

1 Title: An assessment of the biodiversity - ecosystem function rela-
2 tionship in southern African woodlands

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10 **Acknowledgements**

11 **Biosketch**

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

Running title: Woodland functionality in southern Africa

Abstract

Aim: Positive correlations between tree biodiversity and ecosystem function have been widely documented, but the nature of the relationship in highly disturbed and ecophysiologicaly stressful systems is less clear. Here, we explore the relationship between tree biodiversity and aboveground biomass across southern African savannas and woodlands, with respect to gradients in stem density and resource availability, to build a general understanding of the biodiversity - ecosystem function relationship in this understudied ecological context.

Location: Southern African savannas and woodlands

Time period: 2010-2019

Major taxa studied: Trees

Methods: We used a network of 1767 savanna and woodland plots located across the southern African sub-continent in which each tree >5 cm diameter was measured. We used Structural Equation Modelling and path analysis 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.

Results: A positive effect of tree species diversity on biomass was demonstrated, observed largely as an indirect effect of increasing woodland structural diversity. We also found that the effect of tree species diversity on biomass increases with stem density. Finally, we found that resource availability affects biomass in southern African woodlands largely indirectly via its effect on species diversity.

Main conclusions: Tree species diversity plays an important role in determining the ecosystem functionality and structure of southern African woodlands. Our results demonstrate the importance of considering environmental conditions and woodland structural attributes to more accurately describe the relationship between biodiversity and ecosystem functionality.

Introduction

Numerous studies have shown relationships between biodiversity and ecosystem function (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](#)). These studies support early findings from small scale experimental studies predominantly in grassland patches, which began in earnest during the 1990s as concern grew over the global loss of biodiversity ([Tilman and Downing, 1994](#); [Tilman et al., 2014](#)).

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.

Compared to other forested ecosystems, dry tropical woodlands are highly structured by disturbance, mainly through fire, and in Africa notably by herbivory also (). High levels of 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). This means that interspecific competition and therefore the effect of niche complementarity, which contributes the majority of the observed biodiversity effect on ecosystem function in temperate and wet tropical forests (Wright et al., 2017; Poorter et al., 2015; van der Sande et al., 2017), may not be as apparent in dry woodland ecosystems. 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. 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. This potential mismatch in the contribution of different mechanisms to the BEFR between dry tropical woodlands and other forested ecosystems demands further investigation.

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). A severe lack of study in dry tropical ecosystems, especially given the potential mismatch in BEFR mechanism described above, suggests that a focus on these ecosystems could greatly strengthen our understanding of a general BEFR and its environmental determinants.

Savannas and woodlands are the dominant vegetation type across the southern African region, spanning >4 million km^2 (Ryan et al., 2016) (Figure 1). The carbon stored in this vegetation 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 vegetation, resulting in a diverse range of savanna and 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 savannas and 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.

A small number of studies in southern African savannas and 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). However, 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. 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 geographic and environmental gradients to be able to infer a truly regional scale relationship between diversity and biomass.

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 via 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 across southern African savannas and woodlands, using inventory plots which span environmental and biogeographical gradients (Figure 1). We compared the relative effects of tree species biodiversity with that of environmental factors known to affect ecosystem productivity and biomass accumulation, namely water availability, energy input and soil fertility. We also investigated the potential moderating 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 and assess the generality of our results. We used Structural Equation Modelling (SEM) and path analysis as a preferred method to simultaneously account for environmental and biotic factors, which may interact their effect on ecosystem structure and therefore biomass. Initially, we made three hypotheses: (1) water availability 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, and (3) tree species diversity will increase tree structural diversity, which will provide an indirect path by which tree diversity increases woody biomass.

Materials and methods

Study location

The study used 1767 woodland monitoring plots from the larger SEOSAW network (SEOSAW, 2019) located across 10 countries within southern Africa in so-called miombo woodlands (Figure 1, ?). The study region spans a precipitation gradient from $\sim 460 \text{ mm y}^{-1}$ in southern Mozambique and southern Zimbabwe to $\sim 1700 \text{ mm y}^{-1}$ 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 ?, 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).

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 93,242 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.

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

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

201 m resolution, taking the grid cell value for each plot (Hengl et al., 2017). We extracted Cation
 202 Exchange Capacity (CEC), percentage soil organic carbon by volume (Org. C %), and percentage
 203 soil sand content by volume (Sand %). These data are a modelled product derived from various
 204 remotely sensed and directly measured data sources.

205 Data analysis

206 Estimated tree species richness was calculated for each plot using `ChaoRichness()` from the `iNEXT`
 207 package in R (Hsieh et al., 2016). This procedure extrapolates a species rarefaction curve to its
 208 predicted asymptote and uses this value as its estimated species richness value. Extrapolated species
 209 richness accounts for variation in plot size (0.1-10 ha) and therefore sampling effort among plots.
 210 Larger plots will tend to encompass more individuals, and therefore more species (Dengler, 2009).
 211 To measure tree species abundance evenness, the Shannon Equitability index ($E_{H'}$) (Smith and
 212 Wilson, 1996) (Equation 2) was calculated:

$$E_{H'} = \frac{H'_e}{\ln S} \quad (2)$$

213 Where H'_e is an estimation of the Shannon diversity index of trees by extrapolation of the observed
 214 Shannon diversity index (H') to its asymptote via Hill numbers using the `ChaoShannon()` function
 215 from the `iNEXT` package in R (Hsieh et al., 2016), and S is the extrapolated tree species richness in
 216 the plot, using the `ChaoRichness()` function. We calculated tree structural diversity for each plot
 217 by calculating the coefficient of variation of DBH (DBH CV) and tree height (Height CV).

218 Vegetation clusters

219 Plots were assigned to vegetation type groups based on tree species composition. Groups were
 220 identified in Fayolle et al. (2018) in an Africa wide analysis of floristic units using plot data in
 221 savannas and woodlands with tree species diversity and relative abundance data. Groups were
 222 identified using unconstrained correspondence analysis and ordination, followed by clustering based
 223 on dominant ordination axes. Plot data used in this study occurred in four vegetation type groups.
 224 See Table 1 for a description of each vegetation cluster and Figure 1 for the spatial distribution of
 225 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)
<i>Marginal miombo</i>	<i>Julbernadia</i> spp.	<i>Diplorhynchus condylocarpon</i>	688	11(11.2)	152(135.2)	32.9(30.57)
	<i>Brachystegia spiciformis</i>	<i>Burkea africana</i>				
	<i>Baikiaea plurijuga</i>	<i>Pseudolachnostylis maprouneifolia</i>				
<i>Core miombo</i>	<i>Julbernadia</i> spp.	<i>Julbernardia paniculata</i>	754	18(17.5)	193(174.1)	44.8(41.43)
	<i>Brachystegia</i> spp.	<i>Isobertia angolensis</i>				
	<i>Isobertia angolensis</i>	<i>Brachystegia longifolia</i>				
Baikiaea	<i>Spirostachys africana</i>	<i>Baikiaea plurijuga</i>	226	10(10)	162(152)	45.3(47.36)
	<i>Senegalia</i> spp.	<i>Senegalia ataxacantha</i>				
	<i>Euclea racemosa</i>	<i>Combretum collinum</i>				
Mopane	<i>Colophospermum mopane</i>	<i>Colophospermum mopane</i>	99	7(8.2)	190(155.7)	41.5(36.93)
		<i>Combretum</i> spp.				

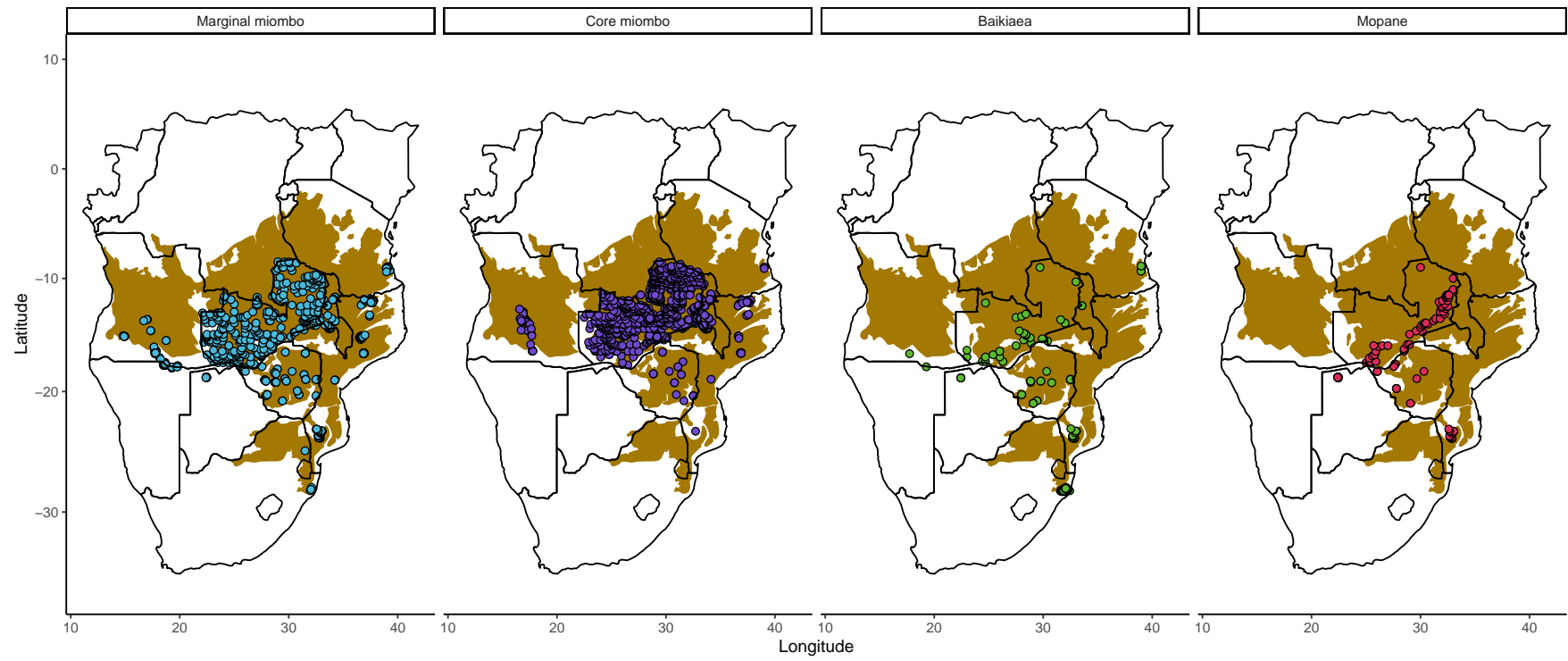


Figure 1: The locations of the 1767 plots used in this study, as points by geographic location with respect to the distribution of miombo woodland vegetation according to ?. Each panel shows plots categorized by their vegetation type as defined by the vegetation types in [Table 1](#).

226 Structural Equation Modelling

227 Structural Equation Models (SEM) investigated the determinants of AGB. All SEMs were con-
 228 structed and analysed in the `lavaan` package (Rosseel, 2012) in R version 3.6.0 (R Core Team,
 229 2019). SEM was used because of its suitability for modelling complex causal interactions in ecologi-
 230 cal systems (Lee, 2007). A key aspect to our decision to use SEMs is that they can explicitly model
 231 and partition variance to indirect effects, which is challenging in standard multiple regression. Using
 232 SEMs also allowed us to describe theoretical latent constructs which have been suggested to act
 233 upon diversity and biomass/productivity in previous studies despite these factors not having single
 234 observable measures in our dataset. Structural equation modelling is also necessary to properly
 235 account for potential feedback mechanisms between aspects of climate and tree species diversity,
 236 which could otherwise increase the chances of Type I error and wrongly attribute inference due to
 237 covariance of explanatory variables when using conventional regression analyses (Nachtigall et al.,
 238 2003).

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

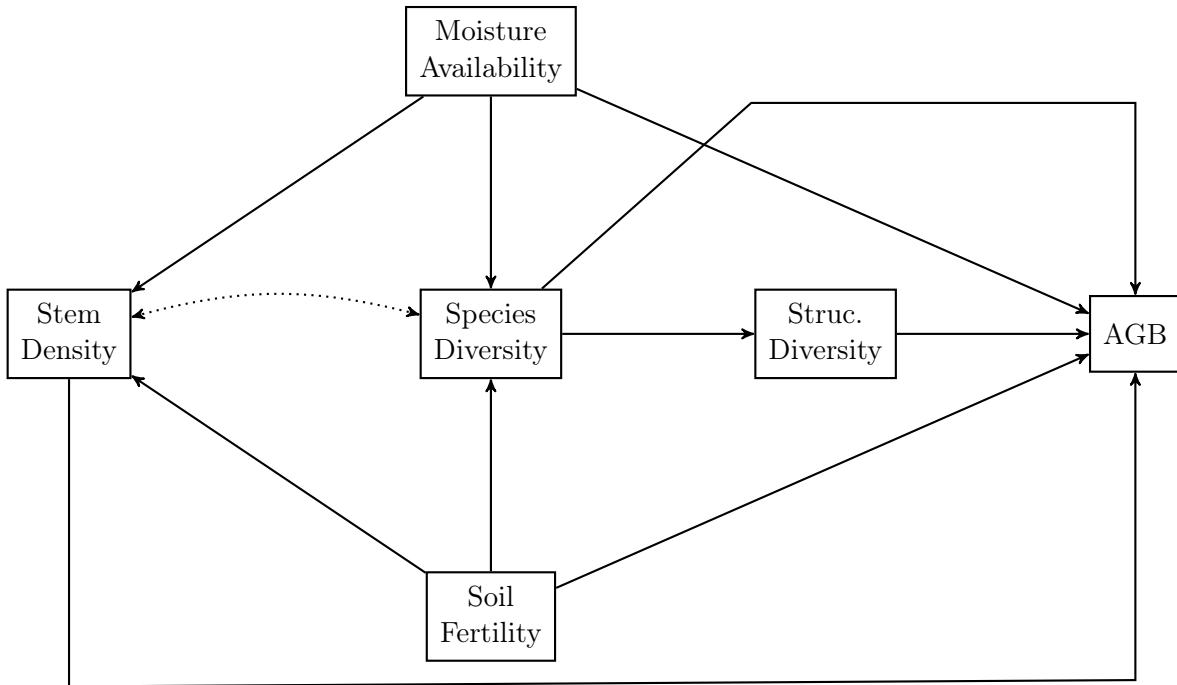


Figure 2: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural diversity, tree stem density, and AGB. Hypothesised paths of causation are depicted as arrows from predictor to response. Correlations are depicted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

241 Observed variables were transformed to achieve normality where necessary and standardised to Z-
 242 scores prior to analysis (Appendix C). Standardisation put each latent variable on the same scale,
 243 with a mean of zero and a standard deviation of one. Standardisation allows path regression coef-
 244 ficients to be easily compared between paths in the same model to assess their relative effect size,
 245 and eliminates confusion in model interpretation arising from the observed variables being on dif-
 246 ferent scales (Beaujean, 2014). Standardisation also controls for variables with different orders of
 247 magnitude which could otherwise prevent adequate model estimation from the covariance matrix
 248 in `lavaan`. To ensure that observed variables within a latent variable had consistent directions of
 249 influence, some observed variables were reversed by multiplying by -1. For example, soil fertility
 250 is expected to decrease as soil sand content increases, so soil percentage sand content was reversed
 251 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.

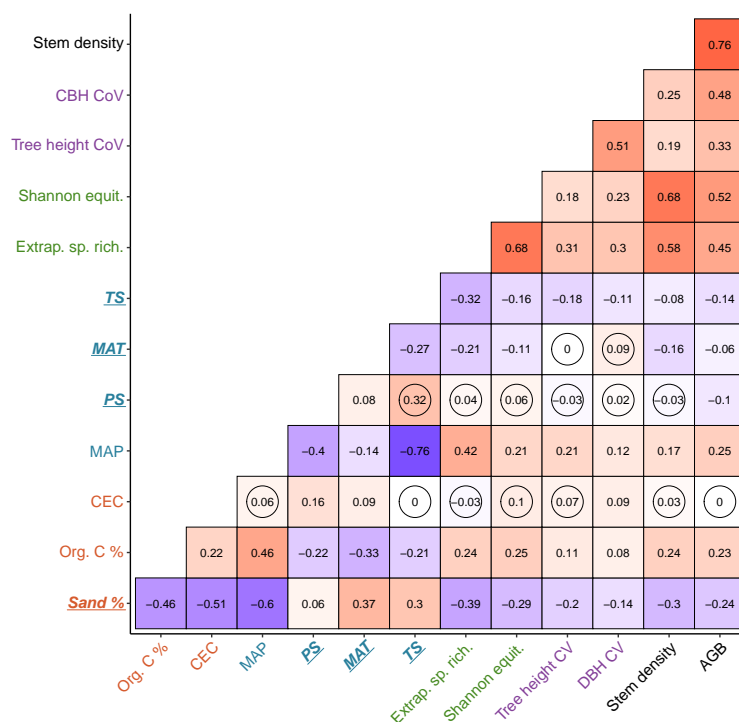


Figure 3: Correlogram of standardised observed variables used in the SEMs, with Pearson correlation coefficients (r) coloured according to sign (+ve red, -ve blue) and shaded by strength of correlation. Variables in bold and underlined on the axis labels were later reversed for SEMs to maintain positive 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 ($r = 0.77$, $p < 0.01$). 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 ($r = 0.22$, $p < 0.01$), and a weak negative correlation between the seasonality of precipitation and AGB ($r = -0.11$, $p < 0.01$). MAT and temperature seasonality (TS) negatively correlated weakly with AGB (MAT: $r = -0.09$, $p < 0.01$; TS: $r = -0.14$, $p < 0.01$). As expected, there was a negative correlation between soil sand content and AGB ($r = -0.27$, $p < 0.01$), and a positive correlation between soil organic carbon and AGB ($r = 0.25$, $p < 0.01$).

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 ($r = 0.09$, $p < 0.01$). MAT had weak correlations with tree species and structural diversity variables. Tree species diversity variables had clear positive correlations with stem density (Species richness: $r = 0.57$, $p < 0.01$; Shannon equitability: $r = 0.48$, $p < 0.01$).

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 ($\beta = 0.11 \pm 0.039$, $p < 0.01$), 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 0.69. The strongest direct effect on AGB was from stem density ($\beta = 0.74 \pm 0.033$, $p < 0.01$).

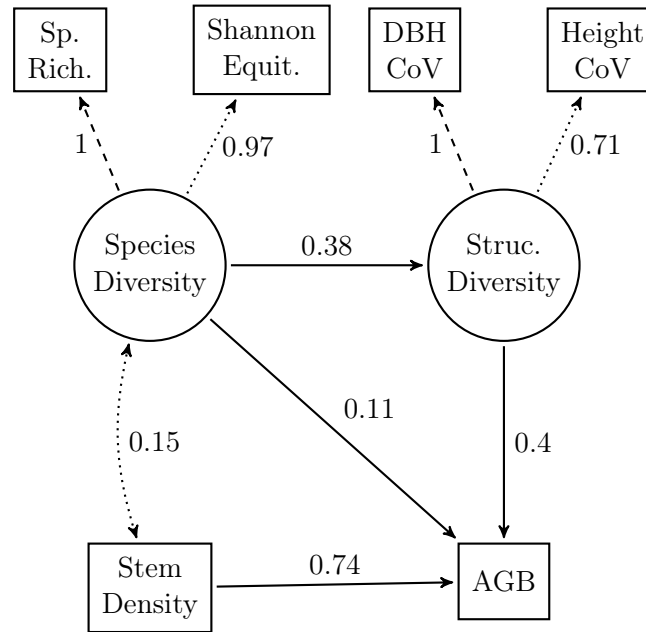


Figure 4: Path diagram with regression coefficients for the tree diversity SEM, including plots from all vegetation clusters. Latent variables are circles while observed variables are rectangles. Standardised path coefficients are solid arrows pointing from predictor to response with the effect size 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.

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 ($\beta = 0.19 \pm 0.154$, $p = 0.22$), 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 ($R^2 = 0.71$) and lowest in the Core miombo ($R^2 = 0.68$).

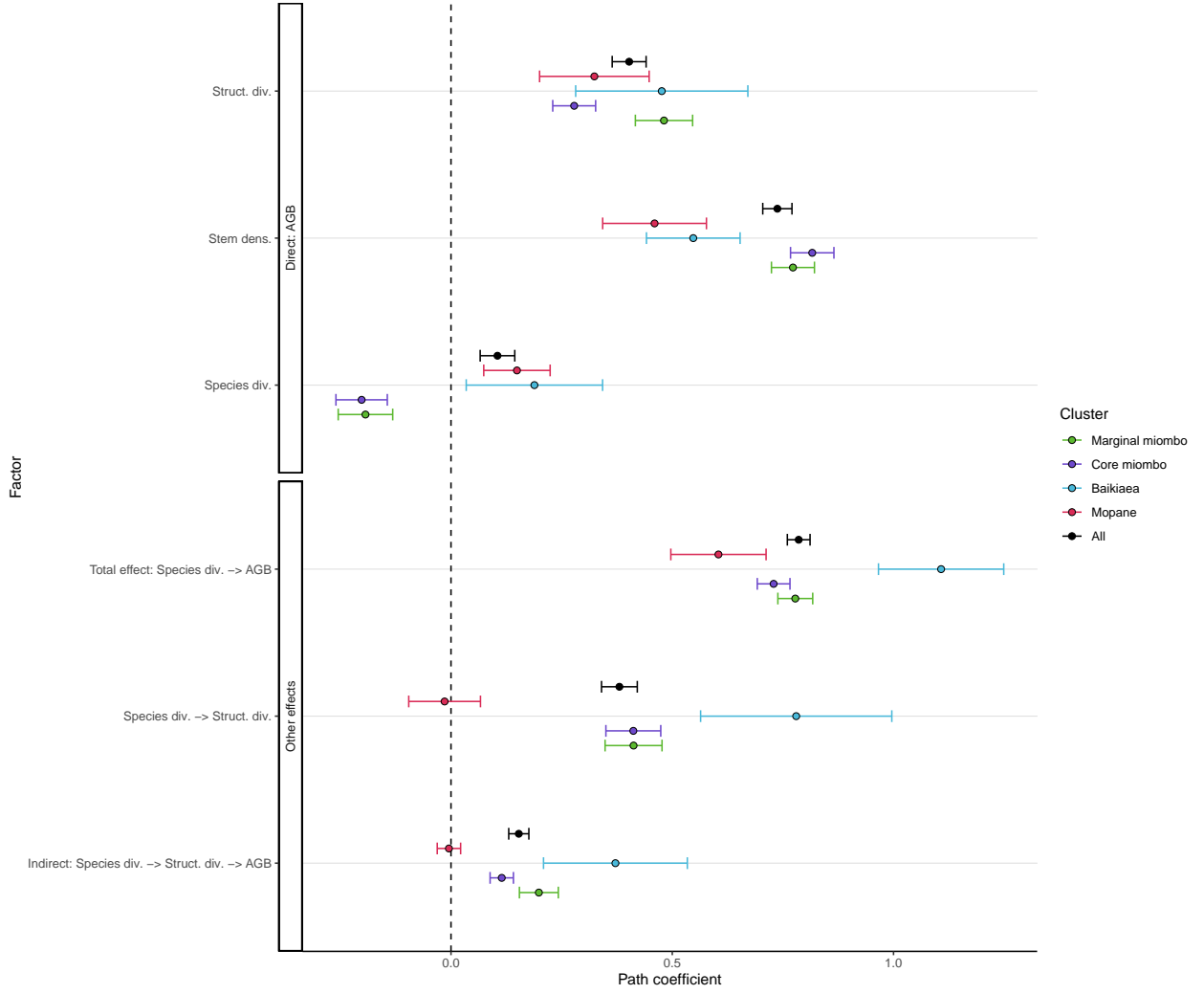


Figure 5: Unstandardised path coefficients for the effects of tree diversity on AGB, mediated by the effect of stand structural diversity. Path coefficients are ± 1 standard error. Path coefficients where the standard error does not overlap zero are considered to be significant effects.

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	44.750	6	0.966	0.916	-3714.000	0.110	0.710
Core miombo	668	57.210	6	0.962	0.904	-4224.000	0.100	0.680
Baikiaea	47	5.860	6	0.998	0.994	-324.600	0.030	0.720
Mopane	84	9.420	6	0.971	0.927	-591.600	0.080	0.450
All	1324	78.430	6	0.975	0.936	-9119.000	0.090	0.690

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 892 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.

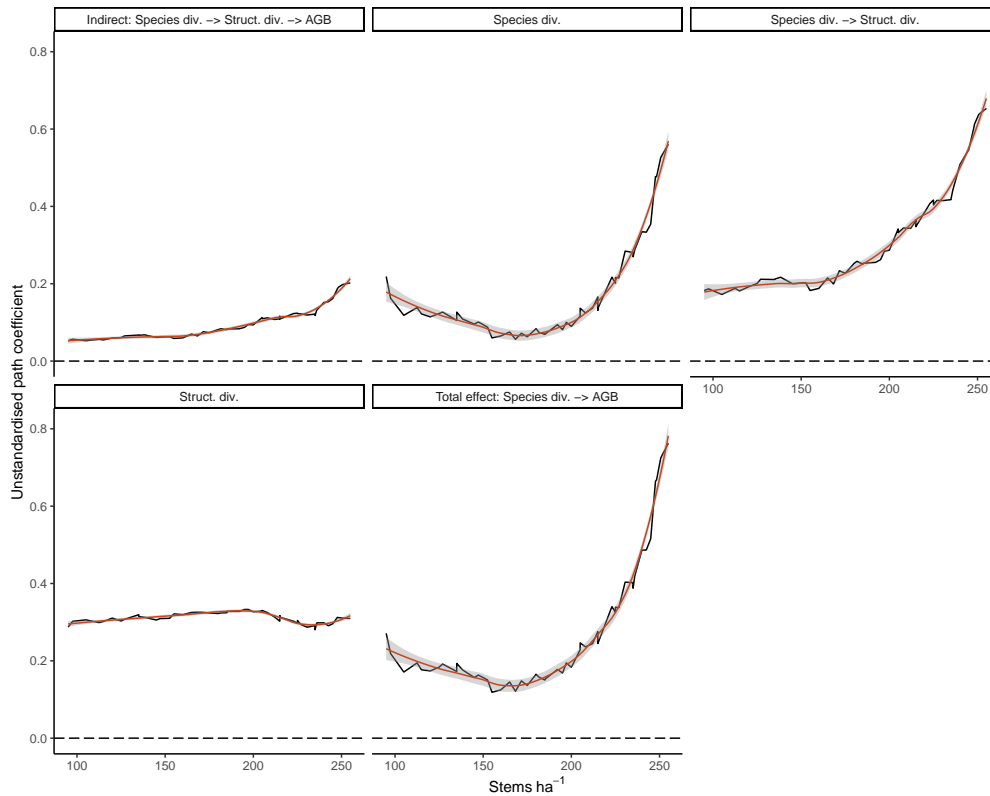


Figure 6: Line plots showing the variation in path coefficients in the SEM, using datasets with different mean stem density. Smoothed lines are loess curves with standard error shaded bars.

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: $\beta = -0.01 \pm 0.005$, $p < 0.01$, soil: $\beta = -0.04 \pm 0.012$, $p < 0.01$). 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 = 0.163, R^2 of AGB = 0.7.

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 ($\beta = 0.16 \pm 0.023$, $p < 0.01$). The total effect of species diversity on AGB was positive ($\beta = 0.64 \pm 0.041$, $p < 0.01$).

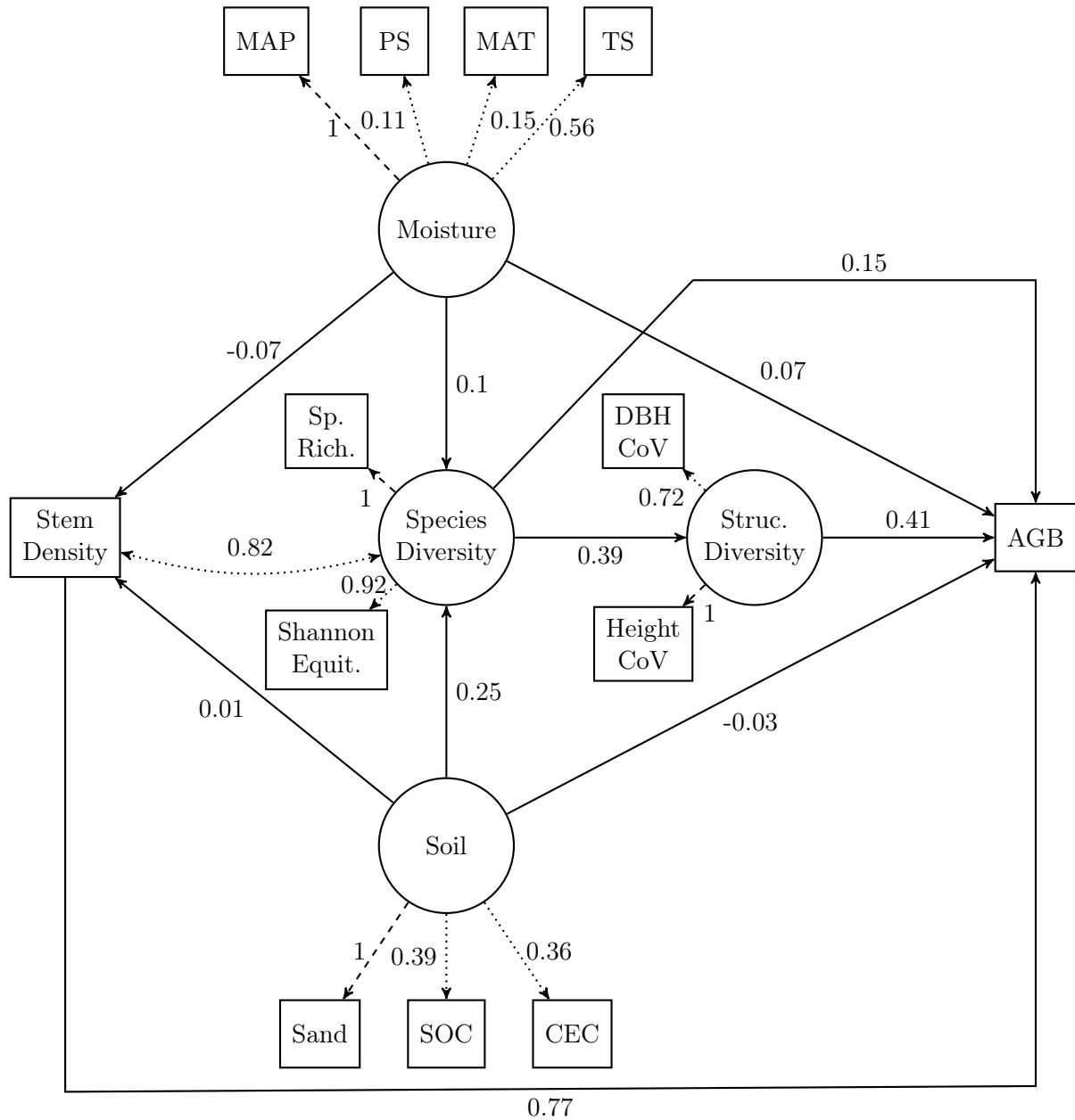


Figure 7: Path diagram with regression coefficients for the SEM incorporating environmental covariates and tree species and structural diversity across all five vegetation types. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are 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.

Discussion

In this study, we assessed the importance of [a] tree species richness, [b] tree structural diversity, [c] resource availability, i.e. 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 1767 woodland survey plots. Using latent variables and Structural Equation Modelling (SEM), we found support for a general positive relationship between tree species diversity and AGB, with an indirect influence of tree species diversity on 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 69% of the variation in AGB across the region, while models for specific vegetation types showed even greater explanatory power (Table 2). The strongest effect on AGB was that of stem density. Interestingly, when the effects of 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 or energy availability or soil fertility, on AGB (H_3).

Inter-related effects of tree species and structural diversity on AGB

We found a consistent positive 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 and evenness causes higher woody AGB. This finding is in agreement with many other studies across different ecosystems and biomes, supporting that there is a generalisable positive association between diversity and ecosystem functionality (Liang et al., 2016; Cardinale et al., 2009). Our study provides a novel dissection of the mechanisms underlying this relationship, particularly in the context of a disturbance-structured and poorly studied ecological system, southern African woodlands and savannas.

Much of the total variation in AGB was driven by variation in 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. The opposite is also plausible however, with increased stem density causing higher species richness through an increased probability of encountering new species. 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.

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 structural diversity of trees, i.e. greater variation in DBH and height. 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. Although we did not measure it here, we would also expect that tree species diversity allows for a greater range of tree functional forms (), i.e. wider variation in canopy shape and overall growth form; bushy understorey vs. emergent canopy, for example. 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). Indeed, our finding that the strength of the effect of tree diversity on AGB increases with stem density supports this. 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).

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} .

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 a greater stem density per unit area, greater productivity per unit area and additionally greater tree species diversity due to niche partitioning (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., 2019a,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.

We expected a positive effect of soil fertility on AGB, but found no evidence of this in our models. We measured soil fertility using the observed variables of soil organic carbon content, sand particle content and Cation Exchange Capacity (CEC). In wet tropical forests a clear relationship has been observed between these variables and AGB (??).

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, incorporating the indirect effect via structural diversity, remained positive in these vegetation types. Compared to Baikiaea and Mopane woodlands, miombo 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 often 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. Alternatively, this

small negative direct effect may be an artefact of particularly noisy data, especially given that the overall effect of diversity on AGB is positive.

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, but the addition of new species appears to make a larger difference to the AGB of these plots than in mopane woodlands. 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.

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, inferring that models of regional and global biodiversity-ecosystem function relationships could benefit from including vegetation type terms and the structural properties of those vegetation types, such as structural diversity and stem density. 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.

Southern African woodlands are relied heavily upon for their ecosystem service provision, which is itself affected by ecosystem functionality. Resource extraction by humans in southern Africa is directly influencing biodiversity via selective tree-felling for timber, among other forest products. Our study shows that biodiversity change through human actions will have the greatest negative impact on ecosystem function in areas of high stem density and Baikiaea woodlands, which are predominantly targeted for tree felling. This raises concerns about the robustness of these ecosystems to further resource extraction and biodiversity loss.

References

- Ali, A., Lin, S., He, J., Kong, F., Yu, J. and Jiang, H. (2019a), ‘Big-sized trees overrule remaining trees’ attributes and species richness as determinants of aboveground biomass in tropical forests’, *Global Change Biology* **25**, 2810–2824.
- Ali, A., Lin, S., He, J., Kong, F., Yu, J. and Jiang, H. (2019b), ‘Climate and soils determine

aboveground biomass indirectly via species diversity and stand structural complexity in tropical forests', *Forest Ecology and Management* **432**, 823–831.

Barthlott, W., Mutke, J., Rafiqpoor, D., Kier, G. and Kreft, H. (2005), 'Global centers of vascular plant diversity', *Nova Acta Leopoldina* **92**(342), 61–83.

Beaujean, A. A. (2014), *Latent variable modeling using R*, Routledge, New York NY, USA.

Byers, B. (2001), *Conserving the miombo ecoregion*, WWF Southern Africa, Harare, Zimbabwe.

Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M., Jouseau, C., Cadotte, M. W., Carroll, I. T., Weis, J. J., Hector, A. and Loreau, M. (2009), 'Effects of biodiversity on the functioning of ecosystems: a summary of 164 experimental manipulations of species richness', *Ecology* **90**(3), 854–854.

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.

Charles-Dominique, T., Midgley, G. F., Tomlinson, K. W. and Bond, W. J. (2018), 'Steal the light: shade vs fire adapted vegetation in forest-savanna mosaics', *New Phytologist* **218**, 1419–1429.

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-Yrizar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Péliissier, 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.

Chidumayo, E. N. (2013), 'Forest degradation and recovery in a miombo woodland landscape in Zambia: 22 years of observations on permanent sample plots', *Forest Ecology and Management* **291**, 154–161.

Chisholm, R. A., Muller-Landau, H. C., Rahman, K. A., Bebbler, D. P., Bin, Y., Bohlman, S. A., Bourg, N. A., Brinks, J., Bunyavejchewin, S., Butt, N., Cao, H., Cao, M., Cárdenas, D., Chang, L., Chiang, J., Chuyong, G., Condit, R., Dattaraja, H. S., Davies, S., Duque, A., Fletcher, C., Gunatilleke, N., Gunatilleke, S., Hao, Z., Harrison, R. D., Howe, R., Hsieh, C., Hubbell, S. P., Itoh, A., Kenfack, D., Kiratiprayoon, S., Larson, A. J., Lian, J., Lin, D., Liu, H., Lutz, J. A., Ma, K., Malhi, Y., McMahon, S., McShea, W., Meegaskumbura, M., Razman, S. M., Morecroft, M. D., Nytech, C. J., Oliveira, A., Parker, G. G., Pulla, S., Punchi-Manage, R., Romero-Saltos, H., Sang, W., Schurman, J., Su, S., Sukumar, R., Sun, I., Suresh, H. S., Tan, S., Thomas, D., Thomas, S., Thompson, J., Valencia, R., Wolf, A., Yap, S., Ye, W., Yuan, Z. and Zimmermann, J. K. (2013), 'Scale-dependent relationships between tree species richness and ecosystem function in forests', *Journal of Ecology* **101**, 1214–1224.

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.

Copernicus Climate Change Service (2017), *ERA5: Fifth generation of ECMWF atmospheric re-analyses of the global climate*, Copernicus Climate Change Service Climate Data Store (CDS). Accessed: 2019-09-03.

- Dengler, J. (2009), ‘Which function describes the species-area relationship best? a review and empirical evaluation’, *Journal of Biogeography* **36**, 728–744.
- Dufrêne, M. and Legendre, P. (1997), ‘Species assemblage and indicator species: the need for a flexible asymmetrical approach’, *Ecological Monographs* **67**(3), 345–366.
- 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., Finkch, 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.
- 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.
- Grime, J. P. (1979), *Plant strategies and vegetation processes*, John Wiley and Sons, Chichester, UK.
- Hardiman, B. S., Bohrer, G., Gough, C. M., Vogel, C. S. and Curtis, P. S. (2011), ‘The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest’, *Ecology* **92**(9), 1818–1827.
- Hector, A. and Bagchi, R. (2007), ‘Biodiversity and ecosystem multifunctionality’, *Nature* **448**, 188–190.
- 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.
- Hill, M. J. and Hanan, N. P., eds (2011), *Ecosystem function in savannas*, CRC Press, Boca Raton FL, USA.
- 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.
- Hooper, D., Coughlan, J. and Mullen, M. R. (2008), ‘Structural equation modelling: guidelines for determining model fit’, *Electronic Journal of Business Research Methods* **6**(1), 53–60.
- Houghton, R. A., Hall, F. and Goetz, S. J. (2009), ‘Importance of biomass in the global carbon cycle’, *Journal of Geophysical Research* **114**, 1–13.
- 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.
- Keddy, P. A. (1990), Competitive hierarchies and centrifugal organization in plant communities, in J. B. Grace and D. Tilman, eds, ‘Perspectives on plant competition’, Academic Press, San Diego CA, USA, pp. 266–287.

- Kraaij, T. and Ward, D. (2006), 'Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa', *Plant Ecology* **186**, 235–246.
- Kunz, M., Fichtner, A., Hardtle, W., Raunonen, P., Bruelheide, H. and von Oheimb, G. (2019), 'Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees', *Ecology Letters* pp. 1–11.
- LaRue, E. A., Hardiman, B. S., Elliott, J. M. and Fei, S. (2019), 'Structural diversity as a predictor of ecosystem function', *Environmental Research Letters* **14**, 114011.
- Lasky, J. R., Uriarte, M., Boukili, V. K., Erickson, D. L., Kress, W. J. and Chazdon, R. L. (2014), 'The relationship between tree biodiversity and biomass dynamic changes with tropical forest succession', *Ecology Letters* **17**, 1158–1167.
- 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.
- Linder, H. P. (2014), 'The evolution of African plant diversity', *Frontiers in Ecology and Evolution* **2**(38), 1–14.
- Mayaux, P., Eva, H., Brink, A., Achard, F. and Belward, A. (2008), Remote sensing of land-cover and land-use dynamics, in 'Earth Observation of Global Change: The Role of Satellite Remote Sensing in Monitoring the Global Environment', Springer-Verlag, Berlin, Germany, pp. 85–108.
- 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 south-eastern Tanzania', *Ecosystems* **21**, 740–754.
- 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.
- Muscolo, A., Bagnato, S., Sidari, M. and Mercurio, R. (2014), 'A review of the roles of forest canopy gaps', *Journal of Forestry Research* **25**(4), 725–736.
- Mutowo, G. and Murwira, A. (2012), 'Relationship between remotely sensed variables and tree species diversity in savanna woodlands of southern Africa', *International Journal of Remote Sensing* **33**(20), 6378–6402.
- Nachtigall, C., Kroehne, U., Funke, F. and Steyer, R. (2003), '(Why) should we use SEM? pros and cons of structural equation modeling', *Methods of Psychological Research* **8**(2), 1–22.
- Otto, W. (2013), *Data analysis in vegetation ecology*, Wiley-Blackwell, Chichester, UK.

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

642 Pasari, J. R., Levi, T., Zavaleta, E. S. and Tilman, D. (2013), ‘Several scales of biodiversity affect
643 ecosystem multifunctionality’, *Proceedings of the National Academy of Sciences* **110**(25), 10219–
644 10222.

645 Poorter, L., van de Sande, M. T., Thompson, J., Arets, E. J. M. M., Alarcón, A., Álvarez-Sánchez,
646 J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G., Boit, A., Bongers, F., Carvalho, F. A.,
647 Casanoves, F., Cornejo-Tenorio, G., Costa, F. R. C., de Castilho, C. V., Duivenvoorden, J. F.,
648 Dutrieux, L. P., Enquist, B. J., Fernández-Méndez, F., Finegan, B., Gormley, L. H. L., Healey,
649 J. R., Hoosbeek, M. R., Ibarra-Manríquez, G., Junqueira, A. B., Levis, C., Licona, J. C., Lisboa,
650 L. S., Magnusson, W. E., Martínez-Ramos, M., Martínez-Yrizar, A., Martorano, L. G., Maskell,
651 L. C., Mazzei, L., Meave, J. A., Mora, F., Muñoz, R., Nytch, C., Pansonato, M. P., Parr, T. W.,
652 Paz, H., Pérez-García, E. A., Rentería, L. Y., Rodríguez-Velázquez, J., Rozendaal, D. M. A.,
653 Ruschel, A. R., Sakschewski, B., Salgado-Negret, B., Schiatti, J., Simões, M., Sinclair, F. L.,
654 Souza, P. F., Souza, F. C., Stropp, J., ter Steege, H., Swenson, N. G., Thonicke, K., Toledo, M.,
655 Uriarte, M., van der Hout, P., Walker, P., Zamora, N. and Peña-Claros, M. (2015), ‘Diversity
656 enhances carbon storage in tropical forests’, *Global Ecology and Biogeography* **24**, 1314–1328.

657 Poorter, L., van der Sande, M. T., Arets, E. J. M. M., Ascarrunz, N., Enquist, B. J., Finegan, B.,
658 Licona, J. C., Martínez-Ramos, M., Mazzei, L., Meave, J. A., Muñoz, R., Nytch, C. J., de Oliveira,
659 A. A., Pérez-García, E. A., Prado-Junior, J., Rodríguez-Velázquez, J., Ruschel, A. R., Salgado-
660 Negret, B., Schiavini, I., Swenson, N. G., Tenorio, E. A., Thompson, J., Toledo, M., Uriarte,
661 M., van der Hout, P., Zimmerman, J. K. and Peña-Claros, M. (2017), ‘Biodiversity and climate
662 determine the functioning of neotropical forests’, *Global Ecology and Biogeography* **26**, 1423–1434.

663 Prado-Junior, J. A., Schiavini, I., Vale, V. S., Arantes, C. S., van der Sande, M. T., Lohbeck, M.
664 and Poorter, L. (2016), ‘Conservative species drive biomass productivity in tropical dry forests’,
665 *Journal of Ecology* **104**, 817–827.

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

668 Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E.,
669 Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C. C., Bauhus, J.,
670 Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Češko, E., Dawud, S. M., de
671 Wandeler, H., Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A., Granier, A., Grossiord,
672 C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F., Kambach, S.,
673 Kolb, S., Koricheva, J., Liebersgesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock,
674 C., Pollastrini, M., Purschke, O., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Ruiz-Benito,
675 P., Seidl, R., Selvi, F., Seiferling, I., Stenlid, J., Valladares, F., Vesterdal, L. and Baeten, L. (2017),
676 ‘Biodiversity and ecosystem functioning relations in European forests depend on environmental
677 context’, *Ecology Letters* **20**, 1414–1426.

678 Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. A., Archibald, S., Lehmann, C. E. R.,
679 Anderson, M. T., Higgins, S. I. and Sankaran, M. (2011), ‘When is a ‘forest’ a savanna, and why
680 does it matter?’, *Global Ecology and Biogeography* **20**, 653–660.

681 Roberts, D. W. (2019), *labdsv: Ordination and Multivariate Analysis for Ecology*. R package version
682 2.0-1.

683 Rosseel, Y. (2012), ‘lavaan: An R package for structural equation modeling’, *Journal of Statistical*
684 *Software* **48**(2), 1–36.

- 685 Ryan, C. M., Pritchard, R., McNicol, I., Owen, M., Fisher, J. A. and Lehmann, C. (2016), ‘Ecosystem
686 services from southern African woodlands and their future under global change’, *Philosophical
687 Transactions of the Royal Society B: Biological Sciences* **371**(1703), 1–16.
- 688 Seidel, D., Ehbrecht, M., Dorji, Y., Jambay, J., Ammer, C. and Annighöfer, P. (2019), ‘Identifying
689 architectural characteristics that determine tree structural complexity’, *Trees* **33**(3), 911–919.
- 690 Selaya, N. G. and Anten, P. R. (2008), ‘Differences in biomass allocation, light interception and
691 mechanical stability between lianas and trees in early secondary tropical forest’, *Functional Ecology*
692 **22**, 30–39.
- 693 SEOSAW (2019), ‘SEOSAW: A Socio-Ecological Observatory for Southern African Woodlands’.
694 [Online; 15-January-2019].
- 695 Shapiro, A. (1983), ‘Asymptotic distribution theory in the analysis of covariance structures (a unified
696 approach)’, *South African Statistical Journal* **17**, 33–81.
- 697 Shirima, D. D., Pfeifer, M., Platts, P. J., Totland, Ø. and Moe, S. R. (2015), ‘Interactions between
698 canopy structure and herbaceous biomass along environmental gradients in moist forest and dry
699 miombo woodland of tanzania’, *PLoS ONE* **10**(11), 1–15.
- 700 Smith, B. and Wilson, J. B. (1996), ‘A consumer’s guide to evenness indices’, *Oikos* **76**(1), 70–82.
- 701 Solbrig, O. T., Medina, E. and Silva, J. F. (1996), *Biodiversity and Savanna Ecosystem Processes*,
702 Springer-Verlag, Berlin, Germany.
- 703 Stark, S. C., Leitold, V., Wu, J. L., Hunter, M. O., de Castilho, C. V., Costa, F. R. C., McMahon,
704 S. M., Parker, G. G., Shimabukuro, M. T., Lefsky, M. A., Keller, M., Alves, L. F., Schietti,
705 J., Shimabukuro, Y. E., Brandão, D. O., Woodcock, T. K., Higuchi, N., de Camargo, P. B., de
706 Oliveira, R. C. and Saleska, S. R. (2012), ‘Amazon forest carbon dynamics predicted by profiles
707 of canopy leaf area and light environment’, *Ecology Letters* **15**, 1406–1414.
- 708 Stegen, J. C., Swenson, N. G., Enquist, B. J., White, E. P., Phillips, O. L., Jørgensen, P. M., Weiser,
709 M. D., Mendoza, A. M. and Vargas, P. N. (2011), ‘Variation in above-ground forest biomass across
710 broad climatic gradients’, *Global Ecology and Biogeography* **20**, 744–754.
- 711 Tilman, D. and Downing, J. A. (1994), ‘Biodiversity and stability in grasslands’, *Nature* **367**, 363–
712 365.
- 713 Tilman, D., Isbell, F. and Cowles, J. M. (2014), ‘Biodiversity and ecosystem functioning’, *Annual
714 Review of Ecology, Evolution, and Systematics* **45**, 471–493.
- 715 Timberlake, J., Chidumayo, E. and Sawadogo, L. (2010), Distribution and characteristics of African
716 dry forests and woodlands, in ‘The Dry Forests and Woodlands of Africa: Managing for Products
717 and Services’, EarthScan, London, United Kingdom, pp. 11–42.
- 718 Tobner, C. M., Paquette, A., Gravel, D., Reich, P. B., Williams, L. J. and Messier, C. (2016),
719 ‘Functional identity is the main driver of diversity effects in young tree communities’, *Ecology
720 Letters* **19**, 638–647.
- 721 van der Sande, M. T., Poorter, L., Kooistra, L., Balvanera, P., Thonicke, K., Thompson, J., Arets,
722 E. J. M. M., Alaniz, N. G., Jones, L., Mora, F., Mwampamba, T. H., Parr, T. and Peña-Claros,
723 M. (2017), ‘Biodiversity in species, traits, and structure determines carbon stocks and uptake in
724 tropical forests’, *Biotropica* **49**(5), 593–603.
- 725 Vilà, M., Inchausti, P., Vayreda, J., Barrantes, O., Gracia, C., Ibàñez, J. J. and Mata, T. (2005),
726 ‘Confounding factors in the observational productivity-diversity relationship in forests’, *Ecological
727 Studies* **176**, 65–86.

- 728 Wildi, O. (2017), *dave: Functions for "Data Analysis in Vegetation Ecology"*. R package version 2.0.
- 729 Wright, A. J., Wardle, W. D. A., Callaway, W. R. and Gaxiola, A. (2017), ‘The overlooked role of
730 facilitation in biodiversity experiments’, *Trends in Ecology and Evolution* **32**(5), 383–390.
- 731 Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S. L., Miller,
732 R. B., Swenson, N. G., Wiemann, M. C. and Chave, J. (2009), *Global wood density database*.
733 <http://hdl.handle.net/10255/dryad.235>.

734 Appendix 1 - Data cleaning process

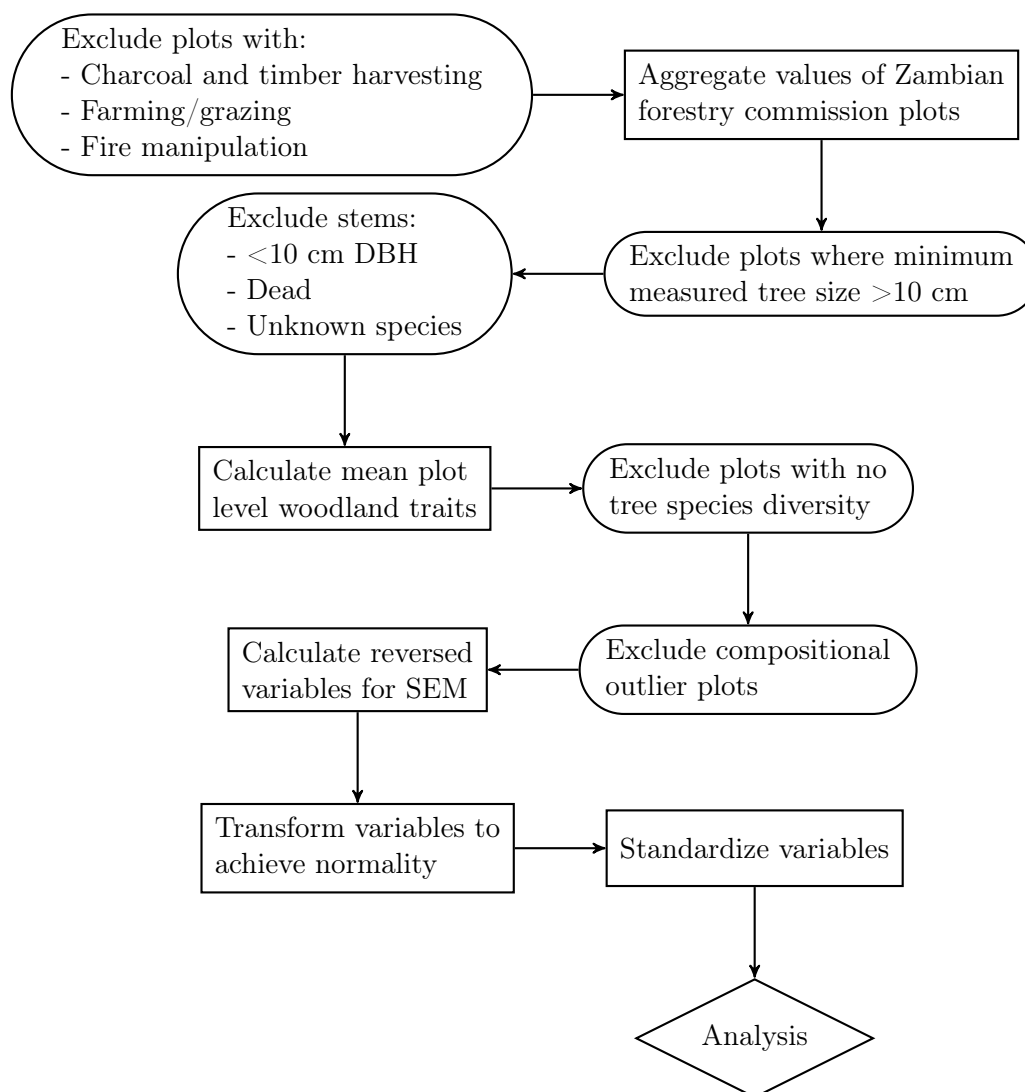


Figure 8: Flow diagram of the data filtering and cleaning process prior to analysis. Rounded boxes indicate filtering events while regular boxes indicate calculation events.

735 Appendix 2 - Estimation of DBH via tree taper

```

736 737 1 ##' @title Stem diameter Point Of Measurement (POM) adjustment
738 2 ##' @description Function to estimate stem diameter at 1.3 given measurements
739 3 ##' at other POMs.
740 4 ##' @author Casey M. Ryan
741 5 ##' @return d130, the estimated diameter at a POM of 1.3 m (in cm).
742 6 ##' @param d_in the diameter measured at the POM (in cm)
743 7 ##' @param POM the height of the POM (in m)
744 8 ##' @details The adjustment is based on a tree taper model developed as part of
745 9 ##' the ACES project (Abrupt Changes in Ecosystem Services
746 0 ##' https://miomboaces.wordpress.com/), using data from the miombo of Niassa.
747 1 ##' The model is a cubic polynomial, with three equations for different sized
748 2 ##' stems.
749 3 ##' @section Warning: The model should not be used for POMs above 1.7 m.
750 4 ##' Extrapolating beyond the training data will give nonsense.
751 5 ##' Thus, POMs >1.7 m are not adjusted.
752 6 ##' @examples
753 7 ##' POMadj(10, 0.3)
  
```

```

7548 ##' POMadj(1, 0.3) # d130 is negative, i.e. the stem probably wasn't 1.3 m tall
7559 ##' POMadj(50, 1.9) # generates warning, as outside calibration data range
7560 ##' \dontrun{
7571 ##'   POMadj(50, 0) # zero or -ve POM is outside range, or nonsense
7582 ##' }
7593 POMadj <- function(d_in, POM) {
7604   stopifnot(is.numeric(d_in),
7615             is.numeric(POM),
7626             POM >= 0,
7637             sum(is.na(POM))==0,
7648             length(POM) == length(d_in))
7659   if (any(POM > 1.7))
7660     warning("POMs >1.7 m are outside the calibration data, no correction applied")
7671
7682   NAS <- is.na(d_in)
7693   d_in_clean <- d_in[!NAS]
7704   POM_clean <- POM[!NAS]
7715   # define the size class edges:
7726   edges <- c(5.0, 15.8, 26.6, 37.4)
7737   sm <- d_in_clean < edges[2]
7748   med <- d_in_clean >= edges[2] & d_in_clean < edges[3]
7759   lg <- d_in_clean >= edges[3]
7760
7771   # compute apredictions for delta_d, for all size classes
7782   delta_d <- data.frame(
7793     # if small:
7804     small = 3.4678+-5.2428 *
7815             POM_clean + 2.9401 *
7826             POM_clean^2+-0.7141 *
7837             POM_clean^3,
7848     # if med
7859     med = 4.918+-8.819 *
7860           POM_clean + 6.367 *
7871           POM_clean^2+-1.871 *
7882           POM_clean^3,
7893     # if large
7904     large = 9.474+-18.257 *
7915            POM_clean + 12.873 *
7926            POM_clean^2+-3.325 *
7937            POM_clean^3
7948   )
7959   # index into the right size class
7960   dd <- NA_real_
7971   dd[sm] <- delta_d$small[sm]
7982   dd[med] <- delta_d$med[med]
7993   dd[lg] <- delta_d$large[lg]
8004   dd[POM_clean > 1.7] <- 0 # to avoid extrapolation mess
8015
8026   # add NAs back in
8037   d130 <- NA
8048   d130[NAS] <- NA
8059   d130[!NAS] <- d_in_clean - dd
8060
8071   if (any(d130[!NAS] < 0))
8082     warning("Negative d130 estimated, repaced with NA")
8093   d130[d130 <= 0 & !is.na(d130)] <- NA
8104   return(d130)
8115 }
812

```

813 Appendix 3 - Frequency distribution of observed variables

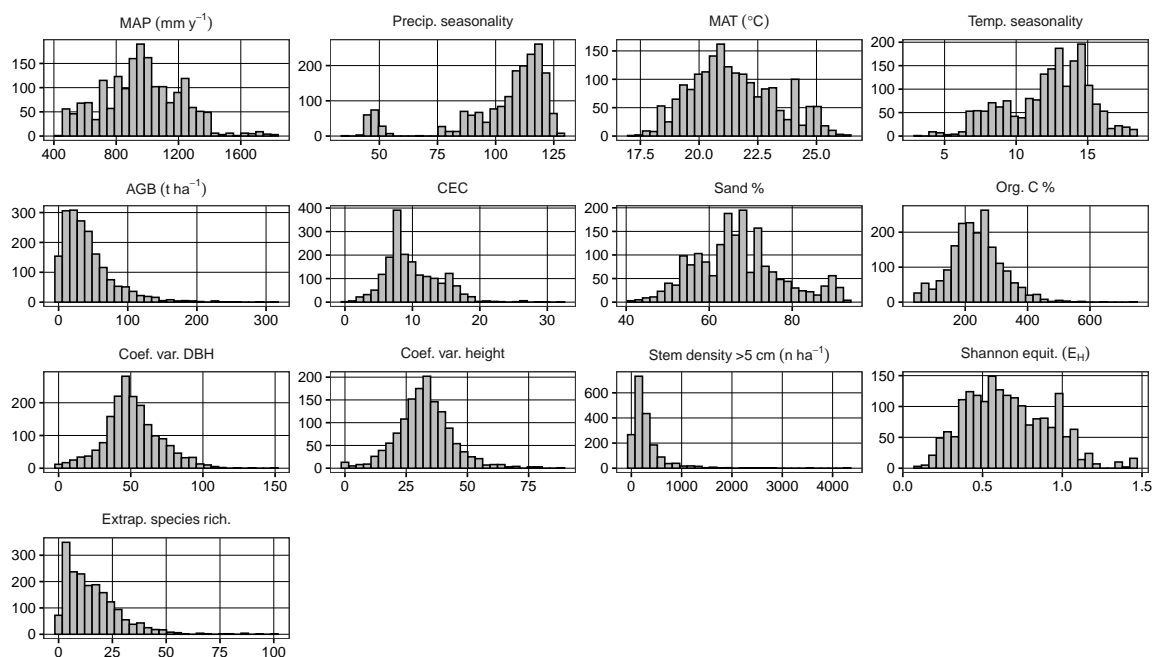


Figure 9: Histograms of raw untransformed observed variables used in final analyses.

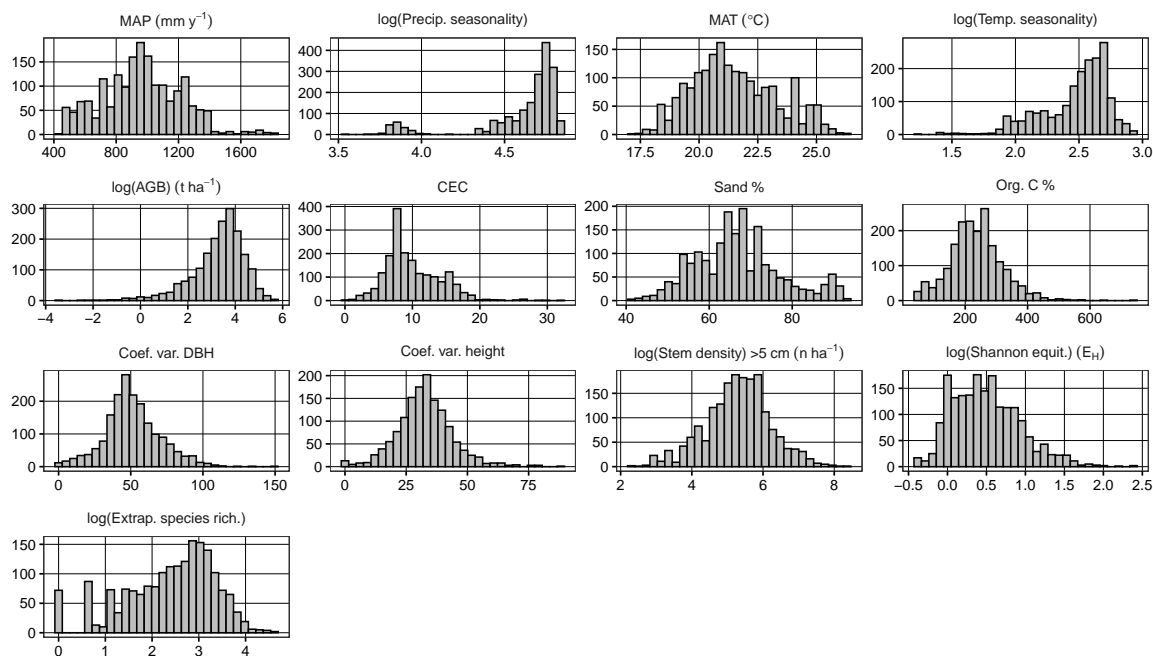


Figure 10: Histograms of observed variables transformed to achieve a normal frequency distribution.

814 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	1767	p < 0.01
Sand %	CEC	-0.560	-0.600	-0.530	1767	p < 0.01
Sand %	MAP	-0.500	-0.530	-0.460	1767	p < 0.01
Sand %	PS	0.320	0.280	0.360	1767	p < 0.01
Sand %	MAT	0.290	0.240	0.330	1767	p < 0.01
Sand %	TS	0.230	0.180	0.270	1767	p < 0.01
Sand %	Sp. rich.	-0.350	-0.390	-0.300	1767	p < 0.01
Sand %	Shannon equit.	-0.240	-0.280	-0.190	1767	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	1742	p < 0.01
Sand %	Stems ha	-0.270	-0.310	-0.220	1767	p < 0.01
Sand %	AGB	-0.270	-0.310	-0.220	1767	p < 0.01
Org. C %	CEC	0.300	0.250	0.340	1767	p < 0.01
Org. C %	MAP	0.450	0.410	0.490	1767	p < 0.01
Org. C %	PS	-0.300	-0.340	-0.260	1767	p < 0.01
Org. C %	MAT	-0.310	-0.350	-0.270	1767	p < 0.01
Org. C %	TS	-0.150	-0.190	-0.100	1767	p < 0.01
Org. C %	Sp. rich.	0.240	0.190	0.280	1767	p < 0.01
Org. C %	Shannon equit.	0.210	0.170	0.260	1767	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	0.140	1742	p < 0.01
Org. C %	Stems ha	0.200	0.160	0.250	1767	p < 0.01
Org. C %	AGB	0.250	0.210	0.290	1767	p < 0.01
CEC	MAP	0	-0.040	0.050	1767	p = 0.85
CEC	PS	-0.510	-0.540	-0.470	1767	p < 0.01
CEC	MAT	0.190	0.150	0.240	1767	p < 0.01
CEC	TS	0.020	-0.020	0.070	1767	p = 0.35
CEC	Sp. rich.	-0.070	-0.110	-0.020	1767	p < 0.01
CEC	Shannon equit.	0.090	0.040	0.130	1767	p < 0.01
CEC	Tree height CV	0.070	0.020	0.130	1324	p < 0.01
CEC	DBH CV	0.110	0.070	0.160	1742	p < 0.01
CEC	Stems ha	0.060	0.020	0.110	1767	p < 0.01
CEC	AGB	0.060	0.020	0.110	1767	p < 0.01
MAP	PS	-0.120	-0.170	-0.080	1767	p < 0.01
MAP	MAT	-0.100	-0.150	-0.060	1767	p < 0.01
MAP	TS	-0.690	-0.720	-0.670	1767	p < 0.01
MAP	Sp. rich.	0.390	0.350	0.430	1767	p < 0.01
MAP	Shannon equit.	0.100	0.050	0.150	1767	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	1742	p < 0.01
MAP	Stems ha	0.090	0.050	0.140	1767	p < 0.01
MAP	AGB	0.220	0.180	0.270	1767	p < 0.01
PS	MAT	-0.170	-0.210	-0.120	1767	p < 0.01
PS	TS	0.070	0.020	0.110	1767	p < 0.01
PS	Sp. rich.	0.080	0.030	0.120	1767	p < 0.01
PS	Shannon equit.	-0.050	-0.100	-0.010	1767	p < 0.05
PS	Tree height CV	-0.030	-0.090	0.020	1324	p = 0.25
PS	DBH CV	-0.070	-0.120	-0.020	1742	p < 0.01
PS	Stems ha	-0.030	-0.080	0.020	1767	p = 0.2

PS	AGB	-0.110	-0.160	-0.070	1767	p < 0.01
MAT	TS	-0.320	-0.360	-0.280	1767	p < 0.01
MAT	Sp. rich.	-0.220	-0.260	-0.180	1767	p < 0.01
MAT	Shannon equit.	-0.110	-0.150	-0.060	1767	p < 0.01
MAT	Tree height CV	0	-0.050	0.050	1324	p = 1
MAT	DBH CV	0.090	0.040	0.130	1742	p < 0.01
MAT	Stems ha	-0.120	-0.160	-0.070	1767	p < 0.01
MAT	AGB	-0.090	-0.130	-0.040	1767	p < 0.01
TS	Sp. rich.	-0.300	-0.350	-0.260	1767	p < 0.01
TS	Shannon equit.	-0.090	-0.130	-0.040	1767	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	1742	p < 0.01
TS	Stems ha	-0.090	-0.140	-0.050	1767	p < 0.01
TS	AGB	-0.140	-0.180	-0.090	1767	p < 0.01
Sp. rich.	Shannon equit.	0.540	0.500	0.570	1767	p < 0.01
Sp. rich.	Tree height CV	0.310	0.260	0.360	1324	p < 0.01
Sp. rich.	DBH CV	0.300	0.260	0.340	1742	p < 0.01
Sp. rich.	Stems ha	0.570	0.540	0.600	1767	p < 0.01
Sp. rich.	AGB	0.500	0.460	0.530	1767	p < 0.01
Shannon equit.	Tree height CV	0.180	0.130	0.230	1324	p < 0.01
Shannon equit.	DBH CV	0.210	0.170	0.260	1742	p < 0.01
Shannon equit.	Stems ha	0.480	0.440	0.520	1767	p < 0.01
Shannon equit.	AGB	0.390	0.350	0.420	1767	p < 0.01
Tree height CV	DBH CV	0.510	0.470	0.550	1324	p < 0.01
Tree height CV	Stems ha	0.190	0.140	0.250	1324	p < 0.01
Tree height CV	AGB	0.330	0.280	0.370	1324	p < 0.01
DBH CV	Stems ha	0.240	0.200	0.280	1742	p < 0.01
DBH CV	AGB	0.490	0.460	0.530	1742	p < 0.01
Stems ha	AGB	0.770	0.750	0.790	1767	p < 0.01
