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Structural diversity consistently mediates species richness effects on aboveground carbon along altitudinal gradients in northern Ethiopian grazing exclosures

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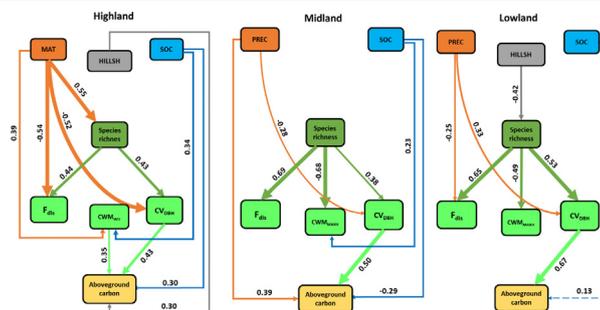
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HIGHLIGHTS

- Carbon storage increases with species richness only in mid- and lowlands.
- Structural diversity, expressed as variances in tree size, consistently mediated the positive effects of diversity on AGC.
- Tree species diversity and their structural complexity should be promoted to enhance C storage.

GRAPHICAL ABSTRACT



Numbers are standardized path coefficients; PREC: Precipitation; HILLSH: Hillshade; SOC: Soil organic carbon; F_{dis}: Functional dispersion; CWM_{max}: Community weighted mean of wood density; CWM_{maxHgt}: Community weighted mean of maximum height; CV_{diam}: Coefficient of variation of tree diameter. The solid arrows represent significant relationships, while the dashed arrows represent non-significant relationships.

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ABSTRACT

Grazing exclosures have been promoted as an effective and low-cost land management strategy to recover vegetation and associated functions in degraded landscapes in the tropics. While grazing exclosures can be important reservoirs of biodiversity and carbon, their potential in playing a dual role of conservation of biodiversity and mitigation of climate change effects is not yet established. To address this gap, we assessed the effect of diversity on aboveground carbon (AGC) and the relative importance of the driving biotic (functional diversity, functional composition and structural diversity) and abiotic (climate, topography and soil) mechanisms. We used a dataset from 133 inventory plots across three altitudinal zones, i.e., highland, midland and lowland, in northern Ethiopia, which allowed local- (within altitudinal zone) and broad- (across altitudinal zones) environmental scale analysis of diversity-AGC relationships. We found that species richness-AGC relationship shifted from neutral in highlands to positive in mid- and lowlands as well as across the altitudinal zones. Structural

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Niche complementarity
Structural diversity
Environmental gradients
Structural equation modelling

diversity was consistently the strongest mediator of the positive effects of species richness on AGC within and across altitudinal zones, whereas functional composition linked species richness to AGC at the broad environmental scale only. Abiotic factors had direct and indirect effects via biotic factors on AGC, but their relative importance varied with altitudinal zones. Our results indicate that the effect of species diversity on AGC was altitude-dependent and operated more strongly through structural diversity (representing niche complementarity effect) than functional composition (representing selection effect). Our study suggests that maintaining high structural diversity and managing functionally important species while promoting favourable climatic and soil conditions can enhance carbon storage in grazing enclosures.

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1. Introduction

Grazing enclosures are the initiatives implemented on communal grazing lands to exclude them from human and animal interferences and promote the natural regeneration of the vegetation, thereby restoring the forest cover and associated biodiversity (Aerts et al., 2009; Birhane et al., 2017; Birhane et al., 2007). Enclosures are therefore important biodiversity and carbon reservoirs (Adem et al., 2020; Gebregergs et al., 2019). Although enclosures have been promoted for the last decades to curb the degradation of natural resources in many tropical countries including Ethiopia (Adem et al., 2020; Birhane et al., 2017), their potential in playing a dual role of biodiversity conservation and climate change mitigation is not well established. More specifically, we still lack fundamental understanding of how species diversity relates to aboveground biomass (AGB) or carbon (AGC) and the underlying ecological mechanisms in enclosure ecosystems.

Empirical investigations of the relationships between tree species diversity and biomass or carbon stocks have reported controversial results of positive and negative patterns in temperate and tropical regions (Mensah et al., 2020d; Ouyang et al., 2019; van der Plas, 2019). There has also been evidence of neutral patterns in natural forests and human-modified ecosystems (Mensah et al., 2020a; Sullivan et al., 2017). This lack of consistency across biogeographical areas suggests that biodiversity and ecosystem functioning (BEF) relationships are controlled by an interplay of complex ecological processes, which may vary with environmental gradients, stand developmental stages, ecosystem type and structure and spatial scale (Grace et al., 2016; Hao et al., 2020; Mensah et al., 2018b, 2020d; Teixeira et al., 2020). For example, the positive effects of diversity on productivity have been reported to be stronger in environments unfavorable for growth such as dry climate and poor soil quality sites (Mori, 2018; Ouyang et al., 2019; Paquette and Messier, 2011). While attempts have been made to explain the shifting biodiversity-ecosystem functioning (BEF) relationships across vegetation type (Mensah et al., 2020a), forest succession stages (Liu et al., 2018; Teixeira et al., 2020) and spatial scales (Chisholm et al., 2013; Sullivan et al., 2017), further insights from a wide range of altitudinal gradients might help resolve this question because the effects of controlling biotic and abiotic factors vary along altitudinal gradients.

Various hypotheses have been proposed to explain the mechanisms that drive BEF relationships across ecosystems and spatial scales. Among them, two non-mutually exclusive mechanisms have received wide support in the literature: the 'niche complementarity effect' (Tilman et al., 1997) and the 'selection effect' (Hector, 1998; Huston, 1997). The complementarity effect occurs when a greater variability in species traits allows for a more efficient acquisition and complementary utilization of resources through niche differentiation and facilitation, resulting in an increased productivity in more diverse communities. The complementary effect can be quantified using functional diversity, which is a measure of the distribution of traits in a multidimensional niche space (Laliberté and Legendre, 2010). As alternative to the niche complementarity, the selection effect has been indicated in part through support for the 'mass-ratio' hypothesis (Grime, 1998; Ruiz-Benito et al., 2014), which postulates that a more diverse community stands a

greater probability of having highly productive and dominant species. The 'mass-ratio' effect can be captured using functional composition, which is quantified by the community-weighted mean (CWM) of functional trait values (Violle et al., 2007). Besides functional diversity and composition, stand 'structural diversity' – expressed as a measure of tree-size variability or complexity – is also increasingly being reported as an important determinant of BEF relationships since high structural diversity can result in a multi-layered stand structure, which would favour efficient use of space and resources through niche differentiation (Ali et al., 2019a; Ali and Mattsson, 2017; Aponte et al., 2020; Mensah et al., 2020a; Zhang and Chen, 2015). Thus, structural diversity may also partly reflect the niche complementarity aspect and can be related to species or functional diversity because increasing species diversity could also lead to the occupation of more spatial niches (Brassard et al., 2008; Zhang and Chen, 2015).

In areas characterized by a rugged topography (e.g., mountain areas), variation in altitude represents an important ecological gradient (Körner, 2007) that could strongly influence BEF relationships because altitude drives changes in abiotic factors such as precipitation and temperature, which in turn, determine plant-environment interactions and plant performance by influencing resource availability (Jucker et al., 2018; Mensah et al., 2018a; Poorter et al., 2015). It is therefore well-accepted that across wide altitudinal gradients, abiotic factors such as climate and soil are important drivers of species diversity and AGB and their effects may obscure the strength of BEF relationships (Ali et al., 2019a, 2019b; Ouyang et al., 2019; van der Plas, 2019). For example, high species diversity and AGB are generally found in areas receiving high precipitation and subsequent water availability (Ali et al., 2019a; Poorter et al., 2015). Soil nutrient availability promotes faster plant growth, thereby enhancing species diversity and AGB accumulation (Quesada et al., 2012). Both climate and soil may however trigger competition, resulting in high mortality and turnover rates (Quesada et al., 2012; Russo et al., 2005). In addition, climate and soil may influence AGB indirectly by altering functional trait diversity and composition and structural diversity. For example, greater soil nutrient availability can increase diversity due to higher complementary resource utilization, but it can also decrease diversity as a result of interspecific competition for available resources in natural forests (Ali et al., 2019a; Paquette and Messier, 2011). Given that species richness and AGC are reportedly influenced by the complex abiotic and biotic factors prevailing along altitudinal gradients, one could ask whether and how species richness-AGC relationships and the controlling biotic and abiotic factors would shift along altitudinal gradients. More importantly, elucidating these mechanisms would be crucial to formulate appropriate strategies and practical guidance for the sustainable management of forest biodiversity and carbon storage.

Although functional diversity, functional composition, structural diversity and abiotic factors have been reported to underlie diversity and AGC patterns in both temperate and tropical secondary forests (Hao et al., 2020; Mensah et al., 2020a; Mensah et al., 2016; Teixeira et al., 2020), their relative importance may vary with forest type, succession age and climatic conditions at various spatial scales (Paquette and Messier, 2011; van der Plas, 2019). This is particularly true in tropical secondary succession, i.e., natural regeneration of vegetation such as

enclosures, as the patterns of the association between biodiversity and biomass as well as the driving mechanisms could depend on processes of ecosystem recovery and anthropogenic activities (Lasky et al., 2014). Secondary succession may lead to a greater structural complexity or competitiveness of dominant species at early- and mid-seral stages (e.g., Brassard et al., 2008; Donato et al., 2012), resulting in stronger effects of structural diversity and functional composition at early succession.

In this study, we used a dataset comprising 1384 trees of 51 species from 133 inventory plots to understand diversity-AGC relationships and the underlying biotic and abiotic mechanisms along altitudinal gradients and environmental conditions in grazing enclosures in the drylands of northern Ethiopia, which is a region that has been less considered in global analyses of BEF relationships. We asked the following questions:

- (1) How does species richness relate to AGC along altitudinal gradients? We hypothesized that AGC would increase with species richness but the strength of the bivariate relationships would increase with decreasing altitude due to reduced climate favourability for plant growth at lower altitudes;
- (2) How do diversity-related biotic attributes (functional diversity, functional composition and structural diversity) mediate species richness-AGC relationships along altitudinal gradients? And what is the relative importance of these diversity dimensions? We hypothesized that structural diversity and functional composition would be stronger mediators of species richness-AGC relationships than functional diversity because the enclosures are at the early stages of succession, where competition for available resources would be a stronger driver of ecosystem productivity;
- (3) How do abiotic factors (climate, topography and soil) influence the species richness-AGC relationships along altitudinal gradients? First, we assumed that the effects of abiotic factors would vary between altitudinal gradients due to variations in climate- and soil-driven plant-plant interactions. Second, we hypothesized that structural diversity would also play a more significant role in mediating the effects of abiotic factors on AGC.

2. Material and methods

2.1. Study area and design

Data were collected from nine grazing enclosure sites, located in the Tigray region (between 12°14'53" to 13°06'08" N and 39°10'45" to 39°53'41") of Northern Ethiopia (Fig. 1). The climate in most of the region is characterized as semi-arid type, with high annual rainfall variability ranging from 450 mm to 980 mm (Birhane et al., 2017). The annual mean temperature ranges between 15 °C and 21 °C, but the maximum daily temperature can reach 42 °C between April and June and declines to 13 °C between July and February. The landscape of the region is complex and characterized by environmental gradients driven mainly by altitude. Consequently, three main agroecological zones were defined based on altitudinal gradients: highlands, midlands and lowlands (Abrha and Simhadri, 2015; Birhane et al., 2017). The highlands cover about 30% of the total area and extend between 2400 and 3400 m.a.s.l. (Abrha and Simhadri, 2015). They are characterized by a relatively higher annual rainfall and cooler temperatures. The midlands represent 29% of the region, extend between 1800 and 2400 m.a.s.l. and experience medium amount of rainfall along with moderate temperatures. The lowland areas are located between 1400 and 1800 m.a.s.l. and experience low amount of rainfall and high temperatures. The region is further characterized by a rugged topography, which includes mountains, plateaus, valleys and gorges (Abrha and Simhadri, 2015). The vegetation is primarily composed of remnant forest patches including forests undergoing restoration (e.g., enclosures) (Birhane et al., 2017).

We used a dataset of 133 inventory plots of 0.02 ha (10 m × 20 m) each, distributed across the three main agroecological zones (hereafter referred to as altitudinal zones) of the region (Table S1). Within each altitudinal zone, three enclosures evaluated as "best" on the basis of well-defined ecological and socio-economic criteria of successful forest restoration and management were selected (Birhane et al., 2017), resulting in a total of nine enclosure sites, distributed across six administrative districts (Fig. 1). More details about the historical land use patterns and vegetation dynamics in the enclosures are provided in Appendix A of the Supplementary Information. The age of each enclosure, i.e., the number of years since the establishment, was recorded (Table S1). The inventory plots were all established inside the enclosures using a systematic transect sampling method (Table S1), with 34 plots in highlands, 54 plots in midlands and 45 plots in lowlands. To avoid edge effects, the first and last transect lines were installed at about 40 m from the borders. In each plot, all individual living trees and shrubs with a diameter ≥ 2.5 cm at stump height, i.e., 30 cm above ground level (DSH) were measured for their DSH, diameter at breast height, i.e., 130 cm above ground level (DBH) and total height (Ht). The minimum diameter for selecting the sample plants was based on the DSH instead of DBH because of the complex architecture of trees and shrubs growing in enclosures (Ubuy et al., 2018b). The DBH and DSH were measured with a digital calliper, while the Ht was measured using a measuring stick. For the trees and shrubs that fork below 130 cm or 30 cm of height, we measured each ramification individually and calculated the DBH and DSH as the average value of the individual stems (Ubuy et al., 2018b). In total, 1384 trees of 51 species were measured. Each individual tree was identified at the species and genus levels using the "Useful Trees and Shrubs for Ethiopia" (Bekele-Tesemma, 2007; Bekele-Tesemma, 1993) and "Useful Trees and Shrubs for Eritrea" (Bein, 1996).

2.2. Aboveground carbon stock

We summed up the AGB of each individual tree and shrub measured within a plot to obtain the plot-level AGB, which was then converted to plot-level AGC stock by applying a carbon fraction of 0.5. We quantified the AGB (kg) of each individual tree and shrub by applying the allometric equation developed by Ubuy et al. (2018b) for the common tree and shrub species found in enclosures in the drylands of Tigray: $AGB = 0.2050 \times DSH^{1.8548} \times Ht^{0.2948}$ where AGB is the aboveground biomass (kg), DSH is the diameter at stump height (cm) and Ht is the total height (m).

2.3. Diversity-related biotic attributes

We considered three main attributes of diversity: taxonomic, functional and structural. We used plot-level species richness, i.e., number of distinct species recorded within each plot, to quantify the taxonomic diversity. Functional diversity and composition were assessed based on two functional traits that determine tree growth and biomass production: wood density (WD, g cm⁻³) and maximum tree height (MAXH, m). Data on specific wood density were obtained from a local study on the wood density of the common tree species found in enclosures in Tigray region, Northern Ethiopia (Ubuy et al., 2018a) and from the Global Wood Density Database (Zanne et al., 2009). Plant maximum height was derived from our dataset for each species. We computed the functional dispersion (F_{dis}), which accounts for the distance of species to the centre of multi-trait functional space (Laliberté and Legendre, 2010; Mouchet et al., 2010) and has been often used as a relevant indicator of functional diversity in many BEF studies (e.g., Aponte et al., 2020; Hisano and Chen, 2020). As functional composition metrics, we computed the plot-level CWM of wood density (CWM_{WD}) and maximum tree height (CWM_{MAXH}). The functional diversity and composition metrics were computed using the 'FD' library in the R statistical

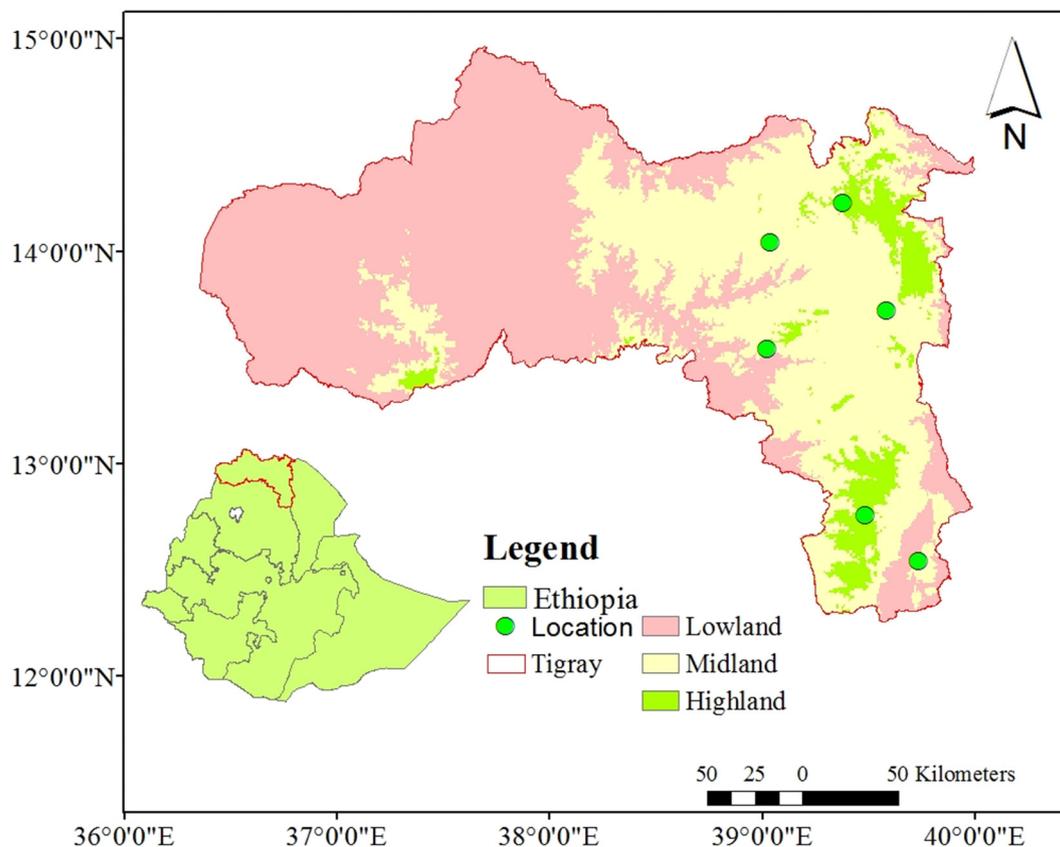


Fig. 1. Location of sampling sites across three altitudinal zones in the Tigray region.

environment based on species relative abundance and the values of the selected traits (Laliberté et al., 2015).

Finally, we used stand structural complexity as a proxy for structural diversity. Stand structural complexity was quantified by calculating two plot-level metrics that relate to the vertical (height) and horizontal (diameter) architectural properties of a tree (Mensah et al., 2020a; Seidel et al., 2019): the coefficient of variation of tree diameter (CV_{DBH}) and the coefficient of variation of tree height (CV_{Ht}).

2.4. Abiotic factors

We considered abiotic factors that can have important influence on plant growth and productivity through their effects on soil mineralization rates and nutrient availability. As such, the environmental data used in this study included climatic, topographic and edaphic factors. The climate data consisted of the 19 Bioclimatic variables (Bio 1 to Bio19), which were downloaded from the climatologies at high resolution for the earth's land surface areas (CHELSA) dataset at a resolution of 1 km (Karger et al., 2017). We used hillshade (HILLSH) as a sole topographic attribute because it is calculated based on the consideration of aspect, slope, mean annual solar azimuth and altitude (Burrough and McDonnell, 1998; Mensah et al., 2020b). The HILLSH characterizes the intensity of illumination at a specific location. Soil organic carbon content (SOC) was also used as the representative variable of edaphic properties and was measured from the 0–30 cm depth layer in each 0.02 ha plot as a composite sample of five subsamples collected from five 1 m² subplots (Table S1).

2.5. Data analysis

We performed all the analyses in the R statistical software, version 4.0.2 (R Core Team, 2020). Age since abandonment has reportedly

influenced ecological processes during secondary forest succession (e.g., Teixeira et al., 2020), but the closure age was not included in our analyses because a preliminary analysis showed that it has no significant effect on species richness and AGC stock (Appendix A and Table S1, Supplementary Information). We also explored how species richness and AGC stock varied along the altitudinal gradients using generalized linear mixed-effects models (GLMMs), with altitudinal zones, i.e., highland, midland and lowland, as the explanatory variable and plot included as a random factor. The GLMMs were performed using the 'lmer' function in the package 'lme4' in R (Bates et al., 2015). AGC was analysed as a continuous response variable using a GLMM with Gaussian distribution, after log-transformation to meet the assumption of normal distribution of residual errors. Species richness was modelled as a count data using a GLMM with Poisson distribution (Mensah et al., 2018b; Zuur et al., 2009). The marginal (R^2_m) and conditional (R^2_c) coefficients of determination were calculated to estimate the variance explained by the fixed and random factors (Nakagawa et al., 2013). We also used boxplots to show the distribution of species richness and AGC between the altitudinal zones (Fig. S1).

In line with our first question, we assessed how species richness relates to AGC along the altitudinal gradients considering two scales of investigation: (i) local scale represented by each altitudinal zone, thereafter referred to as 'within altitudinal zone' and (ii) broad scale represented by the aggregation of the data from the three altitudinal zones, which was thereafter referred to as 'across altitudinal zones'. Thus, we performed simple linear regressions to explore the bivariate relationships between species richness and AGC within and across altitudinal zones. Prior to the analyses, we tested for significant interaction effect of species richness with altitudinal zones. Because we found a significant species richness-altitudinal zone interaction effect, we controlled for the possible confounding effect of altitudinal zone when evaluating the species richness-AGC relationship for the aggregated

data (Table S3). Whether or not the effect of the altitudinal zone was accounted for, we found a similar pattern of species richness-AGC relationship (Table S3) across altitudinal zones'. We used scatterplots and fitted lines to display the patterns of these relationships.

While accounting for the effect of abiotic factors, we evaluated how functional diversity, functional composition, structural diversity mediated species richness effects on AGC by means of Structural Equations Models (SEMs). We chose this modelling approach because it allows making inferences about causal relationships between multiple variables and identifying both direct and indirect causal effects. Our conceptual SEM models aimed to test the relative importance of niche complementarity and mass-ratio as well as the effects of abiotic covariates (Fig. 2). Prior to the analyses, we selected annual mean temperature (MAT or Bio1) and annual precipitation (PREC or Bio12) to represent the main axis of climatic variability in the study area based on their correlations with other bioclimatic variables (Fig. S2). We then standardized all the variables using the 'scale' function in R. Functional diversity was represented by F_{dis} . Because there is more than one metric that can represent functional composition, structural diversity and climatic conditions, we performed separate multi-model inference (MuMIn) analyses for each group of indicators using the 'dredge' function of the MuMIn package in R (Bartoñ, 2018) to select one representative variable per group. The metric with the highest relative importance value was chosen as the most relevant one. We then developed separate SEM for each altitudinal zone and for the pooled dataset using the metrics that were selected from the MuMIn analyses. We started with a full hypothesized model (Fig. 2) and improved the fit of the model by performing a stepwise removal of the non-significant paths and by adding potential correlation paths based on the path modification indices (Luo et al., 2019). We compared the full model versus reduced

models by means of AIC (Akaike Information Criteria) and selected the final model as the model with the lowest AIC (Luo et al., 2019).

All the SEMs were fitted using the "lavaan" package in R (RosseeL, 2012). We used the Chi square p -value, the comparative fit index (CFI), the goodness-of-fit index (GFI) and the standardized root mean square residual (SRMR) to evaluate the goodness-of-fit (GOF) of the models (Mensah et al., 2020a, 2020c; RosseeL, 2012). The strength of the causal paths between the variables was assessed using the standardized parameter values. The bivariate relationships of each causal pathway that was hypothesized in the SEMs were also examined using scatterplots and linear regression analyses.

3. Results

3.1. Species richness-AGC relationships within and across altitudinal zones

Only AGC stocks differed significantly between the three altitudinal zones (Table 1). The largest AGC stock was measured in highlands, followed by lowlands and midlands (Table 1 and Fig. S1). There was a significant interaction between species richness and altitudinal zones on AGC stock ($F = 21.12; p < 0.001$), indicating that the effects of species richness on AGC stock varied between the altitudinal zones. Accordingly, we found that species richness-AGC relationship was significantly positive in lowlands ($\alpha = 0.27; p = 0.000$) and midlands (slope $\alpha = 0.14; p = 0.008$) and non-significant in highlands ($\alpha = 0.12; p = 0.164$; Fig. 3). A significant and positive association ($\alpha = 0.12; p = 0.007$) between species richness and AGC stock was also observed when the data from the three altitudinal zones were pooled together. Moreover, the coefficient of determination (R^2) of the relationship between species richness and AGC increased from highlands to lowlands (Fig. 3).

3.2. Direct and indirect effects of diversity-related biotic attributes and abiotic factors

In midlands, lowlands and across altitudinal zones, CWM_{MAXH} , CV_{DBH} and PREC were the most important metrics of functional diversity, functional composition and climatic conditions, respectively. In highlands, CWM_{WD} and MAT were the most important variables (Fig. 4).

The GOF statistics confirmed that our conceptual models had a good fit to the data, as evidenced by the acceptable range of the values of all GOF indicators (Table 2). The explanatory variables explained 51–65%, 4–30%, 22–59%, 25–59% and 8–43% of the variation in AGC stock, species richness, functional diversity (F_{dis}), functional composition (CWM_{WD} and CWM_{MAXH}) and structural diversity (CV_{DBH}), respectively (Fig. 5).

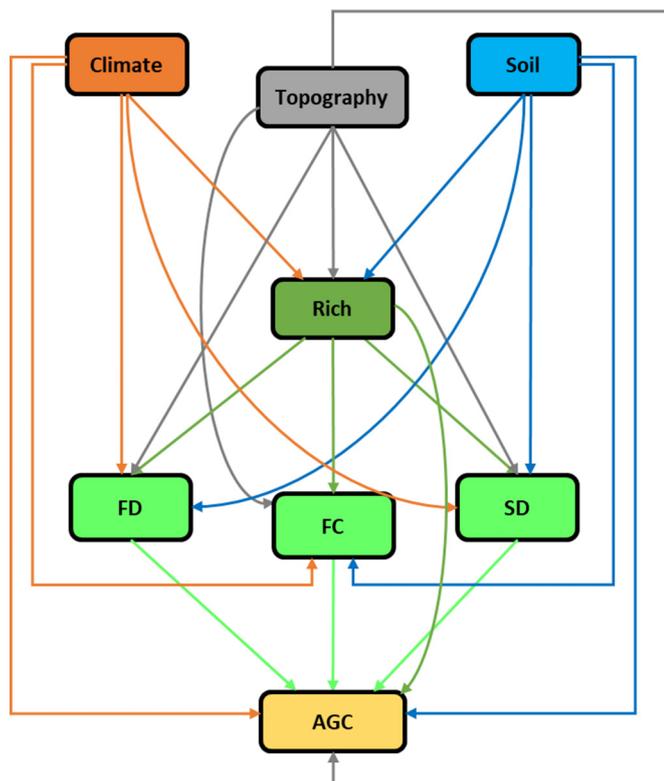


Fig. 2. Conceptual models used to illustrate the multiple interrelated pathways between abiotic factors (soil, climate, and topography) and diversity-related biotic attributes (Rich, FD, FC and SD) controlling aboveground carbon (AGC, $Mg\ ha^{-1}$). The arrows illustrate the hypothesized direct and indirect causal paths. Rich: species richness, FD: functional diversity, FC: functional composition and SD: structural diversity.

Table 1

Results of the generalized linear mixed-effects models testing the effects of altitudinal gradients on species richness and aboveground carbon stock (AGC, $Mg\ ha^{-1}$). The baseline altitudinal zone represented by the intercept is the highland. Significant effects are emboldened.

	Fixed effects			Random effects		R^2	
	Estimate	SE	p-value	σ^2_{Plot}	σ^2_{Resid}	Marg	Cond
Species richness							
Intercept	1.32	0.09	<0.000	0.00	-	0.07	0.11
Midland	0.10	0.11	0.392				
Lowland	-0.22	0.12	0.075				
AGC							
Intercept	2.17	0.13	<0.000	0.22	0.38	0.26	0.53
Midland	-1.13	0.14	<0.000				
Lowland	-0.53	0.14	0.000				

SE: standard errors; σ^2_{Plot} : variance explained by plot, respectively; σ^2_{Resid} : residual variance; Marg: Marginal; Cond: Conditional.

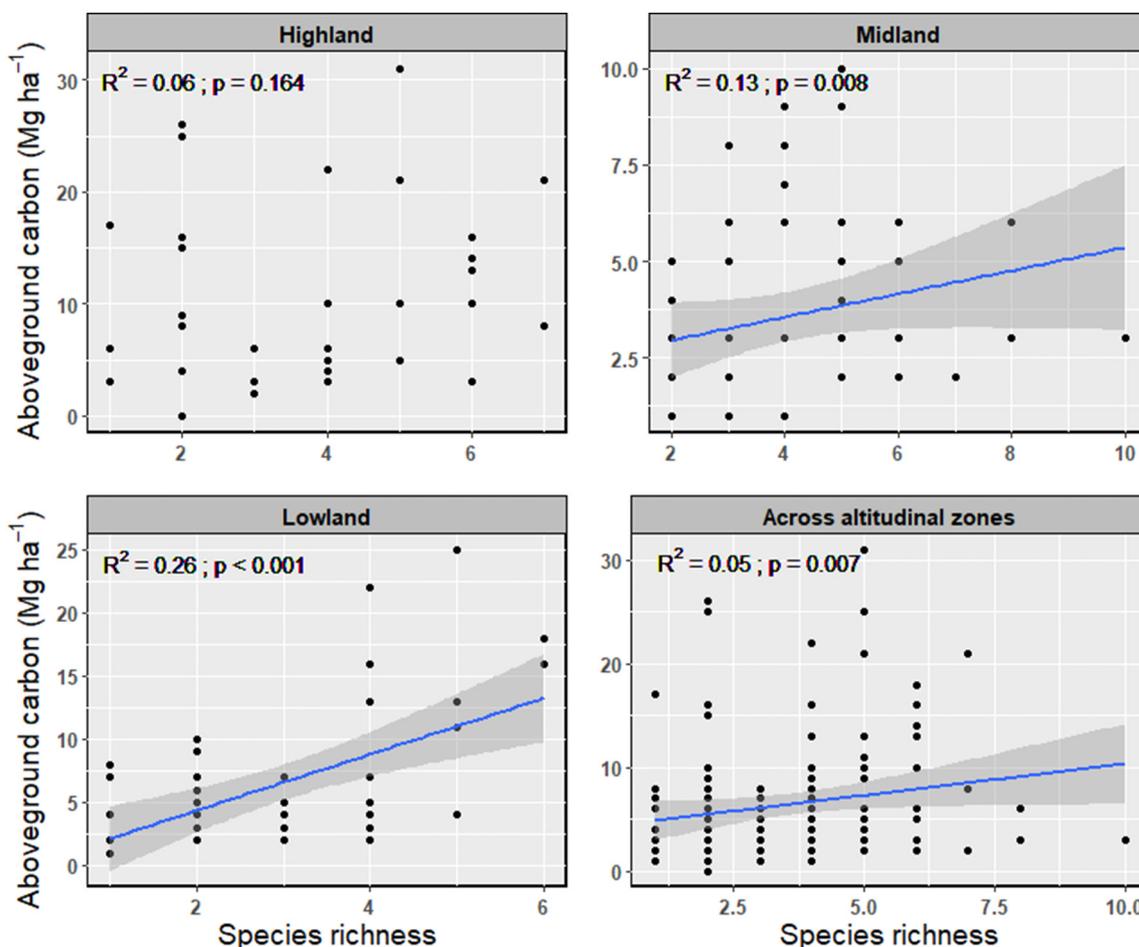


Fig. 3. Bivariate relationships between species richness and aboveground biomass (AGC, Mg ha^{-1}) within and across the altitudinal zones in northern Ethiopian grazing exclosures. The fitted linear regression lines and their pointwise 95% confidence intervals (shaded areas) are shown for significant bivariate relationships only.

Among the biotic variables, CV_{DBH} consistently had a positive direct effect on AGC stock within and across altitudinal zones, which was comparatively stronger than that of CWM_{WD} and CWM_{MAXH} in highlands and across altitudinal zones, respectively (Fig. 5 and Table S4). Similarly, CV_{DBH} mediated the positive effect of species richness on AGC within and across altitudinal zones, as evidenced by the significant positive effect of species richness on CV_{DBH} , which in turn, had a positive effect on AGC. CWM_{MAXH} was also a significant mediator of the effect of species richness on AGC across altitudinal zones only, although the indirect effect of species richness on AGC via CWM_{MAXH} was negative and weaker ($\beta = -0.06$; $p = 0.030$; Fig. 5D) than those via CV_{DBH} ($\beta = 0.13$ – 0.35 ; $p < 0.04$; Fig. 5 and Table S4). Overall, the effect of F_{dis} was negligible (Fig. 5 and Table S4).

Abiotic factors (PREC, MAT, HILLSH, and SOC) affected AGC both directly and indirectly via biotic factors, but the strength and direction of these relationships shifted along the altitudinal gradients (Fig. 5 and Table 3). In highlands, HILLSH directly promoted AGC, while in midlands and across altitudinal zones, precipitation had a direct positive effect on AGC (Fig. 5 and Table S4). The direct effect of SOC on AGC shifted from positive in highlands to negative in midlands and neutral in lowlands (Fig. 5).

The indirect effects of abiotic factors on AGC were mainly reflected through negative indirect effects of MAT and PREC via CV_{DBH} in high- and midlands (Figs. 5A–B), positive indirect effects of MAT and SOC via CWM_{WD} in highlands (Fig. 5A), a positive effect of PREC via CV_{DBH} in lowlands (Fig. 5C) and a negative indirect effect of HILLSH via species richness and CV_{DBH} in lowlands (Fig. 5C). Across altitudinal zones,

PREC and HILLSH indirectly promoted AGC via increasing species richness, CV_{DBH} and CWM_{MAXH} (Fig. 5). Overall, the direct effects of abiotic factors were stronger than their indirect effects and the strength of both direct and indirect effects of abiotic factors was weaker than that of biotic factors (e.g., CV_{DBH}) within and across altitudinal gradients (Fig. 5 and Table S4). The outputs of the SEMs were supported by the results of the linear regression analyses of the bivariate relationships of the causal paths (Figs. S3–S9).

4. Discussion

4.1. Species richness–AGC relationships along the altitudinal gradients

We found that species richness enhanced AGC in mid- and lowlands and across altitudinal gradients, supporting our first hypothesis. This finding is in agreement with previous studies that reported a positive effect of species richness on AGC in tropical ecosystems (Mensah et al., 2020a, 2020d; Poorter et al., 2015) and suggests that C storage is also mediated by species diversity in the exclosures. The positive effect of taxonomic diversity on AGC stock in the exclosures can be linked to increasing tree density with species richness as previously reported (Chisholm et al., 2013; Mensah et al., 2020a). Our results support this observation as we found that species richness correlated positively with tree density, which in turn, increased with AGC (Fig. S10).

We also found that the strength of the relationship between species richness and AGC varied along the altitudinal gradients and environmental scales: a non-significant and weak relationship at high

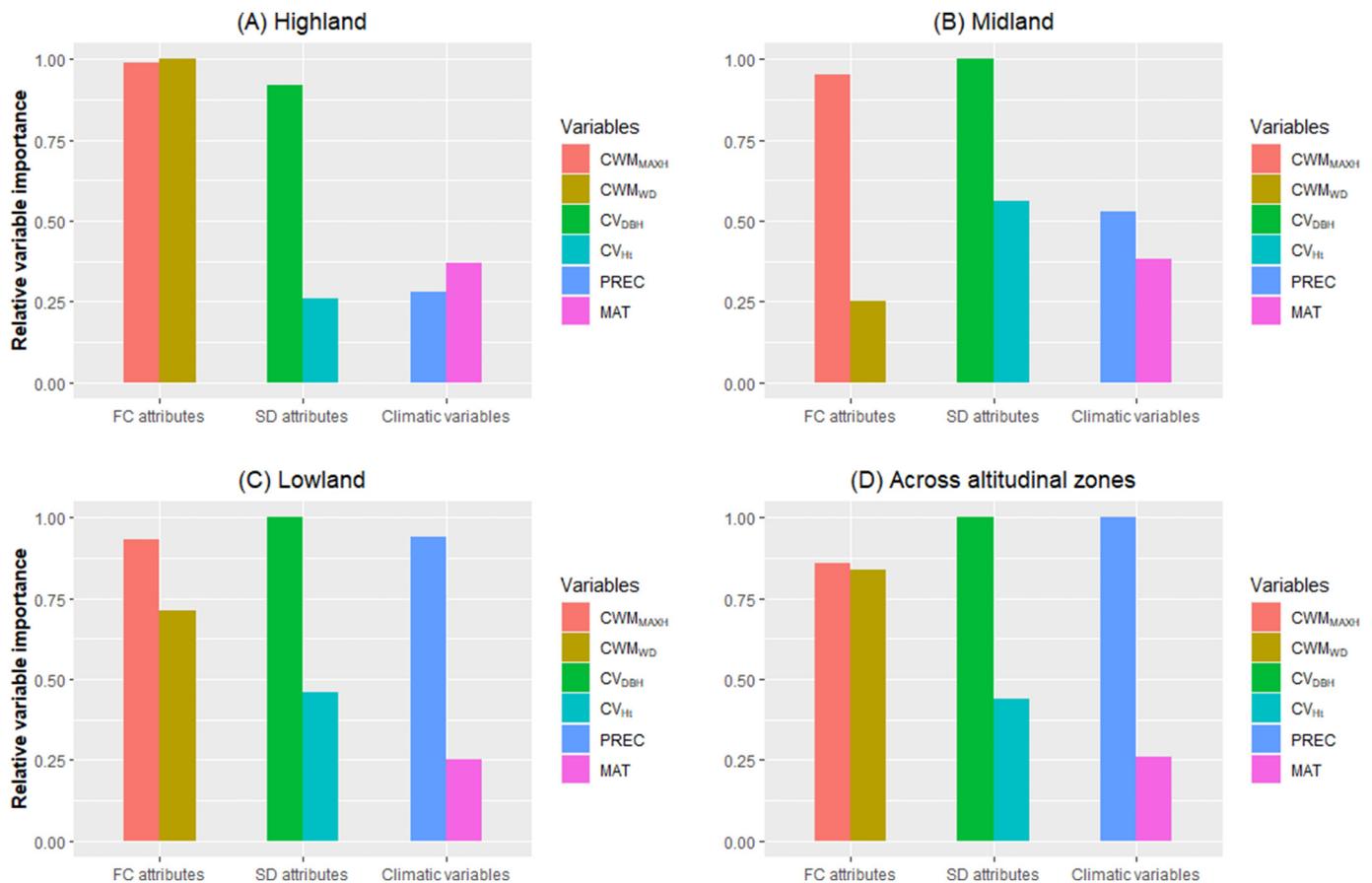


Fig. 4. Relative importance of functional composition (FC) and structural diversity (SD) attributes and climatic variables used as predictors of aboveground carbon (AGC, Mg ha⁻¹) in the multi-model inference analyses. CWM_{MAXH}: community weighted mean of maximum height; CWM_{WD}: community weighted mean of wood density; CV_{DBH}: coefficients of variation of tree diameter; CV_{Ht}: coefficient of variation of tree height; PREC: annual precipitation; MAT: mean annual temperature.

altitudes versus strong positive effects at local environmental scale (mid- and low altitudes) and positive but weak effect at broad environmental scale (across altitudinal zones). These results indicate that altitude may also act as an environmental filter to modulate the effects of species richness on carbon storage. Therefore, our findings support two general opinions: (i) tree species richness-carbon relationships are idiosyncratic and scale-dependent (Chisholm et al., 2013; Mensah et al., 2020a; Sullivan et al., 2017) and (ii) the relationships between diversity and productivity can become stronger when environmental conditions are less favourable for plant growth (Ouyang et al., 2019; Paquette and Messier, 2011). The observed shift in species richness-AGC relationships from weak in highlands to strong positive in mid- and lowlands could therefore be related to the altitude-dependent resource availability driven by climate favourability. In fact, the highland sites had greater climate favourability and resource availability (e.g., higher effective precipitation, i.e., rainfall minus evaporation and SOC) compared to mid- and lowland sites (Fig. S11). This was also evidenced by the higher AGC

potential of highland stands (Table 1 and Fig. S1). Hence, the strong positive effects of diversity on AGC in the mid- and lowland exclosures suggests that under low resource availability conditions, species diversity improves the efficiency of use of the limited resources by niche differentiation or facilitation, in accordance with the stress gradient hypothesis (Maestre et al., 2009).

Moreover, the relationship between species richness and AGC was non-significant in highlands. The lack of taxonomic diversity effect on AGC in highlands may be attributed to the saturation of diversity effects at high diversity in the highland exclosures, particularly if additional species that come into the highland ecosystems are functionally redundant (Chesson et al., 2001; Mensah et al., 2020a; Tilman et al., 1997). Consequently, the number of species may rise without further increase in carbon storage (Poorter et al., 2015), resulting in a non-significant positive effect of diversity on carbon storage as observed at high altitudes. Therefore, our results suggest a potential saturation of diversity effects due to species redundancy from lower to higher altitudinal range.

Table 2

Summary of goodness-of-fit (GOF) statistics for the SEMs relating abiotic factors (ENV), functional diversity (FD), functional composition (FC), structural diversity (SD) to species richness (Rich) and aboveground carbon (AGC, Mg ha⁻¹) within and across altitudinal zones in northern Ethiopian grazing exclosures.

SEM	SEM	Altitudinal gradients	chisq	p-value	cfi	gfi	srmr	AIC
ENV-Rich-(FD, FC, SD)-AGC	Fig. 5A	Highland	4.52	0.95	1.00	0.97	0.08	423.90
ENV-Rich-(FD, FC, SD)-AGC	Fig. 5B	Midland	1.21	0.88	1.00	0.99	0.03	423.21
ENV-Rich-(FD, FC, SD)-AGC	Fig. 5C	Lowland	5.72	0.89	1.00	0.95	0.05	526.99
ENV-Rich-(FD, FC, SD)-AGC	Fig. 5D	Across altitudinal zones	13.10	0.29	0.99	0.96	0.05	1600.544

chisq: Chi-square statistic; cfi: comparative fit index; gfi: goodness of fit index; srmr: standardized root mean residual; AIC: Akaike Information Criteria.

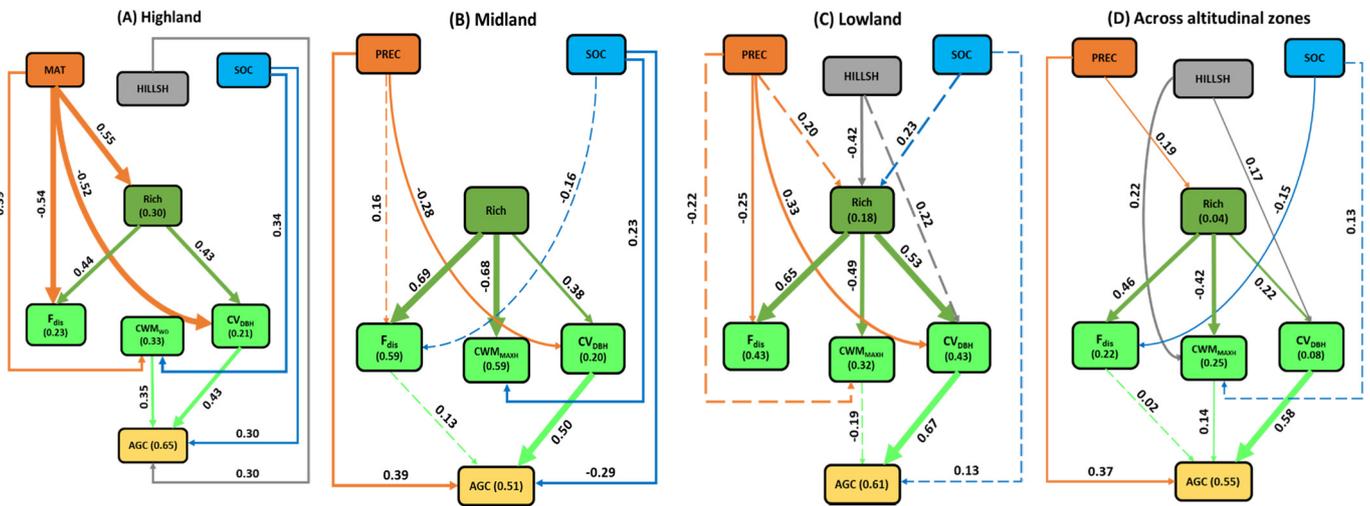


Fig. 5. Results of SEMs relating functional dispersion (F_{dis}), community weighted mean of wood density (CWM_{WD}) and maximum tree height (CWM_{MAXH}), coefficient of variation of tree diameter (CV_{DBH}), precipitation (PREC), mean annual temperature (MAT), hillshade (HILLSH) and soil organic carbon content (SOC) to species richness (Rich) and aboveground biomass (AGC, $Mg\ ha^{-1}$) for highland, midland, lowland and across altitudinal zones. The values without brackets on the graphs are the standardized path coefficients and their significance is presented in the Tables S4. The values within brackets are the coefficients of determination (R^2), shown for the dependent variables. The solid arrows represent the significant ($p < 0.05$) causal paths, while the dashed arrows represent the non-significant ($p > 0.05$) causal paths. The width of an arrow is proportional to the value of its coefficient. The goodness-of-fit (GOF) statistics are summarized in Table 2.

4.2. Structural diversity consistently mediates species richness effects on AGC

We explored the relative importance and contribution of niche complementarity and selection effects to ecosystem functioning by testing whether functional diversity, functional composition and structural diversity could mediate species richness effects on AGC across altitudinal gradients. Interestingly, we found no mediation effect of functional diversity and composition in high-, mid- and lowland stands. On the contrary, we found that structural diversity consistently mediated the species richness–AGC relationships in high-, mid-, lowlands and across sites, supporting partly our second hypothesis. Similar strong and consistent effects of structural diversity on AGC were reported in previous studies conducted in natural forests across biogeographic regions (Ali et al., 2019a; Ali et al., 2016; Aponte et al., 2020; Mensah et al., 2020a). Our results indicate that species richness increased AGC by promoting a diversified stand structure at both local and broad environmental scales (Fig. 5). This was also evidenced by the consistent and significant positive relationships between CV_{DBH} and AGC (Fig. S3) and between species richness and CV_{DBH} (Fig. S4) in mid- and lowlands and further across altitudinal zones. Thus, our finding suggests that higher species diversity promotes greater structural diversity, which optimizes the efficient utilization of space and resources (e.g., light) thereby increasing the potential for carbon storage, in line with the idea that structural diversity is associated with niche complementarity

Table 3

Indirect and total (direct + indirect) standardized effects of precipitation (PREC), mean annual temperature (MAT), hillshade (HILLSH) and soil organic carbon (SOC) on aboveground carbon (AGC, $Mg\ ha^{-1}$) within and across altitudinal gradients in northern Ethiopian grazing exclosures. Significant effects are emboldened. Direct effects are presented in Fig. 5.

Predictor variable	Effects	Highland	Midland	Lowland	Across altitudinal gradients
PREC/MAT	Indirect	0.02	-0.12	0.22	0.35
	Total	0.02	0.27	0.22	0.35
HILLSH	Indirect	-	-	-0.15	-0.15
	Total	0.30	-	-0.15	-0.04
SOC	Indirect	0.12	-0.02	-	0.10
	Total	0.42	-0.31	-	0.24

effects and productivity (Aponte et al., 2020; Mensah et al., 2020a; Zhang and Chen, 2015). The positive mediation of species richness effect on AGC by CV_{DBH} further extends the previously reported importance of structural diversity as a strong predictor of species diversity and AGC to exclusive ecosystems.

We also hypothesized that functional composition would mediate the species richness-AGC relationships in the exclosures. However, we observed a weak mediation effect of functional composition, i.e., CWM_{MAXH} across altitudinal zones only. Consistent with other studies across a range of forest types (Ali et al., 2017; Aponte et al., 2020; Mensah et al., 2021; Villa et al., 2020), this finding provides support to the mass ratio hypothesis and indicates that the selection effect also drives carbon storage in the exclosures. In particular, the negative influence of species richness on CWM_{MAXH} suggests that a few dominant and productive species contribute to higher AGC due to the competitive exclusion effect (Ali et al., 2016; Mensah et al., 2016). That the selection effect operated at the broad environmental scale only stresses the scale-dependency of the biotic mechanisms driving diversity-carbon relationships and reflects the importance of the scale in the analyses of biodiversity effects (e.g., Chisholm et al., 2013). Overall, the effect of structural diversity was stronger than that of functional composition and both structural diversity and functional composition overruled the effect of functional diversity on AGC in the exclosures, as recently reported by Villa et al. (2020).

Although our findings indicate that AGC storage in the exclosures was mainly underpinned by structural diversity, it is worth noting that the limited number of functional traits used for the quantification of functional diversity and composition, i.e., maximum height and wood density, might not be sufficient enough to capture the full range of functional attributes needed to explain AGC storage. Considering other functional traits related to leaf and wood economics (Chave et al., 2009; Wright et al., 2004) such as specific leaf area, leaf mass per area, leaf phenology and hydraulic conductivity could have increased the functional spectrum (Mensah et al., 2020c).

4.3. Effects of abiotic factors on the species richness-AGC relationships

We found that the relative importance of the direct and indirect effects of abiotic factors varied along the altitudinal gradients. For example, precipitation was the most important abiotic factor (as judged by

the total effect) influencing the species richness-AGC relationship across altitudinal zones, whereas SOC and HILLSH were more important drivers at the local environmental scale (Table 3). These results support the general opinion that precipitation is the most important abiotic factors for BEF relationships at global scale (Ratcliffe et al., 2016), whereas topography-driven nutrient availability plays a more important role at local scale (Balvanera et al., 2011). Moreover, when comparing the effects of abiotic and biotic factors, we found that both the direct and indirect effects of abiotic factors were weaker than those of biotic factors (e.g., CV_{DBH}) within and across altitudinal gradients. This indicates that as though environmental filtering acts as a regulator of AGC in the grazing exclosures, biotic mechanisms such as niche complementarity and selection effects remained fundamentally important to explain AGC response to diversity. Of particular importance, environmental effects operated via both positive and negative effects on structural diversity and functional composition, indicating that resource availability may increase stand structural diversity as a result of enhanced growth of individual trees through efficient utilization of resources or favour interspecific competition leading to competitive exclusion and high mortality rates (e.g., Ali et al., 2019a). These findings suggest that niche complementarity and selection effects are modulated by climatic and topographic patterns across altitudinal gradients.

4.4. Implications for the management of exclosures

The relevance of our study extends beyond the identification of the mechanisms underlying diversity-carbon relationships to practical implications for the management of exclosures. Our results suggest that excluding grazing areas can promote co-benefits of diversity conservation and carbon storage. In particular, maintaining and increasing structural diversity as well as promoting functionally important species would be essential to enhance AGC storage and maintain the benefits of species diversity on structural diversity in the grazing exclosures (Ali et al., 2019a; Aponte et al., 2020; Poorter et al., 2015). In addition, the positive direct and indirect effects of precipitation at both local and broad environmental scales suggest that any reduction in precipitation would constrain long-term AGC storage and biodiversity conservation in exclosures in the semi-arid zones of northern Ethiopian (Ali et al., 2019a). Maintaining soil fertility through appropriate management strategies would also be crucial. Because climate, topography and soil modulated the biotic processes underlying species richness-AGC relationships, management and conservation strategies should also consider the conditions that enhances species growth and diversity (Hao et al., 2020).

5. Conclusions

Much debate remains regarding the underlying causes of the shift in BEF relationship across ranges of natural ecosystems. In this study, we show that much of these variations can be explained by variations in the relative importance of the biotic and abiotic mechanisms controlling BEF relationships along altitudinal gradients and across environmental scales using the example of grazing exclosures. Our results emphasize the need of considering altitudinal gradients, environmental scale and biotic-abiotic interactions when analysing the effects of biodiversity on ecosystem functioning in semi-arid secondary forests such as the northern Ethiopian grazing exclosures.

CRedit authorship contribution statement

Florent Noulèkoun: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Emiru Birhane:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Sylvanus Mensah:** Conceptualization, Formal analysis, Writing – review & editing. **Habtemariam Kassa:** Funding acquisition, Project administration,

Supervision, Writing – review & editing. **Alemayehu Berhe:** Resources. **Zefere Mulaw Gebremichael:** Resources. **Nuru Mohammed Adem:** Resources. **Yigremachew Seyoum:** Funding acquisition, Project administration. **Tefera Mengistu:** Funding acquisition, Project administration. **Bekele Lemma:** Funding acquisition, Supervision, Writing – review & editing. **Nigussie Hagazi:** Funding acquisition, Project administration. **Haftu Abrrha:** Formal analysis, Writing – review & editing.

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.

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Appendix A. Supplementary data

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