics and significance of paths are shown in Table 2

vegetation types. Thus the bivariate relationships between AGC and structural complexity metrics were examined for each vegetation type. From the results, significant bivariate relationships were observed only for mixed plantations (Figure 3d,f) and woodlands (Figure 3h).

The outputs of the SEMs testing for AGC response to species richness via structural complexity, revealed good fits of the models to the data for each vegetation type (χ^2 values ranging from 4.55 to 7.66 and $p > 0.05$; Figure 4). Furthermore, the CFI and the RMSEA were within the acceptable range, also indicating very good fits of the models (Figure 4). For both mixed plantations and woodlands, species richness had a significant positive direct effect on structural complexity ($\beta = 0.62$ and 0.46; $p < 0.001$ and 0.001 for mixed plantations and tree/shrub savannas respectively; Table 2; Figure 4), which also showed positive and significant effect ($\beta = 0.55$ and 0.37; $p < 0.001$ and 0.014 for mixed plantations and woodlands respectively; Table 2; Figure 4) on AGC. These results suggest that positive species richness effects on AGC in mixed plantations and woodlands, as shown in Figure 2, are mediated by structural complexity. Contrary to what was observed in mixed plantations and woodlands, we found no significant paths along species richness, structural complexity and AGC for gallery forests and tree/shrub savannas (Table 2; Figure 4).

We further assumed that large-sized trees would play a substantial role in vegetation types with weaker species richness–AGC relationships. Accordingly, we tested for each vegetation type, additional direct and indirect paths between the relative density and AGC. Results showed that for gallery forests, woodlands and shrub/trees savannas, the top 1% large-sized trees relative density had a positive effect on AGC, while in mixed plantations, there was no significant effect of top 1% large-sized trees (Figure 5). Furthermore, the effect of the top 1% large-sized trees on AGC was positive and stronger for gallery forests ($\beta = 0.72$) and shrub/trees savannas ($\beta = 0.57$) than for woodlands ($\beta = 0.50$) and mixed plantations ($\beta = 0.05$; Table 2).

Overall, these results suggest (a) positive structural complexity effects where species richness–AGC relationships were positive (see Figure S6); (b) significant mediation by structural complexity of species richness effects on AGC in mixed plantations and woodlands; (c) that species richness enhanced structural complexity, which in turn promoted AGC in mixed plantations and woodlands; and (d) where species richness–carbon relationships were neutral (i.e. gallery forests and shrub/trees savannas), we found stronger positive large-sized trees' effect on both structural complexity and AGC.

4 | DISCUSSION

In this study, we assessed the role of structural complexity and large-sized trees in explaining diversity–carbon relationship across vegetation types. We found (a) that mixed plantations and gallery forests had the highest AGC stocks, but respectively lower and higher species richness, as compared to tree/shrub savanna and woodland; (b) vegetation-dependent species richness effects on AGC; (c) vegetation-dependent mediation role of structural complexity in linking species richness to AGC; (d) positive structural complexity effects where species richness–AGC relationships were

positive; and (e) stronger positive large-sized trees' effect on both structural complexity and AGC where species richness–AGC relationships were neutral.

4.1 | Diversity, structure and carbon stocks across vegetation types

First, the observed patterns in diversity and structural complexity measured as intensity of inequality in tree size—DBH and total height—and number of primary branches were consistent with our prediction of higher values in natural vegetation types compared to plantations which showed two to four time less species than natural vegetation types. This is a common pattern, especially where plantations are often established with one or a few numbers of species. However, depending on the stage, plantations might have similar diversity to natural vegetation especially when seed dispersal is facilitated between plantations and adjacent species-rich natural forests (Nagaike et al., 2012). Among natural vegetation types, gallery forests were species richer than woodlands followed by tree/shrub savannas. This finding is consistent with a recent study in the West African Sudanian zone where gallery forests and woodlands had higher species diversity compared to tree/shrub savannas (Dimobe et al., 2018). The high diversity in gallery forests compared to the woodlands and tree/shrub savannas is likely due to the better environmental conditions (possibly humidity and nutrients). This might further be due to a higher amount of niches because of water availability gradients with good, medium and lower water supply at the river.

Second, we observed the highest AGC stocks in mixed plantations and gallery forests, 1.5–2 times that of tree/shrub savanna and woodland respectively. The high AGC in plantations is likely the consequence of the (a) commonly high tree planting density in human made vegetation (4–9 times that of other vegetation types, Salako et al., under review), though trees may be of relatively smaller size depending on the plantation age, and (b) the usual plantation of fast growing exotic tree species that rapidly accumulate biomass compared to native species (Brancalion et al., 2019). Such high AGC in plantations has also been reported in a semi-arid savanna watershed in Benin where plantations were made of *T. grandis* and *Eucalyptus grandis* (Chabi et al., 2016). Similarly, the hierarchy of AGC across natural vegetation types is consistent with patterns found elsewhere in Africa semi-arid zone. For instance, higher AGC stocks were reported in gallery forests and woodlands, as compared to tree and shrub savannas in Burkina Faso (Dimobe, Kuyah, Dabré, Ouédraogo, & Thiombiano, 2019). In addition, the observed values for AGC in gallery forests and woodlands are globally similar to those reported for the same vegetation types in Dimobe et al. (2019), but relatively higher for tree/shrub savannas (18.2–28.5 Mg C/ha in our study vs. 2.5–14.1 Mg C/ha in Dimobe et al. (2019)). Higher values in tree/shrub savannas in the present study could be explained by the substantially bigger tree dimensions (DBH: 21.72 ± 0.33 cm) compared to values of 11–13.4 cm reported in Dimobe et al. (2019). However, the high values of AGC in gallery forests compared to other natural vegetation types could be explained by the abundance of large-stature trees in this vegetation type owing to the prevailing environmental conditions: higher humidity, and nutrients that favour tree growth. Nonetheless, the values of AGC were globally low compared to values reported in a semi-deciduous forest in southern Benin (Goussanou, Guendehou, Assogbadjo, & Sinsin, 2018) and in the Miombo woodlands (Ribeiro, Matos, Moura, Washington-Allen, & Ribeiro, 2013; Ryan, Williams, & Grace, 2011) probably resulting from a better rainfall and environmental conditions compared to our study sites (Shackleton & Scholes, 2011).

4.2 | Differential relationship between species richness and AGC across vegetation types

We found strong evidence of vegetation-dependent direct species richness–AGC relationships, confirming the view that tree diversity effects on biomass and carbon stocks are idiosyncratic, especially across complex forests ecosystems. In particular, we observed positive and neutral species richness–AGC relationships in natural forest systems, suggesting that higher species richness may not always promote C stock in the above-ground component, and that management policies that focus on simply increasing species richness might not yield the same results depending on the vegetation types.

Positive species richness effect on AGC can be explained through higher taxonomic diversity promoting higher stem density and forest productivity (Mensah, Veldtman, Assogbadjo, et al., 2016; Ruiz-Benito et al., 2014). Previous studies have also found that an increase in total stem/tree density could be linked to both species richness and AGC (Chisholm et al., 2013; Poorter et al., 2015). Interestingly, our analyses corroborate these patterns; when tree density was incorporated in species richness–AGC relationship for each vegetation type, we found significant and positive tree density effects only where species richness–AGC relationships were initially positive (i.e. mixed plantations and woodlands; see Table S4). Thus, the positive relationship between richness and AGC seemed to result from species richness promoting stocking density in some vegetation types (in this case, mixed plantations and woodlands). The finding that species-rich ecosystems stored more AGC is an evidence for diversity-mediated above-ground C sequestration, and is consistent with previous studies that showed increased productivity or biomass carbon with increasing diversity in plantations (Erskine, Lamb, & Bristow, 2006) and natural forests in tropics (Poorter et al., 2015), subtropics (Liu et al., 2018; Ouyang et al., 2019; Xu et al., 2019) and temperate and boreal regions (Paquette & Messier, 2011; Ruiz-Benito et al., 2014). This finding supports the perspectives that multispecies plantations are more productive than monoculture plantations (Erskine et al., 2006), and maintaining high species diversity in natural forests is beneficial to ecosystem functions and services (Liang et al., 2016; Liu et al., 2018; Poorter et al., 2015). Consequently it highlights the potential negative impacts of biodiversity loss on

ecosystem functions and services, and suggests that afforestation policies should rather change from the current widely practiced monocultures to multispecies plantations to enhance C fixation and therefore mitigate global warming (Liu et al., 2018).

Unlike mixed plantations and woodlands, gallery forests and tree/shrub savanna showed neutral direct relationship with species richness, consistent with other previous studies that also reported neutral or weak species richness–AGC relationships in temperate (mixed/deciduous) forests (Armenteras, Rodríguez, & Retana, 2015; Seidel et al., 2013; Sullivan et al., 2017; Wu et al., 2015). Neutral pattern could result from species number increasing without substantial change in total stem/tree density, as observed in this study for the gallery forest plots (see Figure S7). Neutral pattern could also arise from increased number of small-sized stem not influencing much plot level biomass and carbon (see Figure S7). While the focus on density provides some understanding of why species richness and AGC relationships may shift across vegetation types, this may be of less biological interest as it does not help infer on or distinguish between key ecological mechanisms such as dominance/sampling effects and facilitation/complementary processes (Chisholm et al., 2013). Because tree biomass is size dependent, we argued that particular tree size classes such as large-diameter trees, in addition to tree structural variability at plot level would play a major role in modulating species richness–AGC relationship.

4.3 | Mediation role of structural complexity and large-sized trees in explaining shifting species richness and AGC relationship across vegetation types

We tested whether incorporating stand structural complexity, as a measure accounting for differential structuring among vegetation types would explain differential diversity–carbon patterns across vegetation types. Consistently with Fotis et al. (2018), our data support the view that AGC is positively linked with structural complexity, but this link was valid only where species richness showed positive effects on AGC (i.e. mixed plantations and woodlands; see the bivariate relations). Our SEMs further highlight a vegetation-dependent mediation role of structural complexity in linking species richness to AGC: where positive species richness–AGC relationships were found, high variability in tree DBH, total height and branching were revealed to mediate this effect, confirming that stand structural characteristics mediate the positive effect of species richness on AGC. Zhang and Chen (2015) showed that increasing tree size (diameter and height) variability among and within species indirectly mediates the positive effect of diversity on AGC in sub-tropical forests. Other studies also showed that forests with a diverse structure harbour species that occupy different vertical and horizontal layers, which facilitate better resources utilization (e.g. shade-tolerant vs. light-adapted species) and reduced competition, thus enhancing productivity (Paquette & Messier, 2011; Ruiz-Benito et al., 2014). Indeed, species diversity and composition promotes high intraspecific and interspecific tree size variation, hence multilayered tree canopy structure (i.e. occupation of various light niches in the canopy) and spatial arrangement of leaves, which in turn increase forest productivity through increased light capture and efficient utilization of water and nutrients, thus supporting the niche complementarity and facilitation mechanism, but also sampling effects via plant–plant interactions (Van Pelt et al., 2016; Yachi & Loreau, 2007).

Large-sized trees have shown stronger effects on forest stand biomass and carbon in many previous studies (Lutz et al., 2012, 2013, 2018). Larger trees consistently contributed more to AGC than smaller trees (Xu et al., 2019), and because of their competitive abilities with regard to above- and below-ground resource uptake, impose competitive constraints on small- and medium-sized trees (Mensah, du Toit, et al., 2018). Where neutral species richness–AGC relationships were observed, we expected that large-size trees would exhibit stronger positive effects on AGC. We found evidence for significant positive effects of the density of larger trees across vegetation types (i.e. top 1% larger diameter trees) in affecting stand AGC, either directly as also indicated by Lutz et al. (2018), or indirectly via stand structural complexity. As expected, this effect was stronger where species richness had a neutral relationship with AGC, that is, in tree/shrub savannas and gallery forest clearly showing that the neutral species richness–AGC relationship is attributable to the overruling effect of large-sized and dominant trees.

We also found that the number of species within the top 1% large-size trees ranged from two in mixed species plantations to nine in gallery forests. These patterns are consistent with the study by Lutz et al. (2018), where species that reached the local large-diameter threshold varied greatly in number and percentage across habitats. On a percentage basis, top 1% large-size tree richness was 9% in mixed plantations, 9% in woodlands, 12% in tree/shrub savannas and 19% in gallery forests. The high percentage of top 1% large-size tree richness in tree/shrub savannas and gallery forests explains well, from a dominance perspective, the stronger effect of relative density of larger trees on AGC in these vegetation types, but also implies that tree/shrub savannas and gallery forests might be more resilient to perturbations affecting these large-diameter trees (Lutz et al., 2018; Musavi et al., 2017). Compared to gallery forests, species capable of attaining large diameters in tree/shrub savannas are relatively fewer, but their proportion (12%) and individuals (see Table S2) are relatively considerable. Therefore, irrespective of the species richness or density of top 1% large-size trees, the strong relationship between AGC and the relative density of larger trees in gallery forests and tree/shrub savannas suggests that these vegetation types cannot sequester large amounts of AGB carbon without large trees (Lutz et al., 2018).

All being considered, this study addressed worthwhile aspects of the diversity–AGC relationship in variety of West African ecosystems which are often understudied in global analyses. Although it was conducted at a local scale, consideration of abiotic factors could have provided additional insights; but we believe these factors would have minor impact on AGB variation because the plots were homogenous in terms of climate, topography and soil type within each vegetation

type. Further, we acknowledge that the study may have another limitation: the plot size of 0.18 ha used to study stand AGC may be potentially small to investigate large size tree effects. Previous studies that investigated forest spatial structure and biomass variability have indicated that large-diameter trees patterns and effects could be better elucidated with sample plots of more than 1 ha (Lutz, 2015; Réjou-Méchain et al., 2014). In addition, the conclusions from Réjou-Méchain et al. (2014) suggested that these plots would be too small to capture all the structural variation. Nevertheless, we believe this would also have a minor impact on the conclusions of this study for the following reasons. First is that 0.18 ha was recommended as plot size for structural analyses of the vegetation in woodlands (Salako et al., 2013); these authors compared the ability of smaller and larger plots to capture stand structural variation, and recommended 0.18 ha as the optimal size of inventory plots in West African woodlands. Second, our study was carried out in a Sudanian ecosystem where tree diameter rarely reaches 80 or 100 cm at breast height, as opposed to tropical dense or rain forests. Third, we used a similar plot size across the four vegetation types, which allows for reasonable comparisons among sites. In addition, our results showed interesting insights and trends that could be discussed in the light of existing global scale studies and current knowledge.

5 | CONCLUSIONS

In summary, our study provides evidence for vegetation-dependent species richness–AGC relationships, which operated through differential mediation by structural complexity of the species richness and large trees' effects. Thus, maintaining high stands diversity contributes to the maintenance of greater stand structural complexity that in turn enhances ecosystems services, in particular C storage. Interestingly, we also showed that this mediation does not hold for all vegetation types, and that even relatively higher species richness in diversified ecosystems might not always promote stand AGC, and that neutral pattern may arise as a result of larger dominant individual trees overruling diversity attributes as predictor of AGC. The mechanisms that drive the influence of diversity on AGC are diverse and their relative importance depends on the vegetation types. While conservation of biodiversity is at the forefront of conservation debates and initiatives, the regulation of stand structure can be even more important to maintain ecosystem functioning and services in subtropical and tropical forests either natural or human-made. In forests that showed strong relationship between AGC and the relative density of top 1% large-sized trees, the conservation of large-diameter trees is important to promote or maintain local AGC stock. This is more critical if these large-diameter trees species are relatively few, as observed in woodlands, since their loss (through logging and change in climate and disturbance regime) could also reduce structural complexity and AGC. Policies that target conservation of both large-diameter trees and tree species capable of reaching large-diameter threshold can help promote maintenance of AGC stock.

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AUTHORS' CONTRIBUTIONS

S.M. conceived the research idea and designed methodology; V.K.S. supervised the field work and data collection; S.M. analysed the data and drafted the manuscript with editorial contribution from V.K.S. and T.S. All authors contributed to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.pvmcvdnhr (Mensah, Salako, & Seifert, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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