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

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Abstract

Studies in natural and experimental settings have shown a positive relationship between tree species diversity and ecosystem functionality but many ecosystems are understudied in this regard. In this study we conducted the first regional estimation of the relationship between tree species diversity and above-ground biomass in southern African woodlands, using a network of 1769 woodland plots. We used structural equation modelling (SEM) to determine the relationship between tree species diversity and aboveground biomass, with comparison to the effects of resource availability and along a gradient of stem density. A positive effect of tree species diversity on biomass was demonstrated, with most of this as an indirect effect via woodland structural diversity. We found that the effect of tree species diversity on biomass increases with stem density. Finally, we found that resource availability determines biomass in southern African woodlands largely indirectly via its effect on species diversity.

1 Introduction

A large number of studies have shown relationships between biodiversity and ecosystem functionality (e.g. Liang et al. 2016; Cardinale et al. 2009). 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 (Hector and Bagchi, 2007), and the inclusion of environmental covariates in statistical models (Vilà et al., 2005), 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 wet tropical and temperate forests, and grasslands (Chen et al., 2011).

Ecosystem functions can be defined in broad terms as rate processes and properties of ecosystems 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 measures of function such as resistance of productivity to disturbance, and further to ecosystem properties which themselves influence process, such as trophic complexity and total vegetative biomass. The frequently reported and intuitive relationship between biodiversity and ecosystem functionality invokes three main mechanisms which drive the relationship (Tilman et al., 2014): 1) niche complementarity, whereby communities with greater diversity fill a greater breadth of realised niche space and avoid competition due to differences in their traits, 2) selection effects, whereby communities with greater diversity are more likely to include a species which contributes highly to the measured ecosystem function, and 3) facilitation effects, whereby communities with greater diversity are more likely to include combinations of species which together increase the others functional contribution.

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 generally, with 42% of those being conducted in the wet tropical forests of Costa Rica, which hold many endemic species and unique ecosystem assemblages (Barthlott et al., 2005). In wet tropical forests, much of the observed effect of biodiversity on ecosystem function can be attributed to niche complementarity, which is driven by interspecific competition (Wright et al., 2017; Poorter et al., 2015; van der Sande et al., 2017). 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 great a role in the relationship between biodiversity and ecosystem function. Disturbance may weaken the role of competition in determining local species distribution and allow weak competitors to co-exist where they would normally be excluded (Grime, 1979; Keddy, 1990). Instead, stress tolerance and the functional contribution of more abundant species (selection effects) may be the predominant forces which influence ecosystem functionality (Lasky et al., 2014; Tobner et al., 2016). Similarly, more diverse species assemblages may lead to facilitation effects between certain species combinations in environments which are more hostile to growth (Ratcliffe et al., 2017).

Savannas and sparse woodlands are the dominant vegetation type across the southern African region, spanning >4 million km^2 (Ryan et al., 2016) (Figure Figure 1). The carbon stored in these woodlands is comparable to that found in the wet forests of the Congo basin and is of global importance to the carbon cycle (Houghton et al., 2009; Mayaux et al., 2008). 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. Southern African woodlands are highly diverse, thought to harbour ~8500 plant species of which there are >300 tree species (Frost, 1996), and have been identified by previous studies as a priority for conservation efforts (Byers, 2001; Mittermeier et al., 2003). 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). Despite these efforts however, human actions are driving rapid changes in biodiversity, with largely un-quantified consequences for ecosystem structure and functionality.

Southern African woodlands are relied upon heavily for their ecosystem service provision, which is itself affected by ecosystem functionality (Schulze and Mooney, 1994). This has 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 (Aleman et al., 2016; Ryan et al., 2016). Climate change is also indirectly affecting the biodiversity of southern African woodlands, altering temperature and precipitation, and affecting climate seasonality which heavily influences the degree of seasonal drought and thus woodland structure (Scholes et al., 2004; Eldridge et al., 2012). While rapid biodiversity change is being observed in southern African woodlands (Syampungani et al., 2009), research into the relationship between biodiversity and ecosystem functionality remains scarce.

A small number of studies in southern African woodlands have shown that above ground woody carbon/biomass stocks correlate positively with tree species richness (McNicol et al., 2018; Shirima et al., 2015; Mutowo and Murwira, 2012), but the scientific impact of these studies has been hampered by a restricted climatic and biogeographical range of study sites. Due to the highly variable environmental conditions within which southern African woodlands occur (Frost, 1996), and given the potential importance of environment and biogeography in defining the strength and form of a relationship between biodiversity and woody biomass, it is important to sample across these gradients to be able to infer a truly regional scale relationship between diversity and biomass. Studies conducted over small environmental gradients often find that at local scales, diversity shows a strong effect on ecosystem function, but at large scales diversity effects pale in significance compared to abiotic factors such as climate (Pasari et al., 2013). Small scale studies may therefore be over-estimating the effect of diversity.

In forests, climatic variation is known to affect both woody biomass (Michaletz et al., 2014, 2018) and species diversity independently (Spasojevic et al., 2014). It is important therefore to account for climatic factors and understand how they interact with biomass and diversity to effectively model and correctly attribute the effects of biodiversity on woody biomass in analyses at large spatial scales. 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 positively correlated with biomass (Chisholm et al., 2013; Prado-Junior et al., 2016). Similarly, Condit et al. (2013) found that dry season intensity was the main determinant of tree species distribution and abundance evenness in a wet Panamanian tropical forest. In European forests (Ratcliffe et al., 2017) found stronger positive relationships between tree species richness and various ecosystem functions in more arid environments. They suggest that in dry ecosystems, facilitative effects and selection effects may be more important than niche complementarity in driving the relationship between species diversity and ecosystem function. Stress tolerance rather than competitiveness may be the mechanism by which a tree species' success is measured in dry forested ecosystems.

Solbrig et al. (1996) writes that southern African woodlands possess structurally diverse tree canopies, with trees occupying distinct layers of the canopy at different growth stages and among species.

This structural diversity may be one mechanism through which diversity influences woody biomass. (Kunz et al., 2019) found that crown complementarity and crown plasticity both increased with species richness in a seasonally dry subtropical forest. They also found that trees growing in species rich neighbourhoods exhibited enhanced biomass production. Occupation of multiple canopy layers allows a more full canopy with a greater total foliage density, enhancing productivity and allowing greater standing woody biomass in a smaller area as a form of niche complementarity. This mechanism however, which has been supported by experiments and observational studies in temperate and wet tropical ecosystems (Hardiman et al., 2011; Stark et al., 2012), may not be relevant in savannas, which are structured by disturbance rather than competition. Instead, disturbance history may override the effects of species diversity on structural diversity nullifying the effects of species diversity on structural diversity.

In this study, we made the first known regional estimation of the Biodiversity-Ecosystem Function Relationship in southern African woodlands, using inventory plots which span multi-dimensional environmental and biogeographical gradients (Figure 1). We investigated the relationship between aboveground woody biomass and tree biodiversity. We compared the relative effects of tree species biodiversity with that of environmental factors known to affect ecosystem productivity and biomass accumulation: precipitation, temperature and soil fertility. We also investigated the potential moderation effects of environmental covariates on the relationship between tree species diversity and biomass. We incorporated vegetation type based on major tree species compositional units as a factor in our analyses to understand how species composition as well as species biodiversity affected ecosystem functionality. Initially, we made three hypotheses:

1.1 Hypotheses

1. Precipitation and soil fertility will indirectly positively affect woody biomass via an increase in tree species diversity.

2. The effect size of species diversity on woody biomass will increase with stem density, due to an increased importance of niche complementarity as competition increases.

3. Tree structural diversity will indirectly influence tree species diversity to provide an indirect path of influence between structural diversity and woody biomass.

2 Methods

2.1 Study location

The study used 1769 woodland monitoring plots from the larger SEOSAW network (SEOSAW, 2019) located across 10 countries within southern Africa in so-called miombo woodlands (Figure 1, Hopkins and White 1987). The study region spans a precipitation gradient from ~460 mm y^{-1} in southern Mozambique and southern Zimbabwe to ~1700 mm y^{-1} in northern Zambia, Malawi and northern Mozambique. The study sites span the core climate space of the region as a whole. The 2D convex hull of Mean Annual Precipitation (MAP) and Mean Annual Temperature (MAT) of the study sites covers 94.4% 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).

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 (Ratnam et al., 2011; Hill and Hanan, 2011). Plots with evidence of farming, human resource extraction or experimental treatments such as prescribed burning or herbivore exclusion were excluded 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 (Stegen et al., 2011), leading to inaccurate estimates. Only plots with a stem density >10 stems ha^{-1} (>10 cm stem diameter) 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 each 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 neighbour 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 largest nearest neighbour distances in multidimensional species composition space (Otto, 2013), thus removing 87 plots (Appendix A).

2.2 Data collection

We considered only trees and shrubs in our calculations of above-ground woody biomass (AGB), including woody species such as palms and cycads which are functionally tree-like, but excluding lianas, which fill a different ecological niche (Selaya and Anten, 2008). Only stems >10 cm DBH (Diameter at Breast Height, 1.3 m) were included in analyses. Many plots in the dataset did not include data on stems <10 cm DBH. For those plots with stem measurements <10 cm DBH, those small stems only accounted for a median average of 2.2% of the plot level AGB.

All stems >10 cm DBH were measured within each plot resulting in a total of 93,256 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 we measured species, DBH and tree height to the top of the highest branch material. Height was measured through a variety of means including laser rangefinders, manual clinometers and measuring sticks. 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 C., unpublished) (Appendix B).

AGB 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.

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

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

Climatic data were collected from the ECMWF ERA5 dataset, generated using Copernicus Climate Change Service Information (Copernicus Climate Change Service, 2017). 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 seasonality (TS) and precipitation seasonality (PS) were both calculated as the mean of the coefficient of variation of daily MAT and MAP, respectively, for each of 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), percentage soil organic carbon by volume (Org. C %), and percentage soil sand content by volume (Sand %). These data are a modelled product derived from various remotely 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 extrapolates a species rarefaction curve to its predicted asymptote and uses this value as its estimated species richness value. Extrapolated species richness accounts for variation in plot size (0.1-10 ha) and therefore sampling effort among plots. Larger plots will tend to encompass more individuals, and therefore more species (Dengler, 2009).

To measure tree species abundance evenness, the Shannon Equitability index ($E_{H'}$) (Smith and Wilson, 1996) (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, using the `ChaoRichness()` function. We calculated tree structural diversity for each plot by calculating the coefficient of variation of DBH (DBH CV) and tree height (Height CV).

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) in an Africa wide analysis of floristic units using plot data in savannas and woodlands with tree species diversity and relative abundance data. Groups were identified using unconstrained correspondence analysis and ordination, followed by clustering based on dominant ordination axes. Plot data used in this study occurred in four vegetation type groups. See Table 1 for a description of each vegetation cluster and Figure 1 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 (Dufrêne and Legendre, 1997) implemented with `indval()` from the `labdsv` R package (Roberts, 2019) and represent species which define the given cluster. Dominant species were identified by choosing the species with the largest AGB contribution within each cluster. Numeric values of species richness, stems ha^{-1} and AGB are medians and interquartile ranges (75th percentile - 25th percentile).

Cluster	Dominant species	Indicator species	N plots	Species rich.	Stems ha^{-1}	AGB (t ha^{-1})
Marginal miombo	*Julbernadia* spp. *Brachystegia spiciformis* *Baikeaea plurijuga*	*Diplorhynchus condylocarpon* *Burkea africana* *Pseudolachnostylis maprouneifolia*	687	11(11.2)	170(145.3)	37(34.68)
Core miombo	*Julbernadia* spp. *Brachystegia* spp. *Isoberlinia angolensis*	*Julbernardia paniculata* *Isoberlinia angolensis* *Brachystegia longifolia*	757	18(17.6)	215(171.7)	48.8(43.7)
Baikiaea	*Spirostachys africana* *Senegalia* spp. *Euclea racemosa*	*Baikiaea plurijuga* *Senegalia ataxacantha* *Combretum collinum*	226	10(10)	165(157.5)	46(47.81)
Mopane	*Colophospermum mopane*	*Colophospermum mopane* *Combretum* spp.	99	7(8.2)	190(155.7)	41.5(36.93)

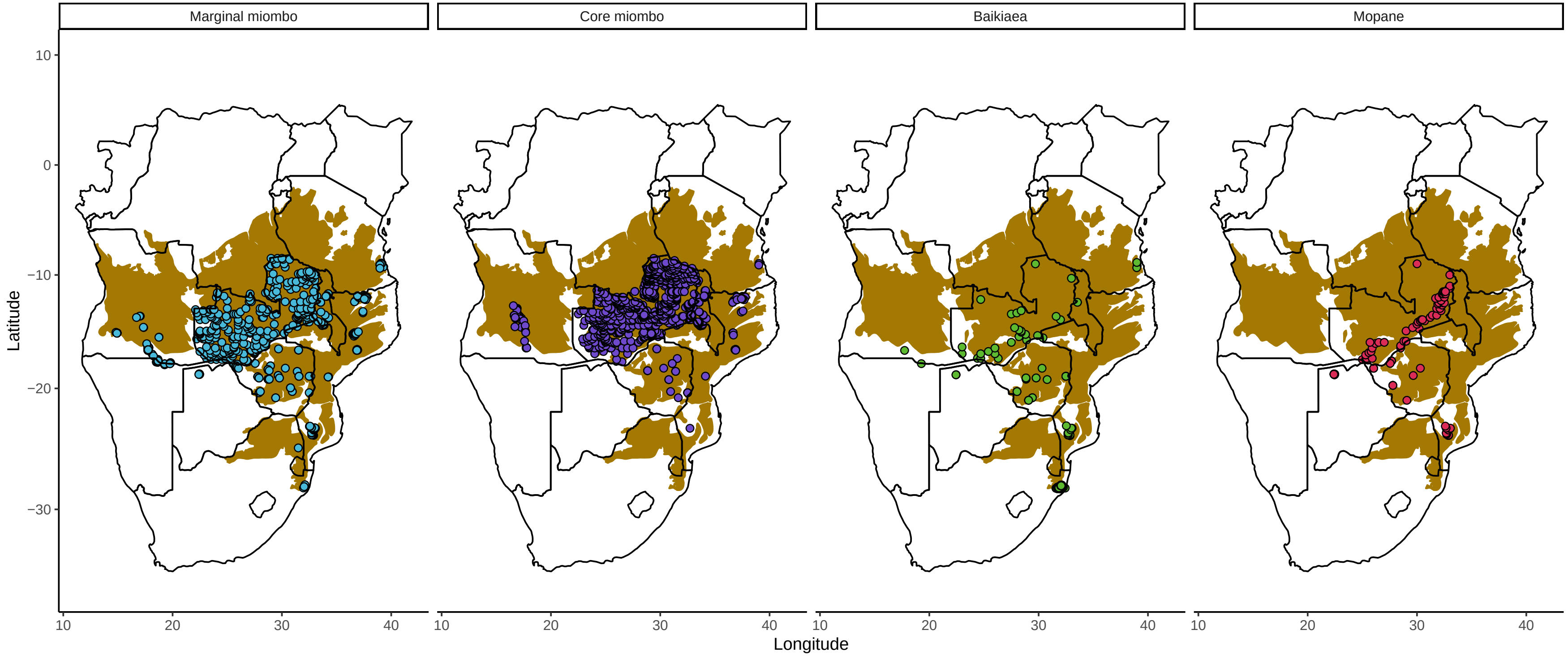

Figure 1: The locations of the 1769 plots used in this study, as points by geographic location with respect to the distribution of miombo woodland vegetation according to Hopkins and White (1987). Each panel shows plots categorized by their vegetation type as defined by the vegetation types in Table 1.

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 (Rosseel, 2012) 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 and partition variance to indirect effects, which is challenging in standard multiple regression. Using SEMs also allowed us to describe theoretical latent constructs which have been suggested to act upon diversity and biomass/productivity in previous studies despite these factors not having single observable measures in our dataset. Structural equation modelling is also necessary to properly account for potential feedback mechanisms between aspects of climate and tree species diversity, which could otherwise increase the chances of Type I error and wrongly attribute inference due to covariance of explanatory variables when using conventional regression analyses (Nachtigall et al., 2003).

Prior to analysis, we specified a conceptual model with factors expected to affect AGB: moisture availability, soil fertility, tree species diversity, tree structural diversity and stem density (Figure 2).

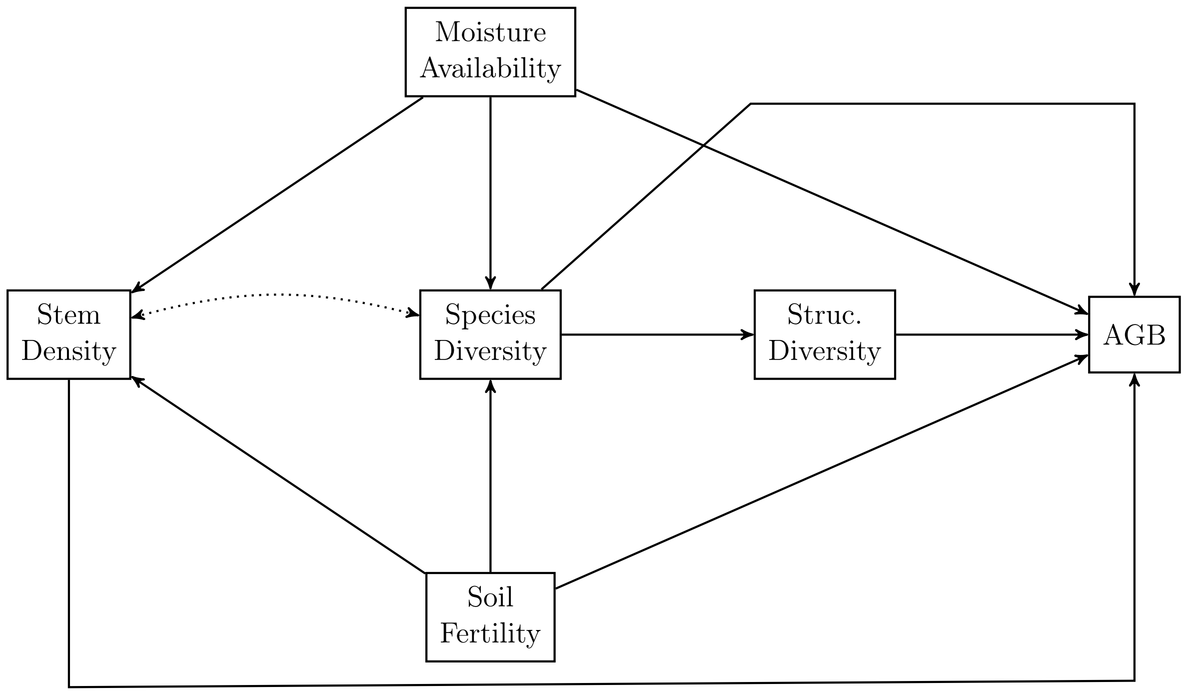

Figure 2: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural diversity, tree stem density, and AGB. Hypothesised paths of causation are depicted as arrows from predictor to response. Correlations are depicted as curved dotted arrows.

Observed variables were transformed to achieve normality where necessary and standardised to Z-scores prior to analysis (Appendix C). Standardisation put each latent variable on the same scale, with a mean of zero and a standard deviation of one. Standardisation allows path regression coefficients to be easily compared between paths in the same model to assess their relative effect size, and eliminates confusion in model interpretation arising from the observed variables being on different scales (Beaujean, 2014). Standardisation 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 for model fitting. Precipitation seasonality (PS), temperature seasonality (TS), and mean annual temperature (MAT) were also reversed in this way to account for the direction of their effect on moisture availability.

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 (Beaujean, 2014). We tested the robustness of our assumptions with a chi-squared test of all possible combinations of observed variable factor loadings set to 1, while ensuring no factor loadings were in excess of 1. We found no significant difference between model specifications. 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).

First, we assessed the role 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. To account for variation in stem density which may covary with species diversity we also included it as an predictor in our model. 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 unstandardised path coefficients among these vegetation cluster scale models to understand the effect that vegetation type has on the relationship between tree species diversity, structural diversity, stem density and AGB. Path coefficients show the effect of a path with other paths of inference held constant. Models were estimated using the "MLM" estimator, because it is robust to multivariate non-normality (Shapiro, 1983). Model fit was evaluated using the robust Comparative Fit Index (CFI), the robust Tucker Lewis Index (TLI), the Root Mean Squared Error (RMSEA) and the R^2 coefficient of determination for AGB. We critically assess model fit in each case, taking into consideration the recommendations of Hu and Bentler (1999) which define threshold values of acceptability for these model fit indices: CFI >0.85, TLI >0.85, RMSEA <0.15, alongside our judgement of the model estimates.

To explore the hypothesis that complementarity effects increase in strength as stem density increases, we repeatedly sub-sampled the available plot dataset to create 50 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. We excluded the effect of stem density on AGB and the correlation between stem density and species diversity from this model. We then examined how the unstandardised path coefficients for each path in the SEM varied according to the median stem density of subsampled dataset.

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. We compared standardised path coefficients between paths in the model to understand the relative contribution of each path to explain variance in AGB. Vegetation type specific 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 Results

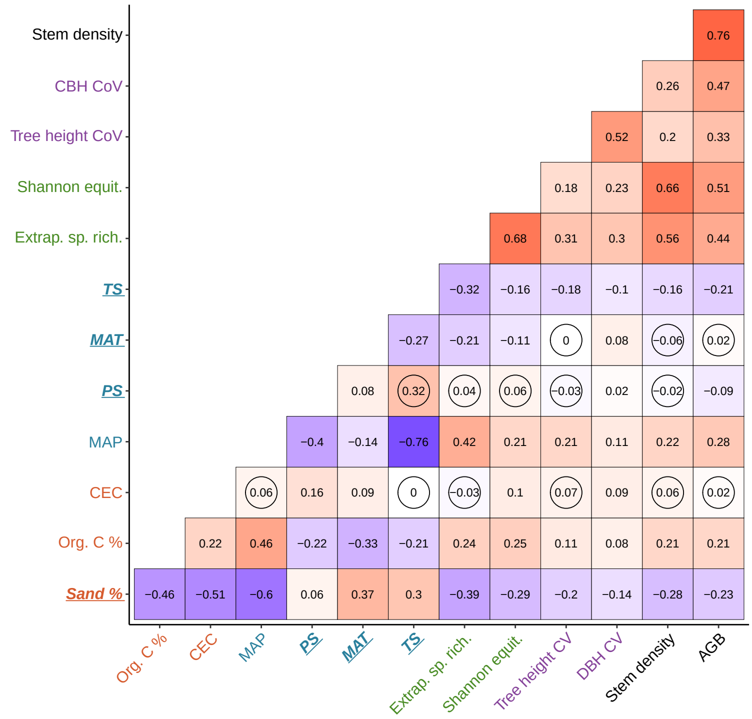

Figure 3: Correlogram of standardised observed variables used in the SEMs, with Pearson correlation coefficients (r) coloured according to sign (+ve red, −ve blue) and shaded by strength of correlation. Variables in bold and underlined on the axis labels were later reversed for SEMs to maintain positive correlations for all 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 = tree species diversity, purple = tree structural diversity. See Appendix D for a full assessment of correlation fit statistics.

Pairwise 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 (r = 0.78, p <0.01). Environmental variables had weaker correlations with AGB than diversity variables, with all environmental variables having significant correlations with AGB, except CEC and MAT.

The direction of these correlations was used as a test of our assumptions of the direction of influence of latent variables later used in the SEMs. As expected, there was a positive correlation between MAP and AGB (r = 0.24, p <0.01), and a weak negative correlation between the seasonality of precipitation and AGB (r = -0.09, p <0.01). MAT and temperature seasonality (TS) negatively correlated weakly with AGB (MAT: r = -0.05, p <0.05; TS: r = -0.19, p <0.01). As expected, there was a negative correlation between soil sand content and AGB (r = -0.25, p <0.01), and a positive correlation between soil organic carbon and AGB (r = 0.23, p <0.01).

MAP had positive correlations with tree species richness (r = 0.39, p <0.01), abundance evenness (r = 0.1, p <0.01), tree height diversity (r = 0.21, p <0.01) and tree stem density (r = 0.12, p <0.01). MAT had weak correlations with tree species and structural diversity variables. Tree species diversity variables had clear positive correlations with stem density (Species richness: r = 0.54, p <0.01; Shannon equitability: r = 0.47, p <0.01).

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 4), species diversity had a small positive direct effect on AGB ($\beta = 0.12 \pm 0.036$, p <0.01), and indirectly via structural diversity ($\beta = 0.15 \pm 0.023$, p <0.01) (Figure 4). Tree species diversity had a positive correlation with stem density. Model fit was good with high factor loadings for all observed variables, all path coefficients were significant (p <0.01) (Table 2). The R^2 of AGB was 0.7. The strongest direct effect on AGB was from stem density ($\beta = 0.76 \pm 0.031$, p <0.01).

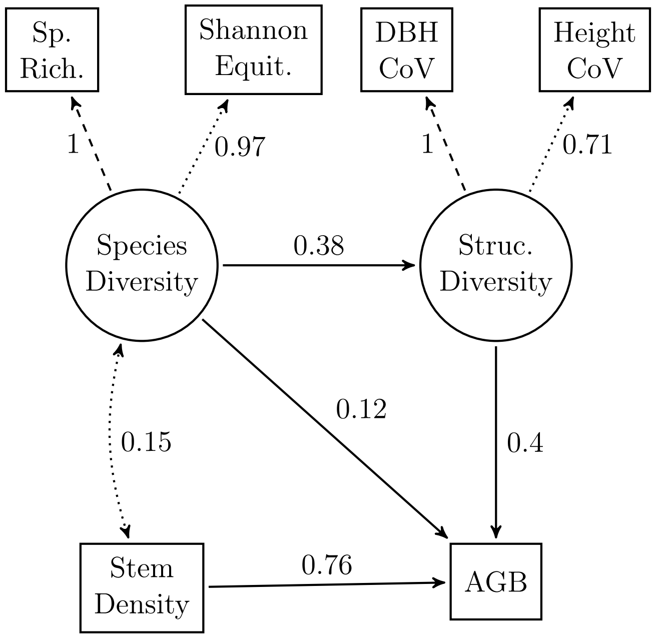

Figure 4: Path diagram with regression coefficients for the tree diversity SEM, including plots from all vegetation clusters. Latent variables are circles while observed variables are rectangles. Standardised path coefficients are solid arrows pointing from predictor to response with the effect size of the path coefficient expressed in terms of standard deviations on the latent variable response scale. The observed variables which inform the latent variables are connected by dotted arrows, observed variables with loading set to 1 are connected by dashed arrows. Correlations between variables are depicted as dotted curved arrows. Measurement errors of exogenous variables are omitted for clarity.

3.2 Variation among vegetation types

When the tree species and structural diversity model (Figure 4) was refitted separately using data from each of the 4 vegetation types the strengths of unstandardised path coefficients varied. The direct effect of tree species diversity on AGB was positive in Baikiaea and Mopane, but negative in Marginal and Core miombo (Figure 5). Relationships between structural diversity and AGB remained generally similar with the same sign and significant overlap between the 95% confidence intervals of path coefficients. The total effect of species diversity on AGB remained strongly positive for all vegetation types. All vegetation types except Mopane exhibited a positive effect of species diversity on structural diversity. All models had adequate goodness-of-fit (Table 2), though confidence intervals around the unstandardised path coefficients were wide particularly for Mopane and Baikiaea. χ^2 statistics were high for some vegetation types, but this appears to be highly correlated with sample size for each vegetation type (Hooper et al., 2008).

The strongest total effect of tree species diversity on AGB was in Baikiaea woodland ($\beta = 0.19 \pm 0.152$, p = 0.22), which was species rich but highly variable in species diversity compared to other vegetation types (Table 1). The R^2 of AGB was highest in Marginal miombo ($R^2 = 0.73$) and lowest in the Core miombo ($R^2 = 0.68$).

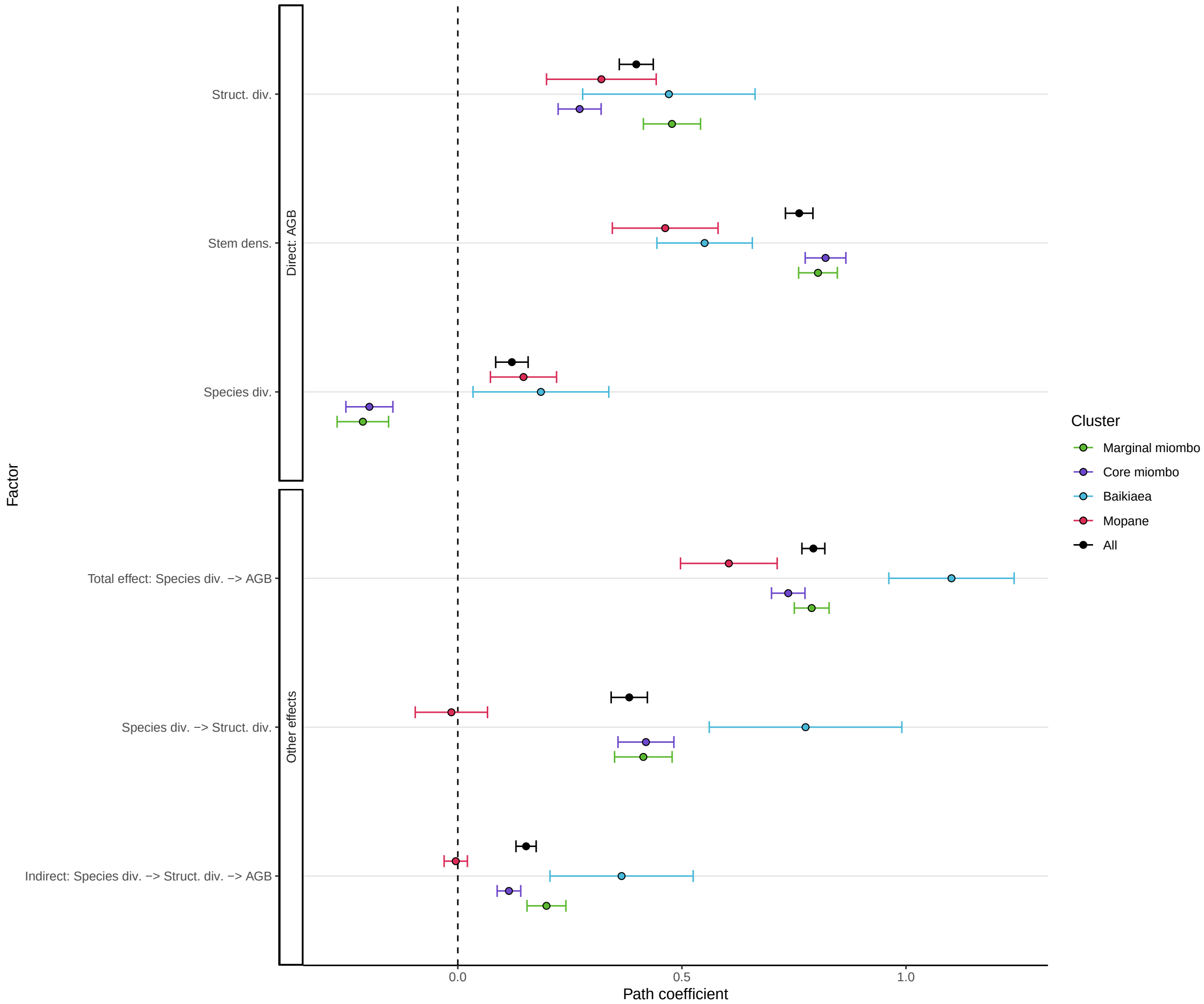

Figure 5: Unstandardised path coefficients for the effects of tree diversity on AGB, mediated by the effect of stand structural diversity. Path coefficients are ±1 standard error. Path coefficients where the standard error does not overlap zero are considered to be significant effects.

Table 2: Model fit statistics for SEMs investigating the effects of tree diversity and stem density on AGB (Figure 4).

Cluster	n	χ^2	DoF	CFI	TLI	LogLik	RMSEA	R^2 AGB
Marginal miombo	525	47.480	6	0.964	0.910	-3730.100	0.110	0.730
Core miombo	668	59.440	6	0.958	0.895	-4219	0.100	0.680
Baikiaea	47	5.860	6	0.998	0.994	-323.100	0.030	0.720
Mopane	84	9.420	6	0.971	0.927	-588.900	0.080	0.450
All	1324	82.020	6	0.973	0.932	-9122.800	0.090	0.700

3.3 Moderation of Diversity-AGB relationship by stem density

We repeatedly sub-sampled the plot dataset to build 50 datasets of varying mean stem density in order to test how the relationship between species diversity, structural diversity and biomass varied with stem density. Each dataset consisted of approximately 893 plots with overlap of plot identity between subsampled datasets. Figure 6 shows a positive effect of tree species diversity on AGB as stem density increases. There appears to be a minimum stem density threshold at ~180 stems ha^{-1} below which there appears to be a reasonably constant low baseline effect of tree diversity on biomass. The effect of structural diversity on AGB appears to remain constant with increasing stem density. The indirect effect of species diversity on AGB via structural diversity climbs slightly as stem density increases.

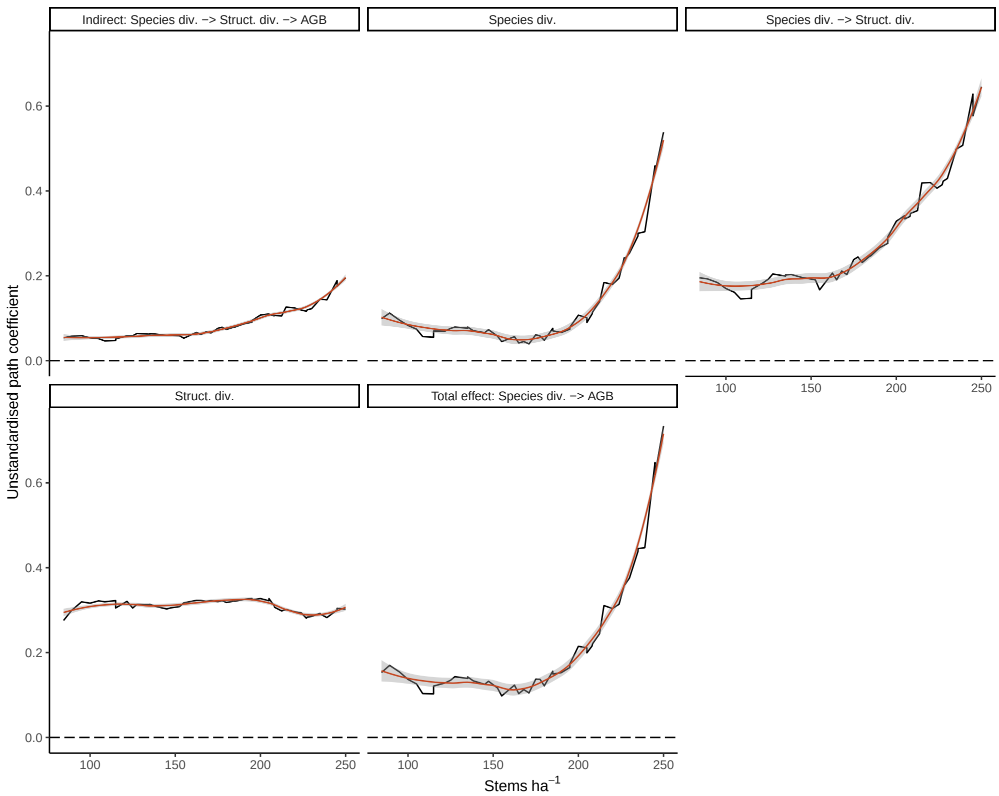

Figure 6: Line plots showing the variation in path coefficients in the SEM, using datasets with different mean stem density. Smoothed lines are loess curves with standard error shaded bars.

3.4 Environmental covariates and diversity

A model incorporating the latent variables of moisture availability and soil fertility showed that the total effect of species diversity on biomass was greater than that of both moisture availability and soil fertility (Figure 7). 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 (moisture: β = -0.01±0.004, p <0.01, soil: β = -0.04±0.011, p <0.01). MAP and temperature seasonality (TS) had the greatest contributions to the latent variable of moisture availability. Moisture availability and soil fertility also had negligible direct effects on stem density. Model fit was acceptable: CFI = 0.924, TLI = 0.905, and RMSEA = 0.162, R^2 of AGB = 0.71.

Similar to the model which only considered tree species and structural diversity (Figure 4), the direct effect of species diversity on structural diversity was positive, while structural diversity itself had a positive effect on AGB, leading to a strong positive indirect effect of species diversity on AGB via structural diversity (β = 0.16±0.023, p <0.01). The total effect of species diversity on AGB was positive (β = 0.62±0.041, p <0.01).

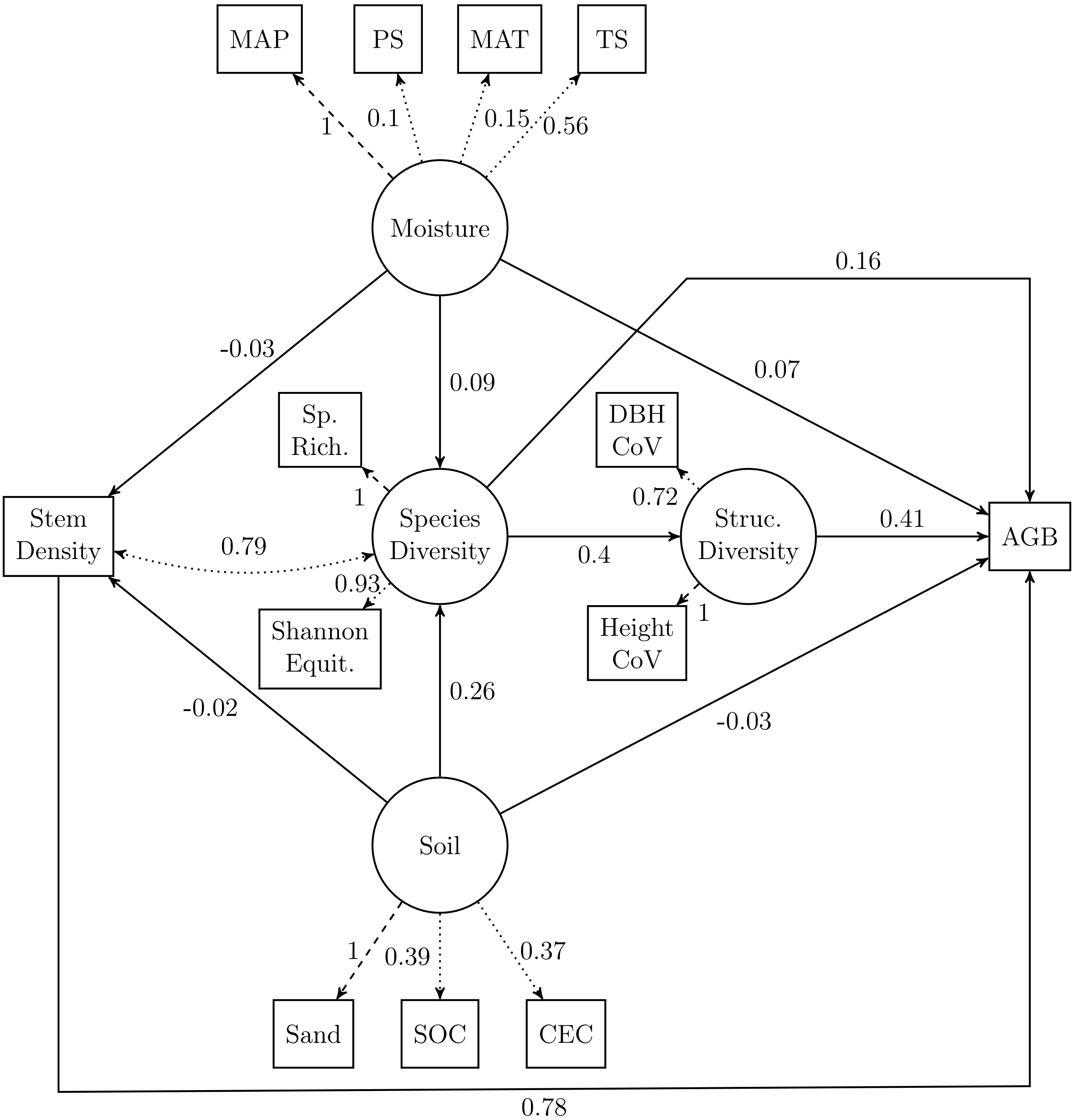

Figure 7: Path diagram with regression coefficients for the SEM incorporating environmental covariates and tree species and structural diversity across all five vegetation types. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are solid arrows pointing from predictor to response with the effect size of the path coefficient expressed in terms of standard deviations on the latent variable response scale. 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. Correlations between variables are depicted as dotted curved arrows. Measurement errors of exogenous variables are omitted for clarity.

4 Discussion

In this study, we assessed the importance of [a] tree species richness, [b] tree structural diversity, [c] resource availability via moisture availability and soil fertility, [d] stem density and their interactions on above ground woody biomass (AGB) across southern African woodlands, using a network of 1769 woodland survey plots. Using latent variables and Structural Equation Modelling (SEM), we found support for a general relationship between tree species diversity and AGB, with an indirect relationship between tree species diversity and AGB via structural diversity (H_1). We found that the effect size of tree species diversity on AGB increased with stem density (H_2). Tree diversity, structural diversity and stem density accounted for 70% of the variation in AGB across the region, while models for certain vegetation types showed even greater explanatory power (Table 2). The strongest effect on AGB was that of stem density. Interestingly, when tree species diversity, structural diversity and stem density were controlled for, we found little evidence of an effect of resource availability, in the form of moisture availability and soil fertility, on AGB (H_3). We found that vegetation composition in the form of discrete vegetation types affected the relationship between tree species diversity and AGB.

4.1 Effect of tree species diversity on AGB

We found a consistent positive total effect of tree species diversity on AGB across all models in this study. Within the savanna woodlands of southern Africa we therefore find support 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 (Liang et al., 2016; Cardinale et al., 2009). In addition however, our study provides a novel dissection of the mechanisms underlying this relationship and their interaction with resource availability and vegetation type in southern African woodlands as an understudied biome.

Much of the total variation in AGB was caused by stem density. Stem density also correlated with species diversity in our SEMs. It is possible that within southern African woodlands a higher species diversity allows for a greater density of tree stems, leading to an increase in total AGB. Reverse causation is plausible however, with increased stem density causing higher species richness through an increased probability of encountering new species. In our extrapolation of species richness according to sampling effort (stem density) we partially accounted for this effect, but our analyses cannot properly assess to what extent a real effect of species diversity on stem density exists. We cannot decompose the relative effects of tree species richness and abundance evenness in our model, but previous studies have shown that both richness and evenness have similar importance in their effects on ecosystem function (Valéry et al., 2009; Zhang et al., 2012). We suggest that an increase in tree species diversity through species richness and evenness produces an assemblage of species which can occupy a greater proportion of the total woodland canopy volume with leaf area, utilising more of the available light resulting in greater total AGB at the plot level. This is supported by the moderately strong positive effect of tree species diversity on AGB via structural diversity.

While we did not explicitly measure Net Primary Productivity (NPP) in this study, other studies have shown a strong positive correlation between woody AGB and NPP in woodland and forest ecosystems (Chisholm et al., 2013; Prado-Junior et al., 2016). This suggests that as has been found in many other woodland/forest ecosystems, woody biomass and woody productivity in southern African woodlands can be maximised by increasing species diversity.

4.2 Structural diversity as a mechanism for the BEFR

We found evidence that tree species diversity led to an increase in AGB indirectly via tree structural diversity and we therefore find support for our hypothesis (H_2). A higher tree species diversity allows for a greater diversity of tree functional forms within a plot and this may act as a mechanism of niche complementarity, with a highly diverse canopy being able to take advantage of a greater proportion of the available light. Variation in structural diversity may be a joint result of disturbance history and tree species diversity, with highly disturbed plots generally having a less structurally diverse canopy (LaRue et al., 2019). In forests, where the tree canopy is effectively closed, as the stand matures a more diverse canopy emerges via competition and tree mortality events which open canopy gaps (Muscolo et al., 2014). In frequently disturbed woodlands such as those studied here however, a tree canopy similar to that of a forest is frequently not reached, Instead, a simple open canopy is maintained that can be made more complex and productive via an increase in species diversity.

While we did not have access to adequate data on disturbance history in our plots, previous studies have found that southern African woodlands with higher species diversity tend to be less disturbed and tend to form a more closed canopy (Chidumayo, 2013; Mutowo and Murwira, 2012).

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 resource partitioning among individual trees and a greater stem density per unit area (Kraaij and Ward, 2006; Shirima et al., 2015).

Previous studies in tropical forests have shown that moisture availability increases AGB both directly and indirectly via increasing tree species diversity and via increasing stand structural diversity (Ali et al., 2019*a*,*b*; Poorter et al., 2017). In this study, while we observed weak indirect effects via species diversity, we saw no evidence for a direct effect on AGB. Compared to moist tropical forests, moisture availability is more of a limiting factor to tree growth in southern African woodlands, which are frequently droughted. It is possible that the range of observed moisture availability in this study (~460-1700 mm y^{-1}) may not have been able to capture variation in AGB. We deliberately excluded plots with very low stem density as they are not considered woodlands, but grassy savannas. It may be that by excluding the bottom end of this stem density continuum we prevented a relationship being observed between moisture and AGB/stem density. Additionally, due to the high levels of adaptation of tree species to drought conditions in southern Africa, at the large scale we conducted our experiment turnover in species composition may have prevented a direct relationship being observed between resource availability and AGB.

In southern African woodlands moisture availability is closely linked with the intensity of disturbance from seasonal fires. The growth of C4 grasses in wetter woodlands leads to more intense seasonal fires which limit tree growth (Charles-Dominique et al., 2018), and may also limit species diversity (Linder, 2014). It is possible therefore that the effect of moisture availability, which is expected to increase AGB, is confounded in its effect on AGB with the unmeasured variable of fire regime intensity, which is expected to decrease AGB. The direct effect of moisture availability on stem density may also be confounded in this way. This may also have caused us to not observe a stronger effect between moisture availability and AGB.

4.4 Vegetation type specific responses

Core miombo and marginal miombo woodland vegetation exhibited a small negative direct effect of tree species diversity on AGB, while the total effect via structural diversity remained positive in these vegetation types. Compared to Baikiaea and Mopane woodlands these woodlands have higher median tree species richness. Baikiaea and Mopane woodlands are also dominated by fewer tree species, notably *Baikiaea plurijuga* in Baikiaea woodlands and *Colophospermum mopane* in Mopane woodlands which tend to produce large canopy dominating trees. We postulate that this negative effect of tree species richness on AGB in miombo woodlands may be due to an increase in interspecific competition through canopy crowding, but that this effect is not present in Baikiaea and Mopane woodlands, where the woodland canopy is dominated often by a single species. Higher functional redundancy among tree species in miombo woodlands may lead to smaller trees with lower AGB in the most diverse plots, more resembling thicket vegetation. Again, these highly diverse plots in miombo woodlands may be the result of disturbance which can promote a mosaic of woodland of different successional stages and stem densities.

Despite Mopane woodland having very low species diversity generally, with often monospecific stands (Timberlake et al., 2010), a positive effect of tree species diversity on AGB was observed. In previous studies across ecosystem types it has been found often that the effect on ecosystem function of adding species is stronger in low diversity assemblages (Hector and Bagchi, 2007). This has been attributed to an increase in functional redundancy as species diversity increases. *I.e.* with more species, it is more likely that the addition of a new species will occupy the same ecological niche space as an existing species, meaning niche complementarity will not occur and competition will lead to niche partitioning, while making little difference to overall ecosystem functioning. Mopane woodlands also have a negligible effect of species diversity on structural diversity. This may be due to the species which tend to co-exist with *C. mopane*, many of which are small shrub-like trees which do not grow into large canopy trees (Timberlake et al., 2010). Larger canopy trees tend to have greater variation in physical structure (Seidel et al., 2019).

Baikiaea woodland had the strongest total effect of species diversity on AGB. Baikiaea also has relatively low median species richness compared to miombo and Mopane woodlands, but the addition of new species appears to make a larger difference to the AGB of these plots than mopane. We suggest that this is due mostly to the particular identity of species found in Baikiaea woodlands and their contribution to ecosystem functioning. Unlike mopane woodlands, Baikiaea woodlands do sometimes contain species other than *B. plurijuga* which grow to be high biomass canopy trees.

4.5 Stem density effects

We found a non linear positive effect of stem density on the relationship between tree species diversity and AGB (Figure 6). At low stem densities competition between trees may not occur, meaning that the niche complementarity provided by an increase in tree species richness might not make any difference to plot level AGB, accounting for the low and constant effect of tree species diversity on AGB below ~180 stems ha^{-1}.

At high stem densities, where the woodland approaches a more forest-like canopy structure an increase in niche complementarity in canopy occupation may allow a higher AGB per unit area. There may be an effect whereby high stem density plots have many small stems which do not hold much woody biomass, but we did not observe this in our study, possibly because we only considered stems >10 cm DBH. An abundance of small stems may prevent the growth of large trees which hold the majority of the AGB in a plot.

4.6 Conclusion

In this study we found that across southern African woodlands, there is a generalisable positive association between tree species diversity and woody biomass as a measure of ecosystem functionality. Additionally, we found that much of this effect of species diversity on biomass exists as an indirect effect by increasing the structural diversity of woodland tree canopies. We found that the multiple vegetation types which comprise southern African woodlands exhibit variation in the strength of the relationship between species diversity and woody biomass. In contrast to previous studies, we found that across the region, the direct effects of moisture availability and soil fertility on woody biomass were negligible, with most of their effect being indirectly through species and structural diversity. A gap in available data means that we could not incorporate disturbance history into our models adequately, but this factor likely plays a large part in the association between species diversity and woody biomass in southern African woodlands.

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Appendix 1 - Data cleaning process

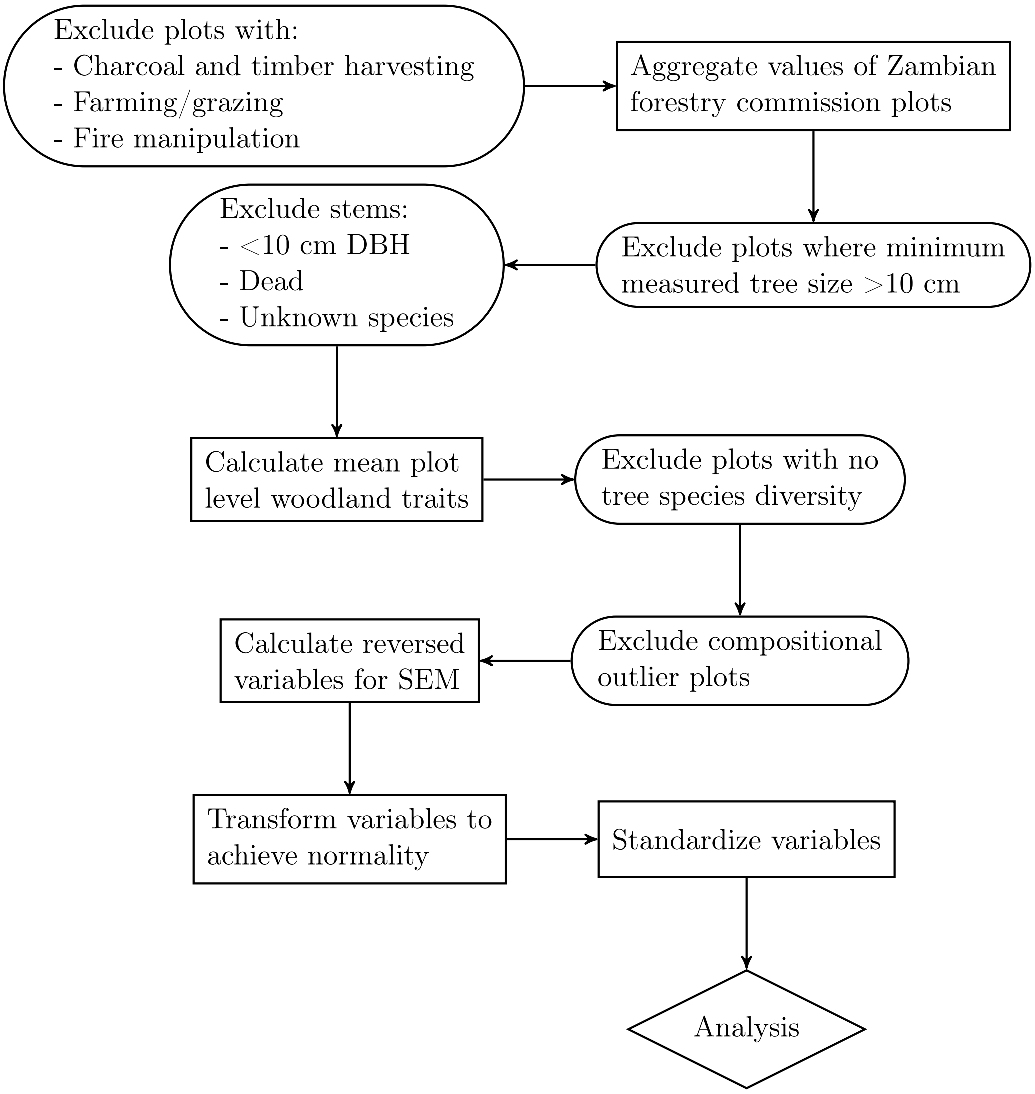

Figure 8: Flow diagram of the data filtering and cleaning process prior to analysis. Rounded boxes indicate filtering events while regular boxes indicate calculation events.

Appendix 2 - Estimation of DBH via tree taper

```
##' @title Stem diameter Point Of Measurement (POM) adjustment
##' @description  Function to estimate stem diameter at 1.3 given measurements
##'   at other POMs.
##' @author Casey M. Ryan
##' @return d130, the estimated diameter at a POM of 1.3 m (in cm).
##' @param d_in the diameter measured at the POM (in cm)
##' @param POM the height of the POM (in m)
##' @details The adjustment is based on a tree taper model developed as part of
##'   the ACES project (Abrupt Changes in Ecosystem Services
##'   https://miomboaces.wordpress.com/), using data from the miombo of Niassa.
##'   The model is a cubic polynomial, with three equations for different sized
##'   stems.
##' @section Warning: The model should not be used for POMs above 1.7 m.
##'   Extrapolating beyond the training data will give nonsense.
##'   Thus, POMs >1.7 m are not adjusted.
##' @examples
##' POMadj(10, 0.3)
```

```r
##' POMadj(1, 0.3)  # d130 is negative, i.e. the stem probably wasn't 1.3 m tall
##' POMadj(50, 1.9)  # generates warning, as outside calibration data range
##' \dontrun{
##'   POMadj(50, 0)  # zero or -ve POM is outside range, or nonsense
##' }
POMadj <- function(d_in, POM) {
  stopifnot(is.numeric(d_in),
    is.numeric(POM),
    POM >= 0,
    sum(is.na(POM))==0,
    length(POM) == length(d_in))
  if (any(POM > 1.7))
    warning("POMs >1.7 m are outside the calibration data, no correction applied")

  NAS <- is.na(d_in)
  d_in_clean <- d_in[!NAS]
  POM_clean <- POM[!NAS]
  # define the size class edges:
  edges <- c(5.0, 15.8, 26.6, 37.4)
  sm <- d_in_clean < edges[2]
  med <- d_in_clean >= edges[2] & d_in_clean < edges[3]
  lg <- d_in_clean >= edges[3]

  # compute apredictions for delta_d, for all size classes
  delta_d <- data.frame(
    # if small:
    small =  3.4678+-5.2428 *
      POM_clean + 2.9401 *
      POM_clean^2+-0.7141 *
      POM_clean^3,
    # if med
    med =  4.918+-8.819 *
      POM_clean + 6.367 *
      POM_clean^2+-1.871 *
      POM_clean^3,
    # if large
    large =  9.474+-18.257 *
      POM_clean + 12.873 *
      POM_clean^2+-3.325 *
      POM_clean^3
  )
  # index into the right size class
  dd <- NA_real_
  dd[sm] <- delta_d$small[sm]
  dd[med] <- delta_d$med[med]
  dd[lg] <- delta_d$large[lg]
  dd[POM_clean > 1.7] <- 0  # to avoid extrapolation mess

  # add NAs back in
  d130 <- NA
  d130[NAS] <- NA
  d130[!NAS] <- d_in_clean - dd

  if (any(d130[!NAS] < 0))
    warning("Negative d130 estimated, repaced with NA")
  d130[d130 <= 0 & !is.na(d130)] <- NA
  return(d130)
}
```

Appendix 3 - Frequency distribution of observed variables

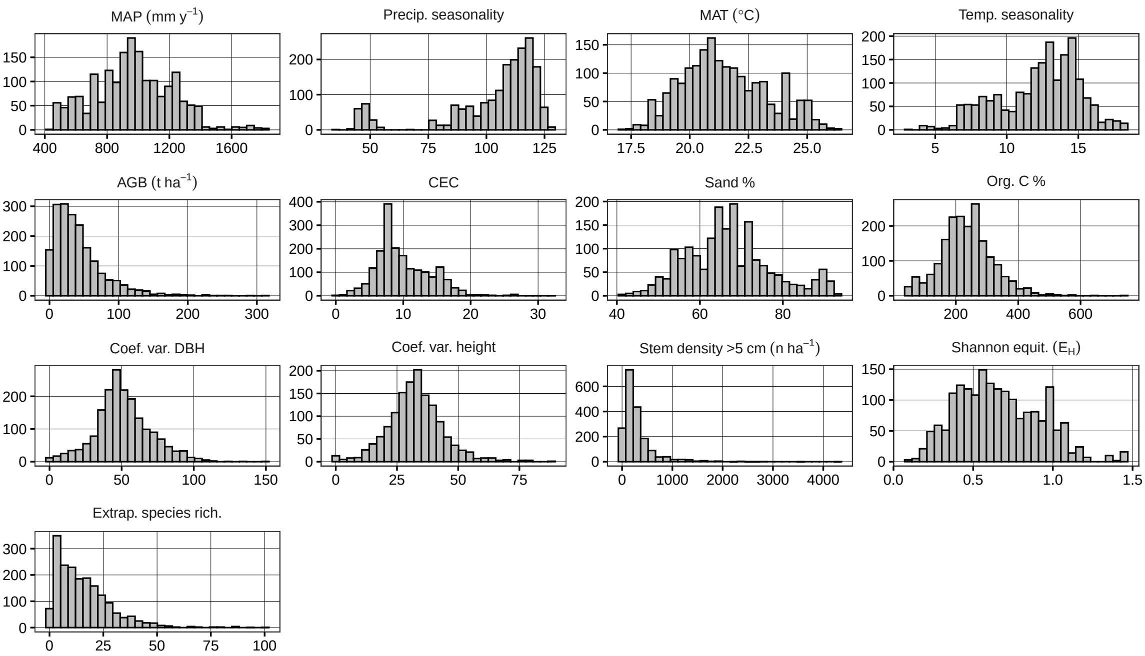

Figure 9: Histograms of raw untransformed observed variables used in final analyses.

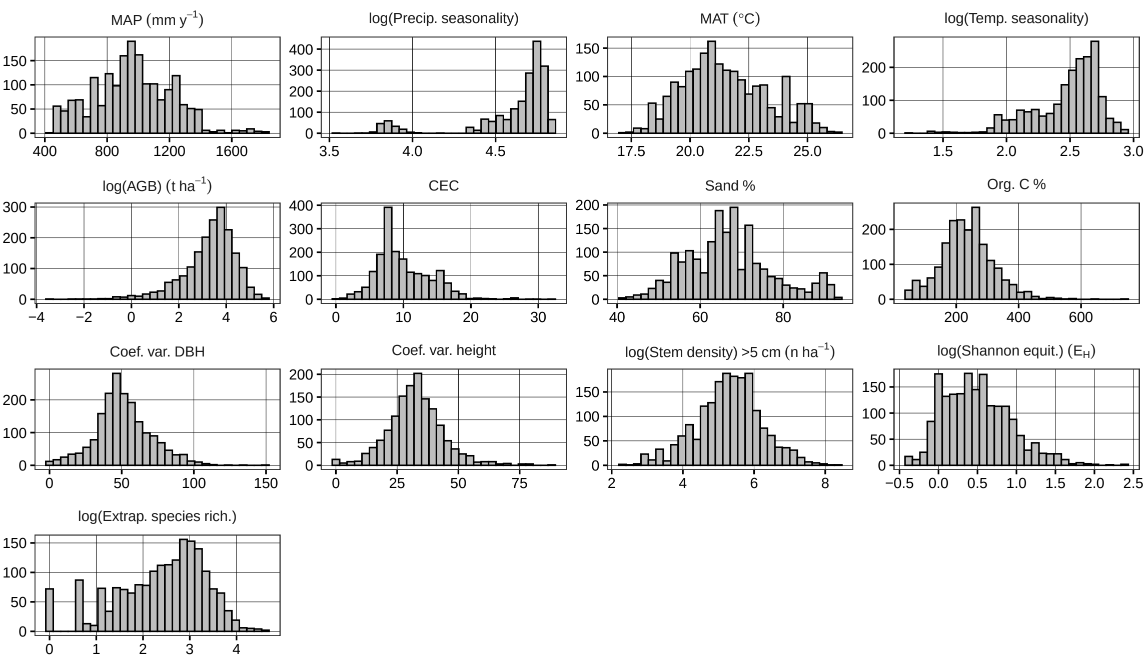

Figure 10: Histograms of observed variables transformed to achieve a normal frequency distribution.

Appendix 4 - 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	r	lower 95% CI	upper 95% CI	n	Prob.
Sand %	Org. C %	-0.510	-0.540	-0.470	1769	p <0.01
Sand %	CEC	-0.560	-0.600	-0.530	1769	p <0.01
Sand %	MAP	-0.500	-0.530	-0.460	1769	p <0.01
Sand %	PS	0.320	0.280	0.360	1769	p <0.01
Sand %	MAT	0.290	0.240	0.330	1769	p <0.01
Sand %	TS	0.230	0.180	0.270	1769	p <0.01
Sand %	Sp. rich.	-0.350	-0.390	-0.300	1769	p <0.01
Sand %	Shannon equit.	-0.240	-0.280	-0.200	1769	p <0.01
Sand %	Tree height CV	-0.200	-0.250	-0.150	1324	p <0.01
Sand %	DBH CV	-0.160	-0.200	-0.110	1744	p <0.01
Sand %	Stems ha	-0.240	-0.290	-0.200	1769	p <0.01
Sand %	AGB	-0.250	-0.290	-0.210	1769	p <0.01
Org. C %	CEC	0.300	0.250	0.340	1769	p <0.01
Org. C %	MAP	0.450	0.410	0.490	1769	p <0.01
Org. C %	PS	-0.300	-0.340	-0.260	1769	p <0.01
Org. C %	MAT	-0.310	-0.350	-0.270	1769	p <0.01
Org. C %	TS	-0.150	-0.190	-0.100	1769	p <0.01
Org. C %	Sp. rich.	0.240	0.190	0.280	1769	p <0.01
Org. C %	Shannon equit.	0.210	0.170	0.260	1769	p <0.01
Org. C %	Tree height CV	0.110	0.060	0.160	1324	p <0.01
Org. C %	DBH CV	0.100	0.050	0.150	1744	p <0.01
Org. C %	Stems ha	0.170	0.130	0.220	1769	p <0.01
Org. C %	AGB	0.230	0.180	0.270	1769	p <0.01
CEC	MAP	0	-0.040	0.050	1769	p = 0.84
CEC	PS	-0.510	-0.540	-0.470	1769	p <0.01
CEC	MAT	0.190	0.150	0.240	1769	p <0.01
CEC	TS	0.020	-0.020	0.070	1769	p = 0.36
CEC	Sp. rich.	-0.070	-0.110	-0.020	1769	p <0.01
CEC	Shannon equit.	0.090	0.040	0.130	1769	p <0.01
CEC	Tree height CV	0.070	0.020	0.130	1324	p <0.01
CEC	DBH CV	0.120	0.070	0.160	1744	p <0.01
CEC	Stems ha	0.060	0.010	0.100	1769	p <0.05
CEC	AGB	0.060	0.010	0.110	1769	p <0.05
MAP	PS	-0.120	-0.170	-0.080	1769	p <0.01
MAP	MAT	-0.100	-0.150	-0.060	1769	p <0.01
MAP	TS	-0.690	-0.720	-0.670	1769	p <0.01
MAP	Sp. rich.	0.390	0.350	0.430	1769	p <0.01
MAP	Shannon equit.	0.100	0.060	0.150	1769	p <0.01
MAP	Tree height CV	0.210	0.160	0.260	1324	p <0.01
MAP	DBH CV	0.110	0.060	0.160	1744	p <0.01
MAP	Stems ha	0.120	0.070	0.170	1769	p <0.01
MAP	AGB	0.240	0.200	0.290	1769	p <0.01
PS	MAT	-0.170	-0.210	-0.120	1769	p <0.01
PS	TS	0.070	0.020	0.110	1769	p <0.01
PS	Sp. rich.	0.080	0.030	0.120	1769	p <0.01
PS	Shannon equit.	-0.060	-0.100	-0.010	1769	p <0.05
PS	Tree height CV	-0.030	-0.090	0.020	1324	p = 0.25
PS	DBH CV	-0.080	-0.120	-0.030	1744	p <0.01
PS	Stems ha	0	-0.050	0.050	1769	p = 0.95

PS	AGB	-0.090	-0.130	-0.040	1769	p <0.01
MAT	TS	-0.320	-0.360	-0.280	1769	p <0.01
MAT	Sp. rich.	-0.220	-0.260	-0.170	1769	p <0.01
MAT	Shannon equit.	-0.100	-0.150	-0.060	1769	p <0.01
MAT	Tree height CV	0	-0.060	0.050	1324	p = 0.95
MAT	DBH CV	0.090	0.040	0.130	1744	p <0.01
MAT	Stems ha	-0.070	-0.120	-0.020	1769	p <0.01
MAT	AGB	-0.050	-0.100	0	1769	p <0.05
TS	Sp. rich.	-0.310	-0.350	-0.260	1769	p <0.01
TS	Shannon equit.	-0.090	-0.140	-0.050	1769	p <0.01
TS	Tree height CV	-0.180	-0.230	-0.130	1324	p <0.01
TS	DBH CV	-0.110	-0.160	-0.070	1744	p <0.01
TS	Stems ha	-0.150	-0.200	-0.110	1769	p <0.01
TS	AGB	-0.190	-0.230	-0.140	1769	p <0.01
Sp. rich.	Shannon equit.	0.540	0.510	0.580	1769	p <0.01
Sp. rich.	Tree height CV	0.310	0.260	0.360	1324	p <0.01
Sp. rich.	DBH CV	0.310	0.260	0.350	1744	p <0.01
Sp. rich.	Stems ha	0.540	0.510	0.570	1769	p <0.01
Sp. rich.	AGB	0.480	0.440	0.510	1769	p <0.01
Shannon equit.	Tree height CV	0.180	0.130	0.230	1324	p <0.01
Shannon equit.	DBH CV	0.230	0.180	0.270	1744	p <0.01
Shannon equit.	Stems ha	0.470	0.440	0.510	1769	p <0.01
Shannon equit.	AGB	0.380	0.340	0.420	1769	p <0.01
Tree height CV	DBH CV	0.520	0.480	0.550	1324	p <0.01
Tree height CV	Stems ha	0.200	0.150	0.250	1324	p <0.01
Tree height CV	AGB	0.330	0.280	0.370	1324	p <0.01
DBH CV	Stems ha	0.230	0.180	0.270	1744	p <0.01
DBH CV	AGB	0.480	0.440	0.510	1744	p <0.01
Stems ha	AGB	0.780	0.760	0.800	1769	p <0.01