An assessment of the biodiversity - ecosystem function relationship in southern African woodlands

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Contents

1 Introduction

A number of studies have shown relationships between biodiversity and ecosystem functionality (**?**). Ecosystem functions can be defined in broad terms as rate processes and properties which describe the degree of biotic activity within an ecosystem (Jax, 2005). This includes basic processes of primary production such as gross primary productivity and atmospheric nitrogen fixation, but can be extended to indirect aggregate measures of function such as resistance of productivity to disturbance (). Ecosystem functionality may also include static ecosystem properties such as forest canopy complexity and trophic complexity, which in turn influence ecosystem processes. The strength and direction of these observed Biodiversity - Ecosystem Function Relationships (BEFRs) varies

depending on the ecosystem being studied (), the ecosystem function(s) of interest (), and the inclusion of environmental covariates in statistical models (), but there appears to be a generalisable positive correlation between biodiversity and ecosystem functionality (Liang et al., 2016). Over the past decade, many observational studies of the BEFR have been conducted, mostly in tropical and temperate forests, and grasslands (Chen et al., 2011). These studies support previous findings from small scale experimental studies which began in earnest during the 1990s as concern grew over the global loss of biodiversity (Tilman and Downing, 1994; Tilman et al., 2014).

The representation of dry tropical ecosystems in the BEFR literature is poor compared to other ecosystems. Clarke et al. (2017) conducted a meta-analysis of 182 published BEFR studies, finding that only 13% were conducted in the tropics, with 42% of those being conducted in the wet tropical forests of Costa Rica, which are unique in terms of species assemblage. In wet tropical forests, much of the observed effect of biodiversity on ecosystem function has been attributed to niche complementarity (), whereby competition between individuals is reduced due to them occupying different niche space, allowing diverse species assemblages to take greater advantage of natural resources (). In the dry tropics however, low precipitation, high seasonality of rainfall and temperature, and high levels of disturbance from fire and herbivory mean that niche complementarity and competition may not play as much of a role in the relationship between biodiversity and ecosystem function. Instead, stress tolerance and productivity of abundant species (selection effects) may be the predominant forces which influence ecosystem functionality (). Similarly, more diverse species assemblages may lead to facilitation effects between certain species combinations in environments which are more hostile to growth ().

Re-assess this paragraph -In the seasonally dry woodlands of southern Africa, human actions are driving rapid changes in biodiversity. This has in turn raised interest in how biodiversity influences ecosystem function in these ecosystems (). Resource extraction by humans directly influences biodiversity via selective tree-felling for timber, charcoal making, non-timber forest products and through land use change to agriculture (Ryan et al., 2016). Climate change is also indirectly affecting the biodiversity of southern African woodlands, altering temperature and precipitation, and affecting climate seasonality (). Savannas and sparse woodlands are the dominant vegetation type across the southern African region, spanning >4 million km^2 (Ryan et al., 2016). The carbon stored in these woodlands is comparable to that found in the wet forests of the Congo basin and are of global importance to the carbon cycle. Climatic conditions and biogeography vary across southern African woodlands, resulting in a diverse range of woodland tree species assemblages, which retain the common features of an open tree canopy and an understorey generally dominated by C4 grass species (Frost, 1996). Southern African woodlands are highly diverse, thought to harbour ~8500 plant species of which there are >300 tree species (Frost, 1996). These ecosystems have been identified by previous studies as a priority for conservation efforts (Brooks et al., 2006; Mittermeier et al., 2003; Frost, 1996). Many conservation projects in the region currently aim to conserve biodiversity and woody biomass stocks simultaneously under the directive of the United Nations REDD+ programme or the similar Forest Carbon Partnership Facility (FCPF) (Hinsley et al., 2015). A small number of academic studies in southern African woodlands have shown that above ground woody carbon/biomass stocks correlate positively with tree species richness (McNicol et al., 2018; ?; ?), but the scientific impact of all these studies has been hampered by a restricted climatic and biogeographical range of study sites, meaning that generalisable regional trends could not be reliably inferred. **Say how the previous studies might have been wrong because of their limited scope, or how in order to really answer the question you need to sample long environmental gradients.**

The role of environmental factors in mediating the BEFR generally is poorly understood (Ratcliffe et al., 2017). In forests, climatic variation is known to affect both woody biomass (Michaletz et al., 2014, 2018) and species diversity (), so it is important to account for these climatic factors and understand how they interact with biomass and diversity to effectively model the effects of biodiversity on biomass stocks in analyses at large spatial scales in savannas. Sankaran et al. (2005) used data from 854 African woodland field sites to show that mean annual precipitation (MAP) sets the upper

limit for woody cover in savannas, which is presumably positively correlated with biomass (), while other factors such as herbivory, fire regime and soil properties also contribute at a local scale to reduce woody cover below this maximum. However, this study did not consider the role of species diversity in the complex interactions between environment and tree cover.

Condit et al. (2013) found that dry season intensity was the main determinant of tree species distribution in Panamanian tropical forests, which may affect ecosystem level productivity and thus woody biomass through selection effects, promoting the growth of a certain highly productive species only under specific environmental conditions. In European forests (Ratcliffe et al., 2017) found a general trend towards stronger positive relationships between tree species richness and various ecosystem functions in more arid environments, suggesting variation in the balance between competitive and facilitative effects along the aridity gradient as the driver of this relationship, an example of the Stress Gradient Hypothesis (Dohn et al., 2013). Water availability imposes a physiological limit on growth rate, which interacts with mortality due to stochastic processes such as fire and herbivory to limit maximum potential woody biomass ().

Temperature imposes a similar physiological limit on woody growth rate by limiting metabolic rates. Temperature and water availability together impact the transpiration rate of a tree, with high temperatures and low water availability limiting growth and potentially causing damage or mortality through cavitation of vessels within the tree (Rowland et al., 2015; Fensham et al., 2009). In southern African woodlands however, many species are drought adapted and lose their leaves in the dry season, limiting water loss (Solbrig et al., 1996), so this effect may not be present in historically droughted areas. The effect of extreme climatic conditions on woody biomass may depend on the degree to which the current biota is adapted to it. Furthermore, across many forested ecosystems, water availability, modulated through precipitation and soil type positively correlates with tree species richness (Vilà et al., 2005), meaning that extremely arid areas may be limited in their potential ecosystem functionality via two effects, the direct effect of resource availability in the form of moisture availability and soil nutrients, and indirectly through the effect of these environmental factors on species composition. Species composition may therefore have a greater effect on the interaction between environment and biodiversity - ecosystem function relationships, than species richness *per se*.

Species abundance evenness and selection effects.

Stand structural complexity

While southern African woodlands are species rich in the herbaceous understorey, the tree layer is relatively species poor (). Solbrig et al. (1996) however, writes that they are structurally diverse in the tree layer, with trees of the same species occupying distinct layers of the canopy at different growth stages. This structural diversity may be one mechanism through which species diversity appears to influence woody biomass. Trees occupying different canopy layers can create a more full canopy with a greater total foliage density, enhancing productivity and allowing greater standing woody biomass in a smaller area. An underpinning principle of the Biodiversity-Ecosystem Function Relationship (BEFR) is that of niche complementarity. Species are assumed to differ in their functional niche by the fact that they may coexist in a steady-state ecological community, therefore the more species are present the greater the area of the total fundamental niche of the ecosystem is filled, allowing more efficient use of natural resources and higher gross primary productivity and biomass (). This theory however, which has been supported by many experiments and observational studies in temperate and wet tropical ecosystems, may not hold in savannas, which are structured by disturbance rather than competition.

High levels of disturbance in the form of seasonal fires and herbivory from large mammals may moderate the strength of observable BEFRs in southern African woodlands (Staver et al., 2009; Bond and Keeley, 2005). Fire disturbance in forests has been linked to abundance dependent mortality among smaller stems (Roques et al., 2001). A dominant and competitive species which tends to produce many small fast-growing stems is more likely to experience mortality during a fire as the higher surface area to volume ratio of the trunk increases the likelihood of combustion (). Such

fast-growing bushy species exist in southern African woodlands and often proliferate when fire is deliberately excluded, leading to the growth of thicket vegetation which precludes the growth of high biomass tree species (Higgins et al., 2007). Additionally, the dominance of a single species is likely to decrease overall functioning by decreasing niche space utilisation (Cardinale et al., 2002).

In this study, we made the first known regional estimation of the Biodiversity-Ecosystem Function Relationship in southern African woodlands, using inventory plots which straddle multi-dimensional environmental and biogeographical gradients (Figure Table 5). We investigated the relationship between aboveground woody biomass and tree biodiversity. We compared the relative effects of tree species biodiversity with that of other environmental factors known to affect ecosystem productivity and biomass accumulation such as precipitation and temperature. We also investigated potential moderation effects of environmental covariates on the relationship between tree species diversity and biomass. We incorporated vegetation type clusters based on tree species composition () into our analyses to understand how species composition as well as species biodiversity affected ecosystem functionality. Initially, we made four hypotheses:

1.1   Hypotheses

1. Plots with a higher tree species diversity will maintain higher above-ground woody biomass stocks.

2. More arid plots and plots with less fertile soil will show a stronger positive effect of tree species richness on above-ground woody biomass.

3. There will be a positive effect of precipitation and soil fertility on AGB and that part of this positive effect will exist as a mediating effect through species diversity.

4. Structural characteristics of the woodland will interact with species diversity to provide an indirect path of influence between species composition and biomass stocks.

5. The observed effect of diversity on AGB will increase in strength as stem density increases owing to an increased importance of niche complementarity as competition increases.

To address these hypotheses we used Structural Equation Models with path analysis as a preferred method to simultaneously account for environmental factors and biotic factors, which may interact in their effect on ecosystem structure and therefore biomass.

2   Methods

2.1   Study location

The study used 1387 woodland monitoring plots from a larger network located across 10 countries within southern Africa in so-called Miombo woodlands (Figure 1a, Hopkins and White 1987). The study region spans a precipitation gradient from ~460 mm y^{-1} in southern Mozambique and southern Zimbabwe and ~1700 mm y^{-1} in northern Zambia, Malawi and northern Mozambique. The study sites straddle the climate space of the region as a whole (Figure 1b). The 2D convex hull of Mean Annual Precipitation (MAP) and Mean Annual Temperature (MAT) of the study sites covers 87.7% of the pixel-wise climate space of the Miombo woodland area as defined by Hopkins and White (1987), using WorldClim estimates of temperature and precipitation between the year 1970 and 2000 with a pixel size of 30 arc seconds (0.86 km^2 at the equator) (Fick and Hijmans, 2017).
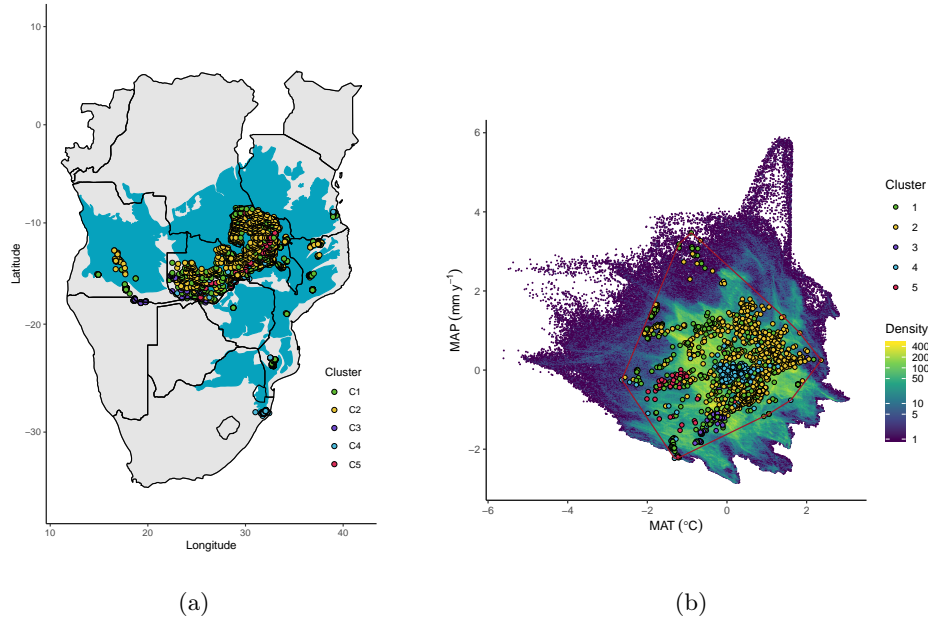
Figure 1: The locations of the 1387 plots used in this study, by geographic location (a) with respect to the distribution of Miombo woodland vegetation according to Hopkins and White (1987), and in climate space (b), showing the plot locations as points compared to the climate space of the whole region as estimated using the WorldClim dataset over the Miombo woodland vegetation extent (Fick and Hijmans, 2017). Note that the density colour scale is log-transformed.

Plots were chosen from a larger pool of 5395 plots based on the quality and completeness of data collection, and plot setup. Plot vegetation was identified under the broad term of "savanna", which includes "woodland", "savanna woodland", and "tree savanna", variously defined in other areas of the scientific literature (). Plots with evidence of farming, human resource extraction or experimental treatments such as prescribed burning or herbivore exclusion were exlcuded from the initial pool. Only plots >0.1 hectares were used in analysis, as area based biomass estimation from small plots is highly influenced by rare large trees (), leading to inaccurate estimates. Only plots with a stem density >10 stems ha^{-1} were used, to ensure all plots were within woodland rather than "grassy savanna", which are considered a separate biome with very different species composition (Parr et al., 2014).

Many plots provided by the Zambian Forestry Commission were arranged in clusters of up to four 20x50 m plots, 20 metres apart. Plots within a cluster were aggregated before the plot dataset filtering described above and treated as a single plot in analyses.

After the initial plot data cleaning described above, we conducted an outlier removal procedure of plots with rare tree species composition. We used the `outlier()` function from the `dave` R package (Wildi, 2017), which uses a nearest neighbor criterion for each plot in species abundance ordination space and a threshold value for the minimum nearest neighbour distance to identify outliers. We set the threshold value to remove the top 5% of plots with the highest nearest neighbour distances (**?**), removing 72 plots.

2.2   Data collection

We considered only trees and shrubs in our calculations of AGB, including woody species such as palms and cycads which are functionally tree-like but excluding lianas, which fill a different ecological niche (). Only stems >5 cm DBH (Diameter at Breast Height, 1.3 m) were included in analyses. Most plots in the dataset did not include data on stems <5 cm DBH, with these small stems forming a very small proportion of the total AGB in a plot ().

All stems >5 cm DBH were measured within each plot resulting in a total of 160,076 stems with measurements. A tree may be comprised of multiple stems, but for this analysis each stem is treated as an individual. For each stem, species, DBH and tree height to the top of the highest branch material were recorded. Height was measured through a variety of means including laser rangefinders, manual clinometers and measuring sticks, which may cause varying measurement uncertainty by data source in the dataset. When DBH could not be measured at 1.3 m due to trunk abnormalities, it was measured at the closest regular portion of the trunk to 1.3 m. The height of this measurement was recorded and used to estimate the DBH_e at 1.3 m using a cubic polynomial regression, with parameters estimated using a test dataset from (Ryan, unpublished).

Aboveground biomass for each plot was calculated using Equation 1, taken from Chave et al. (2014). Wood density estimates were taken from the global wood density database for each species where possible (Chave et al., 2009; Zanne et al., 2009). Wood density for species without species level estimates was estimated from the mean of their respective genus.

$$AGB_{est} = 0.0673 \times (\rho D^2 H)^{0.976} \tag{1}$$

Where ρ is the species level mean wood density, D is the DBH at 1.3 m, and H is the tree height.

Climatic data was collected from the ECMWF ERA5 dataset (). Values of mean annual temperature (MAT) and mean annual precipitation (MAP) were calculated from daily data between 2000 and 2018, then averaged across years to provide a single mean annual estimate per plot. Temperature and precipitation seasonality were both calculated as the coefficient of variation of the daily data across the 18 years of available data. Soil fertility data was extracted from the ISRIC gridded soil information data product at 250 m resolution, taking the grid cell value for each plot (Hengl et al., 2017). We extracted Cation Exchange Capacity (CEC), organic carbon density, and the percentage sand content of the soil. These data are a modelled product compiled from various remote sensed and directly measured data sources.

2.3 Data analysis

Estimated tree species richness was calculated for each plot using `ChaoRichness()` from the `iNEXT` package in R (Hsieh et al., 2016). This procedure uses Hill numbers to extrapolate a species rarefaction curve to its predicted asymptote and uses this value as its estimated species richness value. Extrapolated species richness was preferred over raw Hill numbers as they are more interpretable, representing actual species numbers. Extrapolated species richness accounts for variation in plot size (0.1-10 ha) and therefore sampling effort across the region. Larger plots will tend to encompass more individuals, and therefore probabilistically more species ().

To measure tree species abundance evenness, the Shannon Equitability index () (Equation 2) was calculated:

$$E_{H'} = \frac{H'_e}{\ln S} \tag{2}$$

Where H'_e is an estimation of the Shannon diversity index of trees by extrapolation of the observed Shannon diversity index (H') to its asymptote via Hill numbers using the `ChaoShannon()` function from the `iNEXT` package in R (Hsieh et al., 2016), and S is the extrapolated tree species richness in the plot.

We calculated tree stand structural diversity for each plot by calculating the coefficient of variation of DBH and tree height.

2.3.1 Vegetation clusters

Plots were assigned to vegetation type groups based on tree species composition. Groups were identified in Fayolle et al. (2018) using an Africa wide analysis of floristic units using plot data in savannas with tree species diversity and relative abundance data. Groups were identified using unconstrained correspondence analysis and ordination. Plot data used in this study occurred in five vegetation type groups. See Table 1 for a description of each vegetation cluster and Figure 2 for the spatial distribution of plots from each of these clusters .

Table 1: Description of the biogeographical clusters (C1-C5) to which each plot in the study was assigned. Indicator species were generated using Dufrene-Legendre indicator species analysis (?) implemented with `indval()` from the `labdsv` R package (Roberts, 2019). Numeric values are means ± 1 standard deviation.

Cluster	Indicator species	Species richness	Stems ha⁻¹	AGB (t ha⁻¹)
C1	*Diplorhynchus condylocarpon* *Combretum* spp. *Pseudolachnostylis maprouneifolia*	7±4.7	276±345.2	35.3±37.03
C2	*Julbernardia paniculata* *Isoberlinia angolensis* *Albizia antunesiana*	8±4.3	274±245.9	46.8±35.05
C3	*Burkea africana* *Pterocarpus angolensis* *Baikiaea plurijuga*	4±2.3	274±536.5	36.3±27.86
C4	*Baikiaea plurijuga* *Terminalia randii* *Albizia amara*	10±5.9	447±386.3	47±45.41
C5	*Colophospermum mopane* *Pseudolachnostylis maprouneifolia*	4±2.9	322±390.1	43.8±34.45

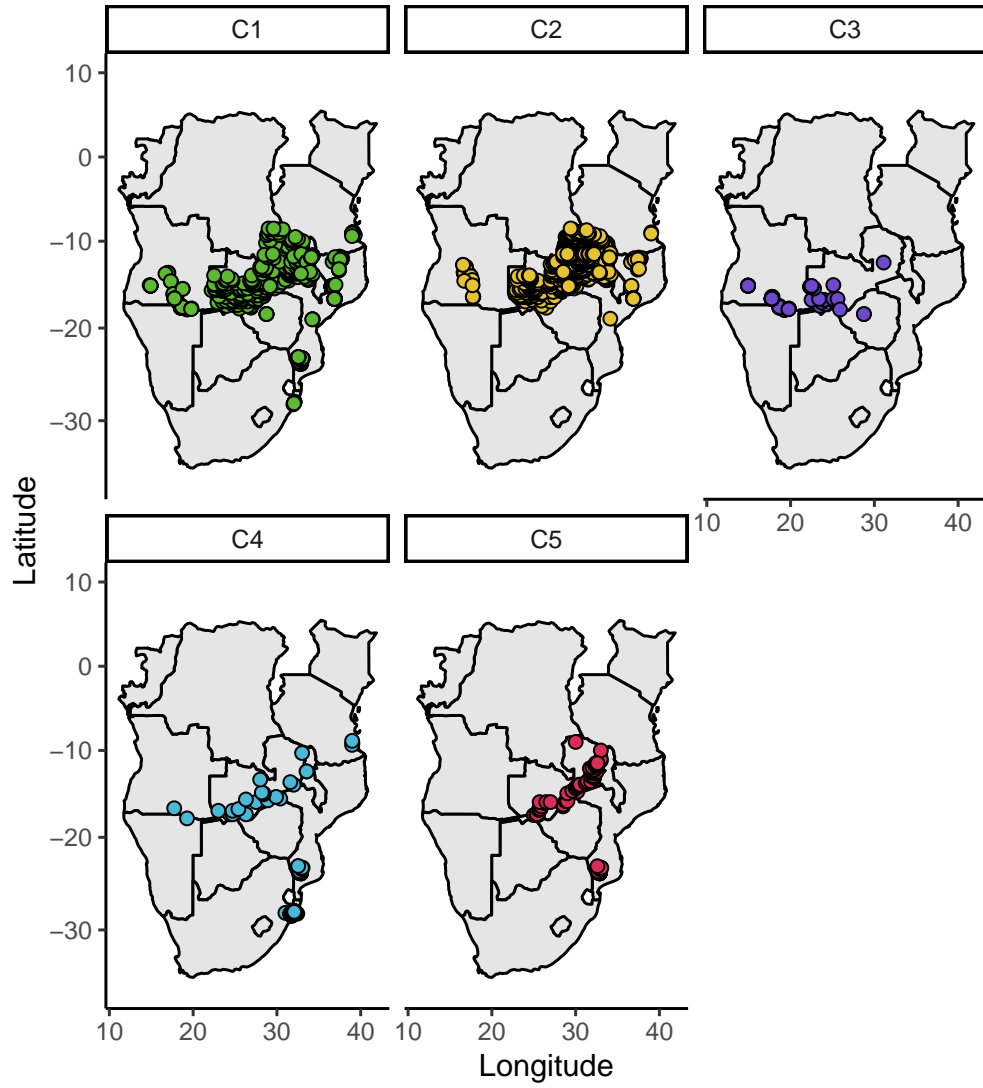Figure 2: The spatial distribution of plots according to vegetation cluster within southern Africa.

2.3.2 Structural Equation Modelling

Structural Equation Models (SEM) investigated the determinants of AGB. All SEMs were constructed and analysed in the `lavaan` package in R version 3.6.0 (R Core Team, 2019). SEM was used because of its suitability for modelling complex causal interactions in ecological systems (Lee,

2007). A key aspect to our decision to use SEMs is that they can explicitly model indirect effects, which is impossible in multiple regression. Using SEMs also allowed us to describe theoretical latent constructs which have been suggested by theory to act upon diversity and biomass/productivity in previous studies despite these factors not having single observable values in our dataset. For example, moisture availability is known to affect productivity (), but it's actual value is determined by the interaction of multiple observable variables over the time scales relevant to tree lifetime growth: precipitation, the seasonality of that precipitation and temperature which affects the rate of evapotranspiration. Independently of total precipitation, precipitation seasonality determines whether water arrives uniformly over a given time period or as a few high volume floods, the latter leading to much water being lost before it can be used for plant growth.

Prior to model fitting, we specified a conceptual model with latent variables based on unmeasured factors known to affect AGB: moisture availability, soil fertility, tree species diversity and tree structural diversity (Figure 3).
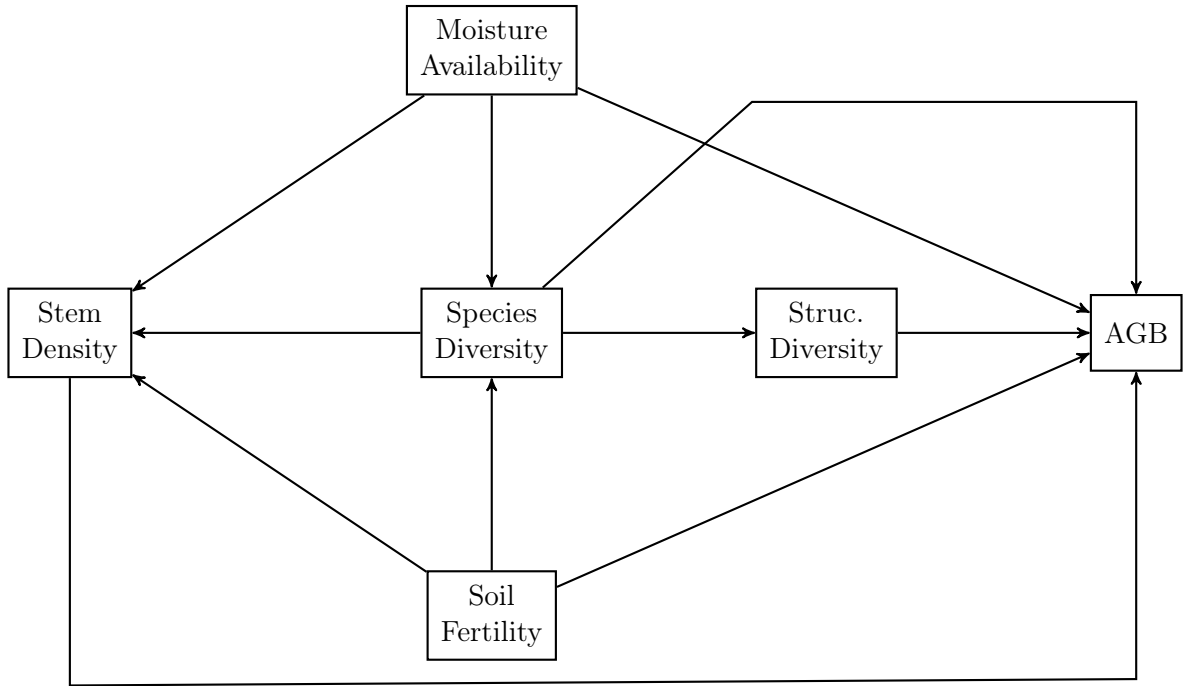

Figure 3: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural iversity, tree stem density, and AGB. Hypothesised paths of causal inference are depicted as arrows from predictor to response.

Observed variables were standardized to Z-scores for the SEMs. Standardization put each latent variable on the same scale, with a mean of zero and a standard deviation of one. Standardization allows path regression coefficients to be easily compared between paths in the same model to assess their relative effect strength, and eliminates confusion in model interpretation arising from the observed variables being on different scales (). Standardization also controls for variables with different orders of magnitude which could otherwise prevent adequate model estimation from the covariance matrix in `lavaan` (). To ensure that observed variables within a latent variable had consistent directions of influence, some observed variables were reversed by multiplying by -1. For example, soil fertility is expected to decrease as soil sand content increases, so soil percentage sand content was reversed. Precipitation seasonality, temperature seasonality, and mean temperature were also reversed in this way.

The factor loadings of the observed variable assumed to contribute most to each latent variable were set to 1 as per convention, with other observed variables being allowed to vary (). While it is recommended by some to set exact factor loadings in the SEM from the regression coefficients of multiple regressions (), because some latent variables were regressed against both structural diversity

and AGB, exact factor loadings from simple multiple regressions could not be used. We therefore allowed factor loadings to be estimated by the SEM itself.

First, we assessed the interacting factors of structural diversity and species diversity in determining AGB. We constructed a simple mediation model which allowed species diversity to influence AGB both directly and indirectly via structural diversity (see orange box Figure 3). To explore variation in the model among woodland vegetation types, we fit the model both at the regional scale and for each vegetation cluster separately. We compared path coefficients among these vegetation cluster scale models to understand the effect that vegetation type has on the relationship between structural diversity, species diversity and AGB. Model fit was evaluated using the Comparative Fit Index (CFI), the Tucker Lewis Index (TLI), the Root Mean Squared Error (RMSEA) and the R^2 coefficient of determination for AGB. We follow the recommendations of Hu and Bentler (1999) which define threshold values of acceptability for these model fit indices: CFI >0.95, TLI >0.95, RMSEA <0.06.

Second, we incorporated environmental covariates into our model to understand the relative effects of moisture availability and soil fertility on AGB both directly and indirectly via species diversity and stem density.

For models of the whole region which included all suitable plots, standardised path coefficients are reported in order to better compare the relative contribution of different paths within the model. When comparing the path coefficients of models using individual vegetation clusters, unstandardised path coefficients are used in order to more readily compare the same path coefficient across different models while accounting for variation in mean values between biogeographical clusters. Full Information Max-Likelihood (FIML) was used in each model to estimate the values of missing data in each latent variable (Cham et al., 2017).

To explore the hypothesis that complementarity effects increase in strength as stem density increases, we repeatedly sub-sampled the available plot dataset to create 900 datasets of similar size with varying median stem density. We used each of these datasets to fit the model including only tree species and structural diversity latent variables to predict AGB (see orange in Figure 3). We then examined how the unstandardised path coefficients for each path in the SEM varied according to the median stem density of the dataset.

We fitted separate moderation models to investigate whether there was an interaction effect whereby the strength of the relationship between species diversity and AGB was influenced by moisture availability and soil fertility. The `lavaan` R package does not natively support moderation of latent variables in its model specification. Instead we manually calculated interaction variables for both soil fertility and moisture availability from the product of predicted values of these latent variables in a Confirmatory Factor Analysis (CFA). Interaction variables were the products: species diversity $\times$ moisture availability, and species diversity $\times$ soil fertility. These interaction variables were included as explanatory variables in multiple regressions alongside the latent variable of species diversity to predict AGB. Regression coefficients and model fit were analysed to determine the presence of interaction effects.
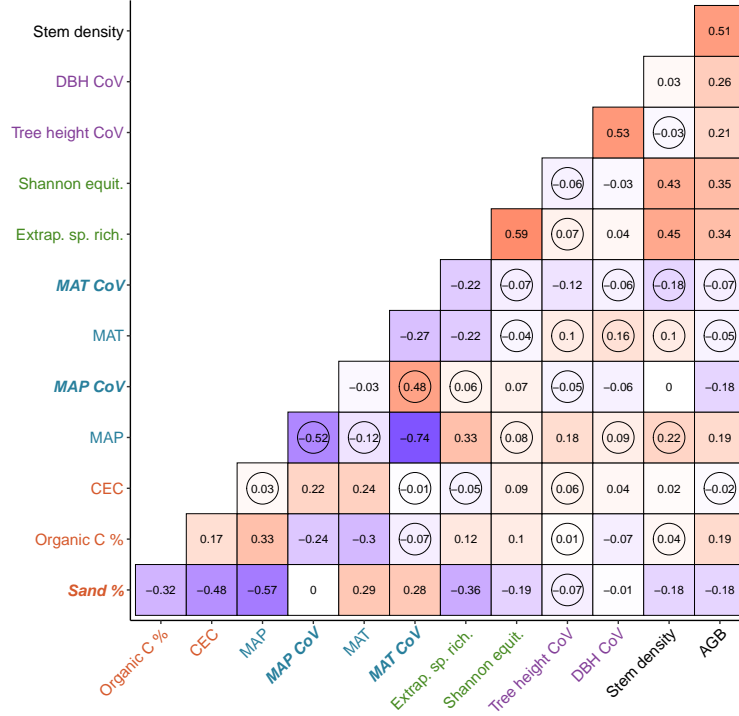
3 Results

Figure 4: Correlogram of standardised observed variables used in the SEMs, with pearson correlation coefficients (ρ) coloured according to sign (+ve red, −ve blue) and shaded by strength of correlation. Variables in bold on the axis labels were later reversed for SEMs to maintain positive correlations between observed variables within each latent variable. Correlation coefficients marked by a circle indicate that the 95% confidence interval of this correlation overlapped zero. Colours of variable names group them into latent variables used in the SEMs: red = Soil fertility, blue = Moisture availability, green = species diversity, purple = structural diversity. See Table 3 for a full table of correlation fit statistics.

A simple set of correlations between all observed variables used in the Structural Equation Models (SEMs) showed that all tree species diversity and structural diversity variables had moderate positive correlations with AGB. Stem density had the strongest correlation with AGB of all variables (ρ = 0.51, n = 1387, p <0.001). Environmental variables had weaker correlations with AGB than diversity variables. Only MAP (ρ = 0.19, n = 1387, p <0.001), MAP seasonality (ρ = -0.18, n = 1387, p <0.001), soil Organic C % (ρ = 0.19, n = 1387, p <0.001) and soil Sand % (ρ = -0.18, n = 1387, p <0.001) had AGB correlation coefficients where the 95% confidence intervals did not overlap zero. (Figure 4).

As expected, there was a positive correlation between MAP and AGB, and a negative correlation between the seasonality of precipitation and AGB. MAT and the seasonality of temperature variation did not correlate with AGB. As expected, there was a negative correlation between soil sand content and AGB, and a positive correlation between soil organic Carbon AGB.

MAP had positive correlations with tree species diversity, tree height diversity and a positive but not significant correlation with tree stem density. MAT had non significant correlations with tree species and structural diversity variables. Tree species diversity variables had clear positive correlations with stem density (Species richness: ρ = 0.45, n = 1387, p <0.001; Shannon equitability: ρ = 0.43, n = 1387, p <0.001).

3.1 Structural and species diversity models

In an SEM describing the effect of tree species diversity on AGB via the mediating effects of stand structural diversity and stem density (Figure 5), species diversity had a positive effect on AGB, both directly and indirectly via stem density, but not via structural diversity (Figure 5, Figure 6). Stand structural diversity had a positive direct effect on AGB independent of species diversity. Tree species diversity had a strong positive effect on stem density. Model fit was good and all paths were significant (p <0.001) (Table 2).
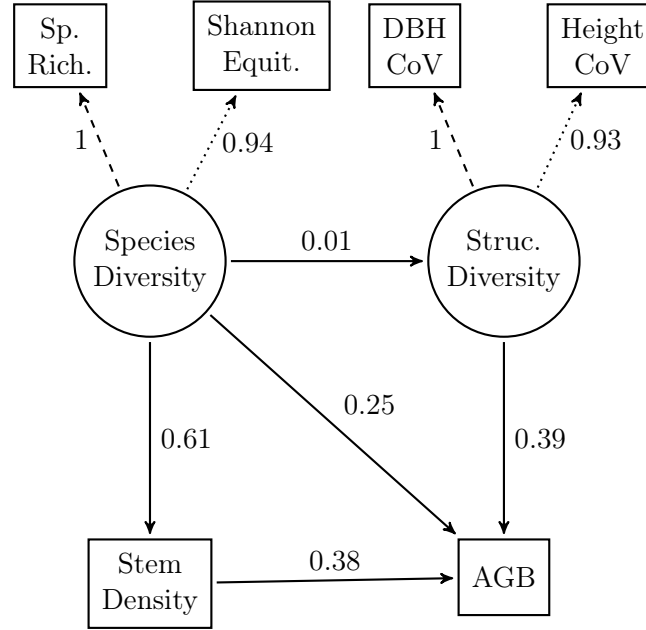
Figure 5: Path diagram with regression coefficients for the tree diversity SEM, including plots from all five vegetation clusters. Latent variables are shown as circles while observed variables are shown as rectangles. Path coefficients are solid arrows pointing from predictor to response. The observed variables which inform the unmeasured latent variables are connected by dotted arrows, observed variables with loading set to one are connected by dashed arrows. Measurement errors of exogenous variables are omitted for clarity.

Figure 6: Standardized path coefficients for the effects of tree diversity on AGB, mediated by the effect of stand structural diversity. Due to all observed variables being standardized and centred, path coefficients are expressed in terms of standard deviations on the latent variable response scale ±1 standard error. Path coefficients where the standard error does not overlap zero are considered to be significant effects.

3.2 Variation among vegetation clusters in structural and species diversity effects

When the structural diversity and species diversity model (Figure 5) was refitted separately using data from each of the 5 vegetation clusters the strengths of unstandardized path coefficients varied but relationships between diversity and AGB remained generally similar with the same sign and significant overlap between the 95% confidence intervals of path coefficients. It should be noted that models for vegetation clusters 4 and 5 did not converge, possibly due to small sample sizes (Figure 7).

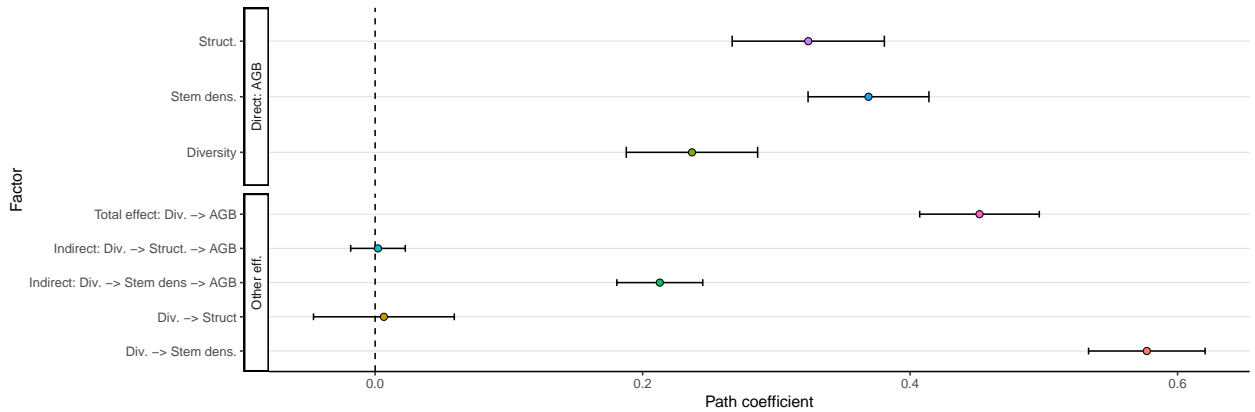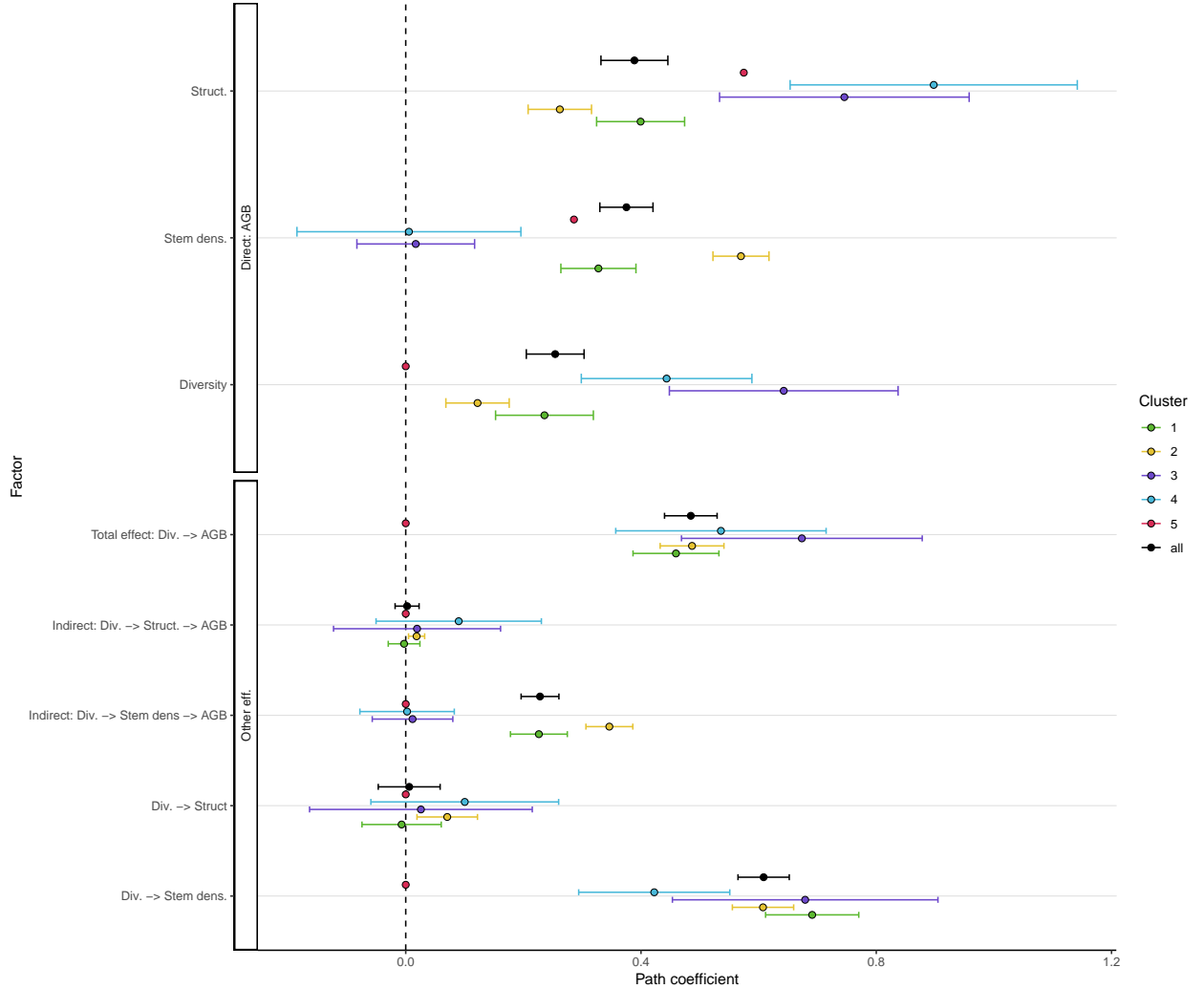
Figure 7: Unstandardised path coefficients for the effects of tree diversity on AGB, mediated by the effect of stand structural diversity. Path coefficients are +/- 1 standard error. Path coefficients where the standard error does not overlap zero are considered to be significant effects.

3.2.1 Moderation of Diversity-AGB relationship by stem density

We repeatedly sub-sampled the dataset of plots to build many datasets of varying mean stem density in order to test how the relationship between species diversity, structural diversity and biomass varied with stem density. The same SEM specification was used as above except that stem density was removed, incorporating the effects of species diversity and structural diversity on AGB (Figure 3). Figure 8 shows that there is a peak in the total effect of tree species diversity on biomass at ~700 stems ha^{-1}. There appears to be a minimum stem density threshold at ~295 stems ha^{-1} below which there appears to be no effect of diversity on biomass. Interestingly, at high stem densities, the

Table 2: Model fit statistics for SEMs investigating the effects of tree diversity and stem density on AGB (Figure 5).

Cluster	Params.	n	χ^2	DoF	CFI	TLI	LogLik	AIC	RMSEA	SRMR
C1	12	420	10.430	3	0.987	0.958	-2630.700	5285.300	0.080	0.029
C2	12	671	50.320	3	0.942	0.806	-3730.200	7484.300	0.150	0.052
C3	12	105	24.970	3	0.880	0.601	-619.100	1262.300	0.260	0.142
C4	12	46	2.710	3	1	1.008	-257.900	539.900	0	0.025
C5	12	84	5.400	3	0.981	0.936	-529.500	1083	0.100	0.085
All	12	1326	62.210	3	0.968	0.895	-8110.500	16245	0.120	0.036

observed effect of species diversity on biomass begins to decline. The effect of structural diversity on biomass appears to decrease slightly with increasing stem density, though the relationship is less clear. At stem densities below ~650 stems ha^{-1} there is no observable effect of tree species diversity on structural diversity.
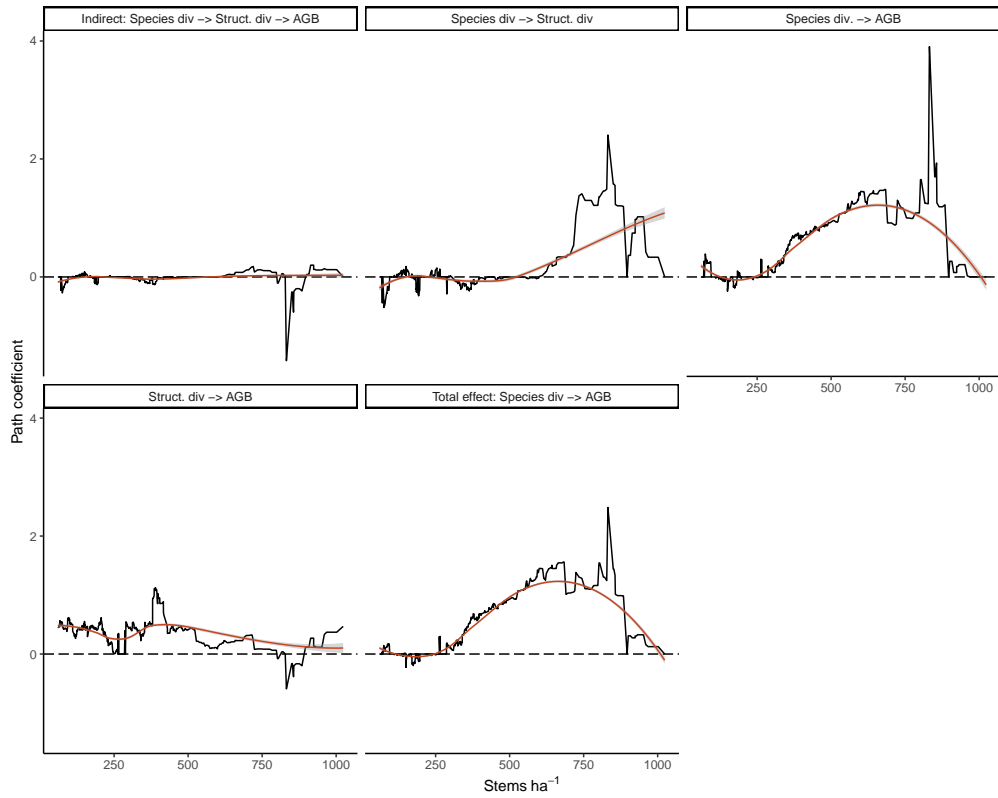
Figure 8: Line plots showing the variation in path coefficients in the SEM, using datasets with different mean stem density. Smoothed lines are loess curves.

3.3 Mediation of environmental covariates via diversity

A model incorporating the latent variables of moisture availability and soil fertility showed that the effect of diversity on biomass was greater than that of both moisture availability and soil fertility (**??**). Surprisingly, the direct effects of moisture availability and soil fertility on biomass were negligible, with nearly all of their observed effect on AGB coming from the indirect path via species diversity (Figure 10).

Moisture availability and soil fertility also had negligible direct effects on stem density, but both had a positive total effect on stem density via species diversity, where species diversity itself had a

strong positive effect on stem density. As species diversity increases, stem density also increases.

Similar to the model which only considered tree species and structural diversity, the direct effect of species diversity on structural diversity was very weakly positive, while structural diversity itself had a positive effect on AGB. Again, stem density had a positive direct effect on AGB.
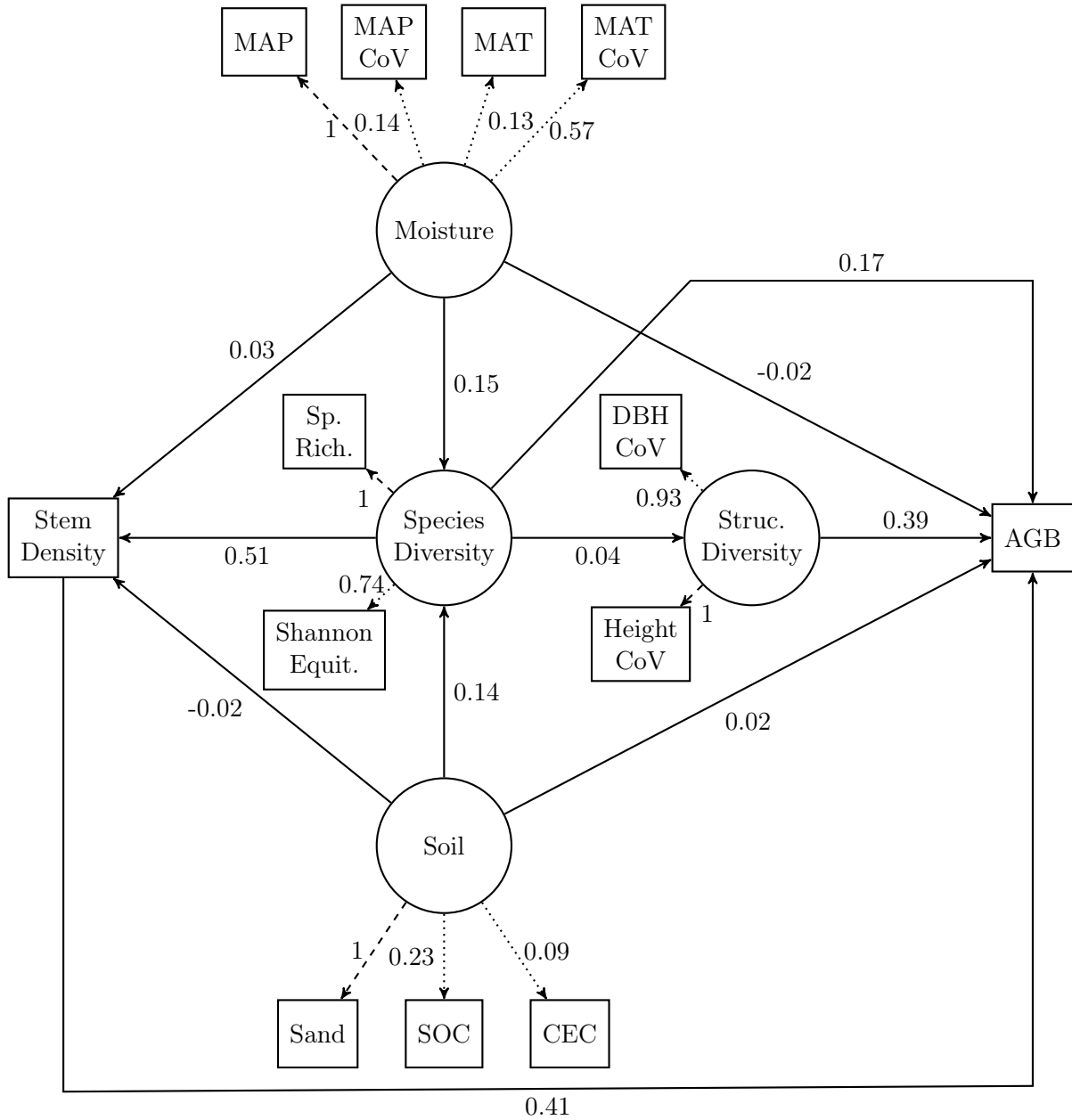
Figure 9: Path diagram with regression coefficients for the full model incorporating environmental covariates and tree species diversity in all five clusters. Latent variables are shown as circles while observed variables are shown as rectangles. Path coefficients are solid arrows pointing from predictor to response. The observed variables which inform the unmeasured latent variables are connected by dotted arrows, observed variables with loading set to one are connected by dashed arrows. Measurement errors of exogenous variables are omitted for clarity.
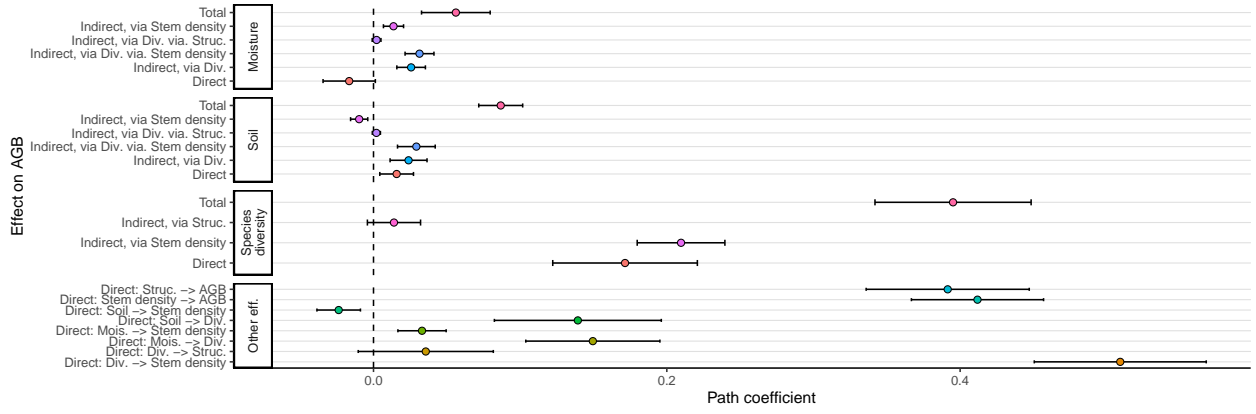
Figure 10: Standardized path coefficients for the interactive effects of abiotic environment and tree diversity on AGB across all plots. Path coefficients are +/- 1 standard error. Path coefficients where the standard error does not overlap zero are considered to be significant effects.

Vegetation cluster level models could not be reliably fitted for this more complex model specification with environmental covariates, due to sample size issues and because some vegetation clusters were narrow in their climate space. leading to a lack of variance particularly in moisture availability.

3.4 Moderation effects of moisture availability and soil

To further address the hypothesis (H_2) that more arid plots and plots with less fertile soil will show a stronger positive effect of tree species richness on above ground woody biomass, we fit separate linear multiple regressions with the latent variables of moisture availability and soil fertility as moderators on the relationship between species diversity and AGB.

Both soil fertility and moisture availability had small positive interaction effects on the strength of the relationship between tree species diversity and biomass. Regression coefficient for the interaction effect of tree species diversity and moisture availability was significant ($\beta = 0.058$, t(1383) = 2.562, p <0.05), while the interaction term of tree species diversity and soil fertility was not ($\beta = 0.034$, t(1383) = 1.452, p = 0.147). As moisture availability increased, the effect of tree species diversity on AGB became stronger. At high tree species diversity, an increase in resource availability led to a larger increase in biomass.

| (a) | (b) |
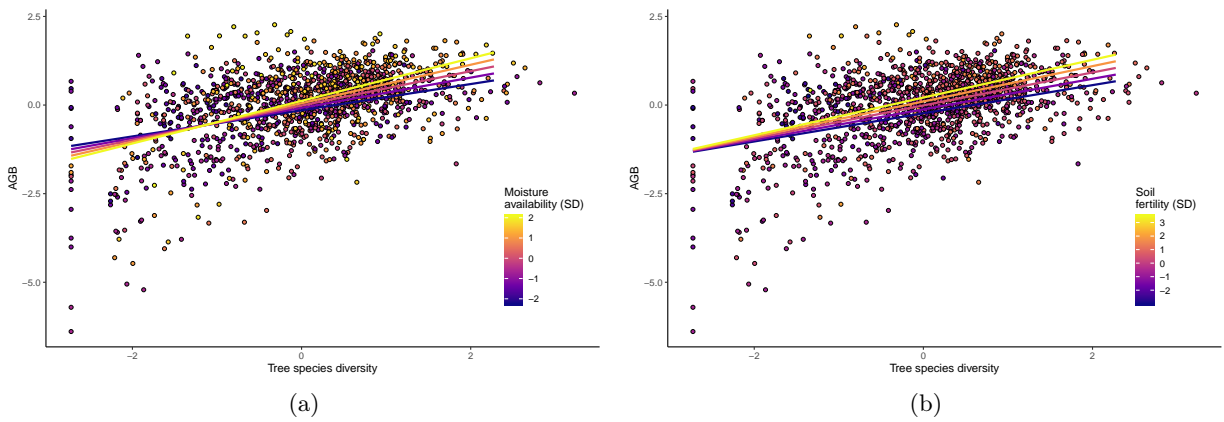
Figure 11: Interaction plots showing variation in the relationship between tree species diversity and AGB with moisture availability (a) and soil fertility (b). All variables are standardised and centred to a mean of zero and a standard deviation of 1. Lines of best fit are drawn for standard deviations of moisture availability and soil fertility between -2 and +2. Moisture availability, tree species diversity and soil fertility are the values of latent variables the same as those used in the SEMs.

4 Discussion

In this study, we assessed the importance of [a] tree species richness, [b] tree structural diversity, [c] moisture availability and soil fertility, and [d] stem density on aboveground woody biomass (AGB) across southern African woodlands. Using latent variables and SEMs, we found support for a general relationship between tree species diversity and AGB, and a relationship between tree structural diversity and AGB that was independent of tree species diversity. Interestingly, when tree species diversity, structural diversity and stem density were controlled for, we found little evidence of a direct effect of resource availability, in the form of moisture availability and soil fertility, on AGB.

4.1 Effect of tree species diversity on AGB

The latent variable of tree species diversity had the strongest positive effect on woody above-ground biomass (AGB) in environment+diversity SEM model (Figure 9). Within the savanna woodlands of southern Africa we therefore find support for our hypothesis (H_1), that higher tree species richness causes higher woody AGB. This finding is in agreement with many other studies across different ecosystems and biomes, showing that there is a generalisable positive association between species richness and ecosystem functionality ().

Most of the total species diversity effect was through the indirect effect via stem density. This suggests that a higher species diversity allows for a greater density of tree stems and that in southern African woodlands, this leads to an increase in total AGB. The effect of increased stem density within forests is variable. The question of whether lots of small stems or a few large stems maximises AGB has yet to be solved ().

While we did not explicitly measure net primary production (NPP) in this study, other studies have shown a strong positive correlation between woody AGB and NPP in woodland and forest ecosystems (). Mechanistically, a higher standing woody biomass results in a greater stand level leaf area index (LAI) (), with leaf area being a primary determinant of productivity ().

As tree species diversity increased, this allowed for greater stem density which in turn led to greater AGB.

4.2 Structural diversity as a mechanism for the BEFR

We found no evidence that species diversity led to an increase in structural diversity. Structural diversity did however have a positive effect on AGB. Our original hpyothesis was that an increase in tree species richness would increase the number of functional forms of trees per unit area due to niche complementarity in growth form of coexisting species. However, it seems more likely that structural diversity is instead merely a result of disturbance history. With highly disturbed plots generally having a less structurally diverse canopy. In forests, where the tree canopy is effectively closed, as the stand matures a more diverse canopy emerges. In highly disturbed woodland plots, maturity in the sense of classical forest succession is never reached, and a simple open canopy is maintained.

4.3 Effects of moisture availability and soil fertility

Surprisingly, moisture availability and soil fertility had only small effects on AGB compared to that of tree species diversity. We expected that higher moisture availability and soil fertility would lead to higher AGB under the assumption that higher resource availability would allow for greater biomass per unit area. We expected that a greater number of stems would be able to coexist in a higher resource availability area.

Previous studies in tropical forests have shown that moisture availability increases AGB both directly

and indirectly via tree species diversity and stand structure **what sort of stand structure?** (**???**). This was not observed in our study however. Compared to most tropical forests, climatic water availability is far more of a limiting factor in southern African woodlands. We expect that an increase in water availability in southern African woodlands would allow for greater tree growth and therefore greater AGB. The range of observed moisture availability in this study however may not have been able to capture this effect. Instead, in southern African woodlands moisture availability is much more closely linked with disturbance from seasonal fires. The growth of C4 grasses in wetter savannas leads to seasonal fires which limit tree growth. Additionally, we may see high local adaptation of tree species andf compositional turnover in response to variation in moisture availability, negating any effects of moisture availability on tree growth. Savannas in Africa have been dry for a long time so it is understnadable that trees may be highly adapted to low rainfall to the point where it doesn't affect their growth.

In a separate set of linear multiple regressions, we found a weak positive interaction effect of moisture availabiltiy on the relationship between tree species diversity and AGB. As moisture availability increased, the relationship between tree species diversity and AGB became stronger. We could not add moderation effects to the SEM framework.

4.4 Vegetation type cluster specific responses

4.5 Stem density effects

We found a non linear effect of stem density on the relationship between tree species diversity and AGB. The effect of tree species diversity on AGB peaked at ~700 stems ha^{-1}. At low stem densities competition between trees may not occur, meaning that the niche complementarity provided by an increase in tree species richness does not make any difference.

It is possible that at very high stem density there are other effects that become more important than tree species diversity in affecting AGB. For example, very high stem density plots may have been found areas of thicket vegetation which are highly structured by disturbance. There may also be an effect whereby the high stem density plots have lots of very small stems, meaning that AGB cannot be high. The largest trees always ahve the bulk of the biomass in a system. Again, this is indicative of thicket vegetation. The peak in species diversity effect may occur at a given stem density because that is the balance between tree species diversity effects and the offsetting effects of stem crowding which preclude high biomass large trees.

4.6 Future work

We hope that this study prompts further investigation of the relationship between woody productuivity and species richness and composition in southern African woodlands. While AGB is correlated with NPP,...

4.7 Conclusion

References

Bond, W. J. and Keeley, J. E. (2005), 'Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems', *Trends in Ecology and Evolution* **20**(7), 387–394.

Brooks, T. M., Mittermeier, R. A., da Fonseca, G. A. B., Gerlach, J., Hoffmann, M., Lamoreux, J. F., Mittermeier, C. G., Pilgrim, J. D. and Rodrigues, S. L. (2006), 'Global biodiversity conservation priorities', *Science* **313**, 58–61.

Cardinale, B. J., Palmer, M. A. and Collins, S. L. (2002), 'Species diversity enhances ecosystem functioning through interspecific facilitation', *Nature* **415**, 426–429.

Cham, H., Reshetnyak, E., Rosenfeld, B. and Breitbart, W. (2017), 'Full information maximum likelihood estimation for latent variable interactions with incomplete indicators', *Multivariate Behavioural Research* **52**(1), 12–30.

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G. and Zanne, A. E. (2009), 'Towards a worldwide wood economics spectrum', *Ecology Letters* **12**, 351–366.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrízar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G. and Vieilledent, G. (2014), 'Improved allometric models to estimate the aboveground biomass of tropical trees', *Global Change Biology* **20**(10), 3177–3190.

Chen, I., Hill, J. K., Ohlemüller, R., Roy, D. B. and Thomas, C. D. (2011), 'Rapid range of species associated with high levels of climate warming', *Science* **333**, 1024–1026.

Clarke, D. A., York, P. H., Rasheed, M. A. and Northfield, T. D. (2017), 'Does biodiversity - ecosystem function literature neglect tropical ecosystems', *Trends in Ecology & Evolution* **32**(5), 320–323.

Condit, R., Engelbrecht, B. M. J., Pino, D., Pérez, R. and Turner, B. L. (2013), 'Species distributions in repsonse to individual soil nutrients and seasonal drought across a community of tropical trees', *Proceedings of the National Academy of Sciences* **110**(13), 5064–5068.

Dohn, J., Dembélé, F., Karembé, M., Moustakas, A., Amévor, K. A. and Hanan, N. P. (2013), 'Tree effects on grass growth in savannas: competition, facilitation and the stress-gradient hypothesis', *Journal of Ecology* **101**, 202–209.

Fayolle, A., Swaine, M. D., Aleman, J., Azihou, A. F., Bauman, D., te Beest, M., Chidumayo, E. N., Cromsigt, J. P. G. M., Dessard, H., Finckh, M., Gonçalves, F. M. P., Gillet, J., Gorel, A., Hick, A., Holdo, R., Kirunda, B., Mahy, G., McNicol, I., Ryan, C. M., Revermann, R., Plumptre, A., Pritchard, R., Nieto-Quintano, P., Schmitt, C. B., Seghieri, J., Swemmer, A., Talila, H. and Woollen, E. (2018), 'A sharp floristic discontinuity revealed by the biogeographic regionalization of african savannas', *Journal of Biogeography* **46**(2), 1–12.

Fensham, R. J., Fairfax, R. J. and Ward, D. P. (2009), 'Drought-induced tree death in savanna', *Global Change Biology* **15**, 380–387.

Fick, S. E. and Hijmans, R. J. (2017), 'Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas', *International Journal of Climatology* **37**(12), 4302–4315.

Frost, P. (1996), The ecology of miombo woodlands, *in* B. Campbell, ed., 'The miombo in transition: woodlands and welfare in Africa', Center for International Forestry Research, Bogor, Indonesia, pp. 11–55.

Hengl, T., Mendes de Jesus, J., Heuvelink, G. B. M., Gonzalez, M. R., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. A., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B., Ribeiro, E., Wheeler, I., Mantel, S. and Kempen, B. (2017), 'Soilgrids250m: Global gridded soil information based on machine learning', *PLoS ONE* **12**(2), 1–40.

Higgins, S. I., Bond, W. J., February, E. C., Bronn, A., Euston-Brown, D. I. W., Enslin, B., Govender, N., Rademan, L., O'Regan, S., Potgieter, A. L. F., Scheiter, S., Sowry, R., Trollope, L. and Trollope, W. S. W. (2007), 'Effects of four decades of fire manipulation on woody vegetation structure in savanna', *Ecology* **88**(5), 1119–1125.

Hinsley, A., Entwistle, A. and Pio, D. V. (2015), 'Does the long-term success of redd+ also depend on biodiversity', *Oryx* **49**(2), 216–221.

Hopkins, B. and White, F. (1987), 'Vegetation map of africa. the vegetation of africa: A descriptive memoir to accompany the unesco/aetfat/unso vegetation map of africa.', *The Journal of Ecology* **75**(4).

Hsieh, T. C., Ma, K. H. and Chao, A. (2016), 'inext: an r package for rarefaction and extrapolation of species diversity (hill numbers)', *Methods in Ecology and Evolution* **7**, 1451–1456.

Hu, L. and Bentler, P. M. (1999), 'Cutoff criteria for fit indexes in covariance structure analysis: conventional criteria versus new alternatives', *Structural Equation Modeling* **6**(1), 1–55.

Jax, K. (2005), 'Function and "functioning" in ecology: what does it mean?', *Oikos* **111**(3), 641–648.

Lee, S. Y. (2007), *Structural Equation Modeling: A Bayesian Approach*, Wiley, New York, USA.

Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A. D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Herault, B., Scherer-Lorenzen, M., Barrett, C. B., Glick, H. B., Hengeveld, G. M., Nabuurs, G.-J., Pfautsch, S., Viana, H., Vibrans, A. C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J. V., Chen, H. Y. H., Lei, X., Schelhaas, M.-J., Lu, H., Gianelle, D., Parfenova, E. I., Salas, C., Lee, E., Lee, B., Kim, H. S., Bruelheide, H., Coomes, D. A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonke, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E. B., Neldner, V. J., Ngugi, M. R., Baraloto, C., Frizzera, L., Ba azy, R., Oleksyn, J., Zawi a Nied wiecki, T., Bouriaud, O., Bussotti, F., Finer, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A. M., Peri, P. L., Gonmadje, C., Marthy, W., OBrien, T., Martin, E. H., Marshall, A. R., Rovero, F., Bitariho, R., Niklaus, P. A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N. L., Ferreira, L. V., Odeke, D. E., Vasquez, R. M., Lewis, S. L. and Reich, P. B. (2016), 'Positive biodiversity-productivity relationship predominant in global forests', *Science* **354**(6309), aaf8957–aaf8957.

McNicol, I. M., Ryan, C. M., Dexter, K. G., Ball, S. M. J. and Williams, M. (2018), 'Aboveground carbon storage and its links to stand structure, tree diversity and floristic composition in southeastern tanzania', *Ecosystems* **21**, 740–754.

Michaletz, S. T., Cheng, D., Kerkhoff, A. J. and Enquist, B. J. (2014), 'Convergence of terrestrial plant production across global climate gradients', *Nature* **512**, 39–43.

Michaletz, S. T., Kerkhoff, A. J. and Enquist, B. J. (2018), 'Drivers of terrestrial plant production across broad geographical gradients', *Global Ecology and Biogeography* **27**, 166–174.

Mittermeier, R. A., Mittermeier, C. G., Brooks, T. M., Pilgrim, J. D., Konstant, W. R., da Fonseca, G. A. B. and Kormos, C. (2003), 'Wilderness and biodiversity conservation', *Proceedings of the National Academy of Sciences* **100**(18), 10309–10313.

Parr, C. L., Lehmann, C. E. R., Bond, W. J., Hoffmann, W. A. and Andersen, A. N. (2014), 'Tropical grassy biomes: misunderstood, neglected, and under threat', *Trends in Ecology and Evolution* **29**(4), 205–213.

R Core Team (2019), *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria.

Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C. C., Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Chećko, E., Dawud, S. M., de Wandeler, H., Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F., Kambach, S., Kolb, S., Koricheva, J., Liebersgesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock, C., Pollastrini, M., Purschke, O., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Ruiz-Benito, P.,

Seidl, R., Selvi, F., Seiferling, I., Stenlid, J., Valladares, F., Vesterdal, L. and Baeten, L. (2017), 'Biodiversity and ecosystem functioning relations in european forests depend on environmental context', *Ecology Letters* **20**, 1414–1426.

Roberts, D. W. (2019), *labdsv: Ordination and Multivariate Analysis for Ecology.* R package version 2.0-1.

Roques, K. G., O'Connor, T. G. and Watkinson, A. R. (2001), 'Dynamics of shrub encroachment in an african savanna: relative influences of fire, herbivory, rainfall and density dependence', *Journal of Applied Ecology* **38**, 268–280.

Rowland, L., da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., Binks, O. J., Oliveira, A. A. R., Pullen, A. M., Doughty, C. E., Metcalfe, D. B., Vasconcelos, S. S., Ferreira, L. V., Malhi, Y., Grace, J., Mencuccini, M. and Meir, P. (2015), 'Death from drought in tropical forests is triggered by hydraulics not carbon starvation', *Nature* **528**, 119–122.

Ryan, C. M., Pritchard, R., McNicol, I., Owen, M., Fisher, J. A. and Lehmann, C. (2016), 'Ecosystem services from southern african woodlands and their future under global change', *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**(1703), 1–16.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K. K., Coughenour, M. B., Diouf, A., Ekaya, W., Feral, C. J., February, E. C., Frost, P. G. H., Hiernaux, P., Hrabar, H., Metzger, K. L., Prins, H. H. T., Ringrose, S., Sea, W., Tews, J., Worden, J. and Zambatis, N. (2005), 'Determinants of woody cover in african savannas', *Nature* **438**(8), 846–849.

Solbrig, O. T., Medina, E. and Silva, J. F. (1996), *Biodiversity and Savanna Ecosystem Processes*, Springer-Verlag, Berlin, Germany.

Staver, A. C., Bond, W. J., Stock, W. D., van Rensburg, S. J. and Waldram, M. S. (2009), 'Browsing and fire interact to suppress tree density in an african savanna', *Ecological Applications* **19**(7), 1909–1919.

Tilman, D. and Downing, J. A. (1994), 'Biodiversity and stability in grasslands', *Nature* **367**, 363–365.

Tilman, D., Isbell, F. and Cowles, J. M. (2014), 'Biodiversity and ecosystem functioning', *Annual Review of Ecology, Evolution, and Systematics* **45**, 471–493.

Vilà, M., Inchausti, P., Vayreda, J., Barrantes, O., Gracia, C., Ibàñez, J. J. and Mata, T. (2005), 'Confounding factors in the observational productivity-diversity relationship in forests', *Ecological Studies* **176**, 65–86.

Wildi, O. (2017), *dave: Functions for "Data Analysis in Vegetation Ecology".* R package version 2.0.

Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S. L., Miller, R. B., Swenson, N. G., Wiemann, M. C. and Chave, J. (2009), *Global wood density database.* http://hdl.handle.net/10255/ dryad.235.

Appendix 1 - Data cleaning process
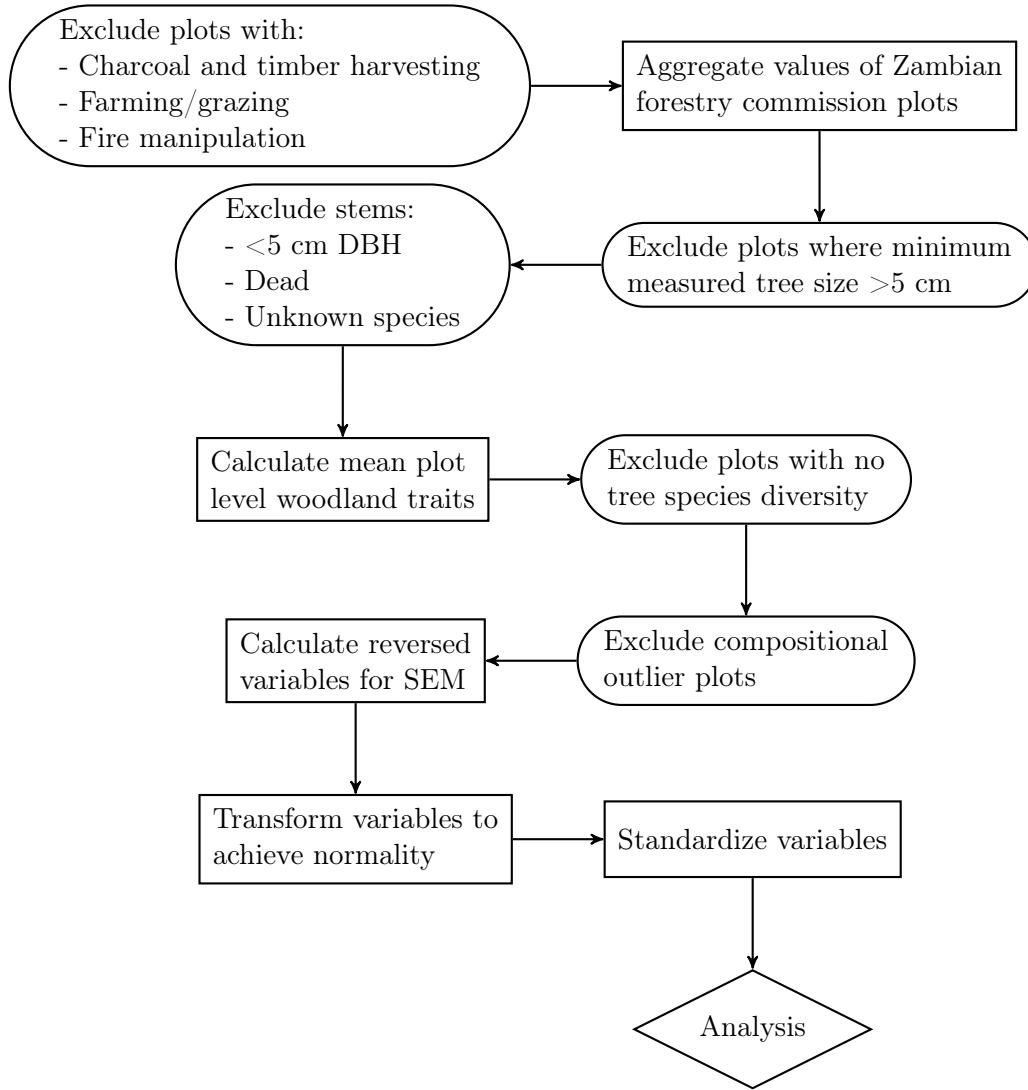
Figure 12: Flow diagram of the data filtering and cleaning process prior to analysis. Rounded boxes indicate filtering events while normal boxes indicate calculation events.

Appendix 2 - Table of correlation fit statistics

Table 3: Table of correlation fit statistics for each pairwise Pearson correlation test of observed variables used in Structural Equation Models.

X	Y	ρ	lower 95% CI	upper 95% CI	n	Prob.
Sand %	Organic C %	-0.430	-0.470	-0.390	1387	0
Sand %	CEC	-0.580	-0.610	-0.540	1387	0
Sand %	MAP	-0.420	-0.460	-0.370	1387	0
Sand %	MAP CoV	0.380	0.330	0.420	1387	0
Sand %	MAT	0.240	0.190	0.290	1387	0
Sand %	MAT CoV	0.140	0.090	0.190	1387	0
Sand %	Extrap. sp. rich.	-0.290	-0.340	-0.240	1387	0
Sand %	Shannon equit.	-0.250	-0.300	-0.200	1387	0
Sand %	Tree height CoV	-0.070	-0.130	-0.010	974	0.024
Sand %	DBH CoV	-0.180	-0.230	-0.130	1387	0

Sand %	Stem density	-0.220	-0.260	-0.160	1387	0
Sand %	AGB	-0.190	-0.240	-0.140	1387	0
Organic C %	CEC	0.300	0.250	0.340	1387	0
Organic C %	MAP	0.330	0.280	0.380	1387	0
Organic C %	MAP CoV	-0.350	-0.390	-0.300	1387	0
Organic C %	MAT	-0.310	-0.350	-0.260	1387	0
Organic C %	MAT CoV	0	-0.050	0.050	1387	0.996
Organic C %	Extrap. sp. rich.	0.150	0.100	0.200	1387	0
Organic C %	Shannon equit.	0.140	0.090	0.190	1387	0
Organic C %	Tree height CoV	0.010	-0.050	0.080	974	0.663
Organic C %	DBH CoV	0.100	0.050	0.160	1387	0
Organic C %	Stem density	0.070	0.010	0.120	1387	0.015
Organic C %	AGB	0.200	0.150	0.250	1387	0
CEC	MAP	-0.060	-0.120	-0.010	1387	0.016
CEC	MAP CoV	-0.560	-0.590	-0.520	1387	0
CEC	MAT	0.240	0.190	0.290	1387	0
CEC	MAT CoV	0.080	0.030	0.130	1387	0.002
CEC	Extrap. sp. rich.	-0.070	-0.120	-0.020	1387	0.011
CEC	Shannon equit.	0.240	0.190	0.280	1387	0
CEC	Tree height CoV	0.060	0	0.130	974	0.044
CEC	DBH CoV	0.250	0.200	0.300	1387	0
CEC	Stem density	0.210	0.160	0.260	1387	0
CEC	AGB	0.050	0	0.100	1387	0.053
MAP	MAP CoV	-0.080	-0.140	-0.030	1387	0.002
MAP	MAT	-0.080	-0.130	-0.030	1387	0.003
MAP	MAT CoV	-0.650	-0.680	-0.620	1387	0
MAP	Extrap. sp. rich.	0.310	0.270	0.360	1387	0
MAP	Shannon equit.	-0.020	-0.080	0.030	1387	0.382
MAP	Tree height CoV	0.180	0.120	0.240	974	0
MAP	DBH CoV	0.060	0.010	0.110	1387	0.025
MAP	Stem density	-0.070	-0.120	-0.010	1387	0.013
MAP	AGB	0.140	0.090	0.190	1387	0
MAP CoV	MAT	-0.170	-0.220	-0.110	1387	0
MAP CoV	MAT CoV	0.020	-0.040	0.070	1387	0.561
MAP CoV	Extrap. sp. rich.	0.080	0.020	0.130	1387	0.005
MAP CoV	Shannon equit.	-0.230	-0.280	-0.180	1387	0
MAP CoV	Tree height CoV	-0.050	-0.110	0.010	974	0.102
MAP CoV	DBH CoV	-0.350	-0.390	-0.300	1387	0
MAP CoV	Stem density	-0.250	-0.300	-0.200	1387	0
MAP CoV	AGB	-0.100	-0.160	-0.050	1387	0
MAT	MAT CoV	-0.330	-0.370	-0.280	1387	0
MAT	Extrap. sp. rich.	-0.230	-0.280	-0.180	1387	0
MAT	Shannon equit.	0.010	-0.040	0.060	1387	0.775
MAT	Tree height CoV	0.100	0.040	0.160	974	0.002
MAT	DBH CoV	0.090	0.040	0.150	1387	0
MAT	Stem density	0.080	0.030	0.130	1387	0.003
MAT	AGB	-0.060	-0.110	0	1387	0.038
MAT CoV	Extrap. sp. rich.	-0.240	-0.290	-0.190	1387	0
MAT CoV	Shannon equit.	-0.030	-0.090	0.020	1387	0.193
MAT CoV	Tree height CoV	-0.120	-0.180	-0.060	974	0
MAT CoV	DBH CoV	-0.020	-0.070	0.030	1387	0.428
MAT CoV	Stem density	-0.070	-0.120	-0.020	1387	0.010
MAT CoV	AGB	-0.080	-0.140	-0.030	1387	0.002

Extrap. sp. rich.	Shannon equit.	0.540	0.500	0.580	1387	0
Extrap. sp. rich.	Tree height CoV	0.070	0	0.130	974	0.038
Extrap. sp. rich.	DBH CoV	0.160	0.110	0.210	1387	0
Extrap. sp. rich.	Stem density	0.390	0.350	0.440	1387	0
Extrap. sp. rich.	AGB	0.460	0.420	0.500	1387	0
Shannon equit.	Tree height CoV	-0.060	-0.130	0	974	0.046
Shannon equit.	DBH CoV	0.140	0.090	0.190	1387	0
Shannon equit.	Stem density	0.540	0.500	0.580	1387	0
Shannon equit.	AGB	0.400	0.350	0.440	1387	0
Tree height CoV	DBH CoV	0.530	0.480	0.570	974	0
Tree height CoV	Stem density	-0.030	-0.100	0.030	974	0.311
Tree height CoV	AGB	0.210	0.150	0.270	974	0
DBH CoV	Stem density	0.190	0.140	0.240	1387	0
DBH CoV	AGB	0.420	0.380	0.470	1387	0
Stem density	AGB	0.510	0.470	0.540	1387	0

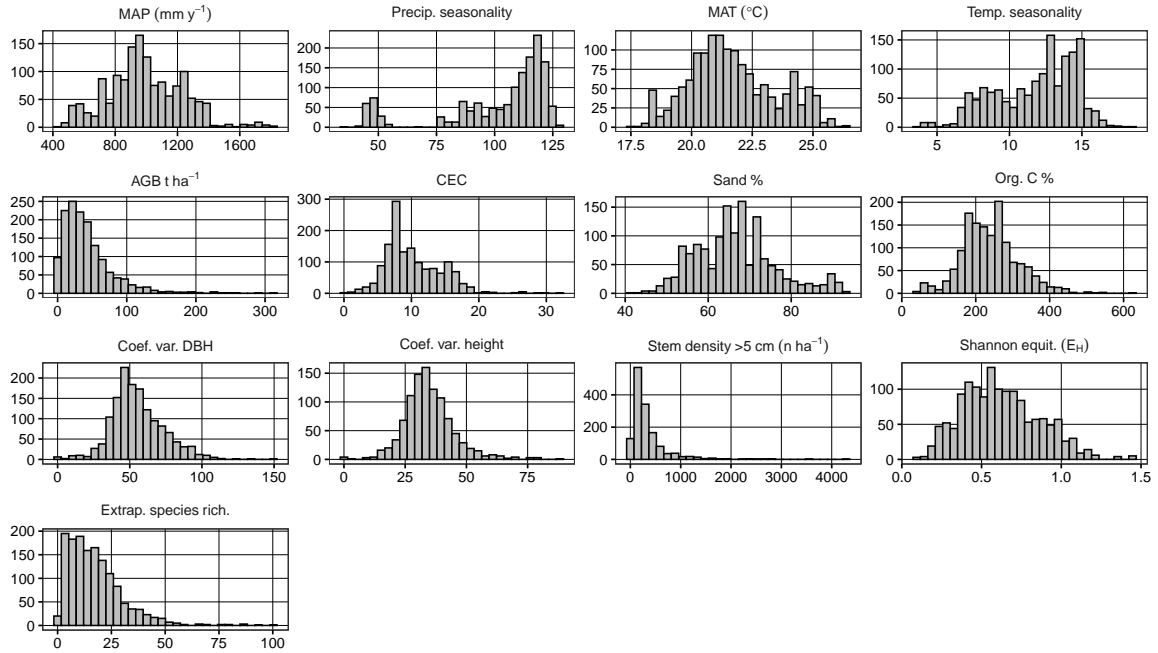# Appendix 3 - Frequency distribution of observed variables

Figure 13: Histograms of raw untransformed observed variables used in final analyses.
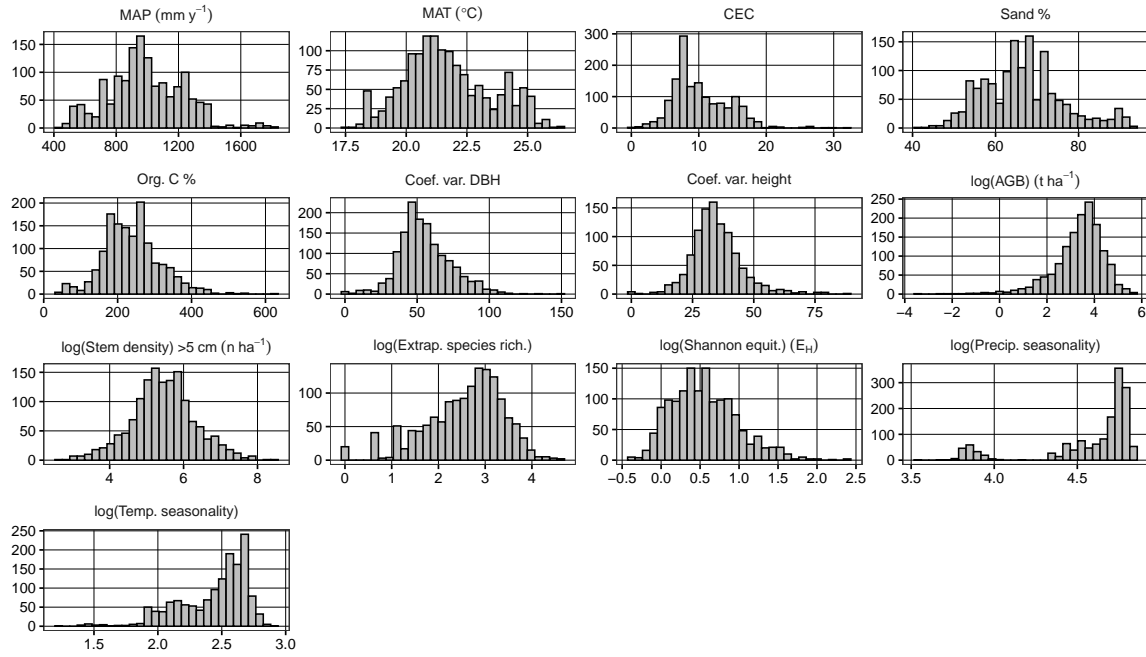
Figure 14: Histograms of observed variables transformed to achieve a normal frequency distribution.

Appendix 4 - Regression tables for moderation by environmental variables

Table 4: Regression fit for a linear multiple refression including the latent variables of moisture availbility, tree species diversity and their interaction term on AGB.

	bchave_std
Tree sp. div.	0.485*** (0.024)
Moisture avail.	0.066*** (0.024)
Tree sp. div. * Moisture avail.	0.058** (0.023)
Constant	−0.015 (0.024)
Observations	1,387
R^2	0.251
Residual Std. Error	0.867 (df = 1383)
F Statistic	154.241***

*p<0.1; **p<0.05; ***p<0.01

Table 5: Regression fit for a linear multiple refression including the latent variables of soil fertility, tree species diversity and their interaction term on AGB.

	bchave_std
Tree sp. div.	0.465*** (0.025)
Soil fert.	0.111*** (0.025)
Tree sp. div. * Soil fert.	0.034 (0.023)
Constant	−0.010 (0.024)
Observations	1,387
R^2	0.254
Residual Std. Error	0.864 (df = 1383)
F Statistic	157.245***

*p<0.1; **p<0.05; ***p<0.01