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

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1 Acknowledgements

2 Biosketch

SEOSAW (A Socio-Ecological Observatory for Southern African Woodlands, https://seosaw.github.io) aims to understand the response of southern African woodlands to global change. The goal of SEOSAW is to produce novel analyses of the determinants of ecosystem structure and function for the southern Africa region, based on syntheses of plot data. Additionally the group hopes to develop infrastructure for a long-term regional plan for plot remeasurement in the southern African region. While working on a multitude of diverse projects in the dry tropics at large, all authors have a broad interest in community ecology and ecosystem assemblage in southern African woodlands.

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

Running title: Ecosystem function in southern African woodlands

3   Abstract

Aim: Positive correlations between tree ~~biodiversity~~species diversity and ecosystem function have been widely documented, but the nature of the relationship ~~in highly disturbed and ecophysiologically stressful systems is less clear~~in southern African savanna/woodlands, which experience high levels of disturbance through fire and ecophysiological stress, is less clear. In disturbed systems it is posited that high levels of disturbance may allow the presence of poor competitors, weakening the correlation between biodiversity and niche complementarity which drives ecosystem function. Here, we explore the relationship between tree species diversity and aboveground biomass across southern African savannas and woodlands, ~~with respect to~~while controlling for gradients in stocking density, resource availability, disturbance through fire, and across vegetation types 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 1235 ~~savanna and woodland~~savanna/woodland tree plots located across the southern African sub-continent ~~in which each tree >10 cm diameter was measured and identified to species level~~. We used Structural Equation Modelling with path analysis to determine the relationship between tree species diversity and aboveground woody biomass, while accounting for the interactive effects of resource availability , disturbance by fire, and stocking density.

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

Main conclusions: The study underlines the close association between tree diversity, ecosystem structure and ecosystem function of highly disturbed southern African savannas and woodlands. Our results demonstrate the importance of ~~including~~accounting for environmental conditions and vegetation type in order to accurately model a general relationship between biodiversity and ecosystem function at a regional level. Biodiversity loss, predominantly ~~by~~through human actions in southern Africa may have detrimental outcomes for ecosystem function, particularly in tree species-poor ex-Acacia woodlands, which showed the strongest biodiversity - ecosystem function relationship.

4   Introduction

In order to understand the effects of global biodiversity change, it is necessary to explore the relationship between biodiversity and ecosystem function (Tilman et al., 2014). Numerous studies have shown relationships between biodiversity and ecosystem function (e.g. Liang et al. 2016; Hooper et al. 2012; Cardinale et al. 2009). The strength and direction of the Biodiversity-Ecosystem Function (BEF) relationship varies depending on the ecosystem being studied, the ecosystem func-

tion(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 function (Liang et al., 2016). Over the past decade, many observational studies of the BEF relationship 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 conducted 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). Despite these concerted efforts, we continue to lack a nuanced, ecosystem agnostic understanding of the complex interactions between biodiversity, environment, and ecosystem function.

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~~processes 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 function invokes three main mechanisms ~~which drive~~to explain the relationship (Tilman et al., 2014): 1) niche complementarity, whereby communities with greater biodiversity fill a greater breadth of realised niche space and avoid competition due to differences in their traits; 2) selection effects, whereby communities with greater biodiversity are more likely to include a species that contributes highly to the measured ecosystem function; and 3) facilitation effects, whereby communities with greater biodiversity are more likely to include combinations of species which together increase the others' functional contribution.

Compared to ~~other forested~~forest ecosystems, dry tropical woodlands and savannas are highly structured by disturbance, mainly through fire ~~and in Africa notably by herbivory also~~and herbivory, with African savannas possessing large herbivores absent from other savannas (Sankaran et al., 2008; Levick et al., 2009). Disturbance via human activities such as timber extraction and charcoal processing is also common in African woodlands, often causing high levels of disturbance in localised areas (). High levels of disturbance by fire 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~~important in dry woodland/savanna ecosystems. Instead, stress tolerance and the functional contribution of more abundant species (selection effects) may be the predominant forces influencing ecosystem function (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~~under limiting environmental conditions such as low water availability () or high maximum temperature (). Across 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 water-limited ecosystems, facilitative effects and selection effects may be more important than niche complementarity in driving the relationship between species diversity and ecosystem function, as competition diminishes in ecosystems where environmental stress limits individual species reaching the bounds of their fundamental niche space, thus reducing the competition which drives niche complementarity effects. This potential mismatch in the contribution of different mechanisms to the BEF relationship between dry tropical woodlands and other forested ecosystems demands further investigation ~~in order to characterise~~if we are to derive a generalisable BEF relationship.

The representation of dry tropical ecosystems in the BEF relationship literature is poor compared to other ecosystems. Clarke et al. (2017) conducted a meta-analysis of 182 published BEF relationship 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 BEF relationship mechanisms described above, suggests that a focus on these ecosystems could greatly strengthen our understanding of a general BEF relationship and its environmental determinants. Savannas and woodlands are the dominant vegetation type across the southern African region, spanning >4 million km^2 (Hopkins and White, 1987; Ratnam et al., 2011; 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. These retain the common features of an open tree canopy and an understorey generally dominated by C4 grass species grasses. Southern African savannas and woodlands are highly diverse, thought to harbour ~8500 plant species of which there are >300 are tree species trees (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 unquantified consequences for ecosystem structure and function.

A small number of studies in southern African woodlands, all of which were restricted in the spatial scope to a small region of miombo woodland, have found 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). The results of these fine scale studies concur with similar studies in other biomes (). Studies of the BEF relationship often find that at fine scales, biodiversity shows a strong effect on ecosystem function, but at broad scales biodiversity effects pale in significance compared to abiotic factors such as climate (Pasari et al., 2013). Due to the variable environmental conditions within which southern African woodlands occur (Frost, 1996), with wide variation in precipitation, diurnal and annual temperature range and given the potential importance of environment and biogeography in defining the strength and form of a relationship between biodiversity and above ground woody biomass (), it is important to sample across geographic and environmental gradients to gain understanding of the spatial variation in the relationship between biodiversity and biomass.

In forests, climatic variation is known to affect both woody biomass (Michaletz et al., 2014, 2018) and tree species diversity independently (Spasojevic et al., 2014). It is important therefore to account for climatic factors and understand how they interact with biomass and biodiversity to effectively model and correctly attribute the effects of biodiversity on woody biomass in analyses at broad spatial scales. Sankaran et al. (2005) used data from 854 African woodland field sites to show that below a threshold of ~650 mm MAP, precipitation sets 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.

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 tree species 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 Occupancy of multiple canopy layers allows a more full fuller 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. Instead, the overriding importance of disturbance history may negate the effects of tree species diversity on structural diversity (Grime and Pierce, 2012).

High levels of disturbance in southern African woodlands may moderate the observable BEF relationship through its effect on ecosystem composition. Fire disturbance in forests has been linked to abundance-dependent mortality among smaller trees (Roques et al., 2001; Staver et al., 2009; Bond and Keeley, 2005). Some species in the regional species pool may be excluded from woodland plots with high levels of disturbance if they are unable to escape the fire bottleneck and grow to become a large tree. Selection effects may therefore be more important in maximising ecosystem function in disturbance prone woodlands. If the regional species pool contains a large number of species, it is more likely that one of them will possess the necessary growth strategy to grow to a large tree with high biomass under an intense disturbance regime.

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 used aboveground woody biomass of trees as our metric of ecosystem function, and compared the relative effects of tree species diversity 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 (via clustering of plot-level tree species composition), as a factor in our analyses to understand how tree species composition as well as diversity affected ecosystem function and to assess the generality of our results. We used Structural Equation Modelling (SEM) ~~and~~with path analysis as a preferred method to simultaneously account for environmental and biotic factors, ~~which may interact their effect~~which may have interacting effects on ecosystem structure and therefore biomass. Initially, we ~~made~~posited 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~~the strength of the effect of tree species diversity on woody biomass will increase with plot level stocking density, due to an increased importance of niche complementarity as competition increases, and (3) tree species diversity will increase tree structural diversity (i.e. physiognomic diversity), which will provide an indirect path by which tree diversity increases woody biomass.

5 Materials and methods

5.1 Study location

The study used 1235 woodland monitoring plots from the larger SEOSAW network (SEOSAW, 2019) located across 10 countries within southern Africa in the ~~so-called miombo woodland eco-region~~miombo ecoregion (Figure 1, Hopkins and White 1987). The study ~~region spans~~area spans the core climate space of the region, with 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 2D convex hull of Mean Annual Precipitation (MAP) and Mean Annual Temperature (MAT) of the study sites covers 96.5% of the pixel-wise climate space of the miombo woodland ecoregion ~~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 and here referred to collectively as southern African woodlands (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 stocking density >50 trees 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 2005-2008 Zambian Integrated Land Use Assessment (Mukosha and Siampale, 2009) 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 citepdave, 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 citepOtto2013, thus removing noutliers plots (hyperref[appendixa~~

5.2 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 which contained stem measurements <10 cm DBH, small stems only accounted for a median of 2.1% of the plot level AGB.

All stems >10 cm DBH were measured within each plot resulting in a total of 66,758 stems with measurements. A tree may be comprised of multiple stems and so tree-level diversity estimates were used to prevent bias towards species which readily coppice. For each tree, we ~~measured~~recorded 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), see Godlee et al. (2020).

AGB for each plot was calculated using Equation 1, taken from Chave et al. (2014):

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

where ρ is the species level mean wood density, D is the DBH$_e$ at 1.3 m, and H is the tree height. 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 means of their respective ~~genus~~genera. For stems where tree height was unknown, the plot location was used to estimate tree height, according to Chave et al. (2014).

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)~~MAT and ~~Mean Annual Precipitation (MAP)~~MAP was calculated from daily data between 2000 and 2018, then averaged across years to provide a single mean annual estimate per plot. Temperature stress was calculated as the mean of daily delta temperature variation, and precipitation seasonality was calculated as the mean of the coefficient of variation of daily mean precipitation, for each of the 18 years of available data. Soil fertility data was ex-

tracted from the ISRIC gridded soil information data product at 250 m resolution, taking the grid cell value for each plot centre (Hengl et al., 2017). We extracted Cation Exchange Capacity (CEC), percentage soil organic carbon stocks (kg m^{-2}) percentage soil sand content by volume (Sand g kg^{-1}) and soil nitrogen content (g kg^{-1}). These data are a modelled product derived from various remotely sensed and directly measured data sources.

5.3 Data analysis

5.3.1 Species diversity and structural diversity metrics

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) was calculated as the ratio of the estimated Shannon diversity index to the natural log of estimated species richness. Abundance evenness allows for greater niche complementarity at small scales due to an increased spatial heterogeneity of functional traits. We calculated tree structural diversity for each plot by calculating the coefficient of variation of DBH (DBH CV) and tree height (Height CV).

5.3.2 Vegetation clusters

Plots were assigned to vegetation type groups based on tree species composition. Groups were defined 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. Group identification was conducted 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. Cluster names were assigned post-hoc based on the dominant and indicator species in each cluster.

Table 1: Description of the biogeographical clusters 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 mean plot level proportional AGB within each cluster. Numeric values of species richness, stems ha^{-1} and AGB represent medians and interquartile ranges (75th percentile - 25th percentile).

| Cluster	Dominant species	Indicator species	N plots	Species rich.	Stems ha^{-1}	AGB (t ha^{-1})
Core miombo	*Baikiaea plurijuga* *Burkea africana* *Pterocarpus angolensis*	*Burkea africana* *Baikiaea plurijuga* *Pterocarpus angolensis*	523	20(16.9)	204(142.5)	44.2(36.11)
ex-Acacia	*Colophospermum mopane* *Androstachys johnsonii* *Kirkia acuminata*	*Colophospermum mopane* *Psuedolachnostylis maprouneifolia* *Lannea discolor*	188	12(10.3)	181(166.5)	54.5(61.33)
Mopane	Spirostachys africana *Senegalia burkei* *Senegalia nigrescens*	*Euclea racemosa* *Vachellia nilotica* *Spirostachys africana*	58	10(10.2)	186(125.6)	42.7(32.83)
Sparse miombo / Baikiaea	*Brachystegia spiciformis* *Julbernardia paniculata* *Brachystegia boehmii*	*Parinari curatellifolia* *Uapaca kirkiana* *Brachystegia spiciformis*	466	12(13.7)	178(129.5)	36.9(26.98)

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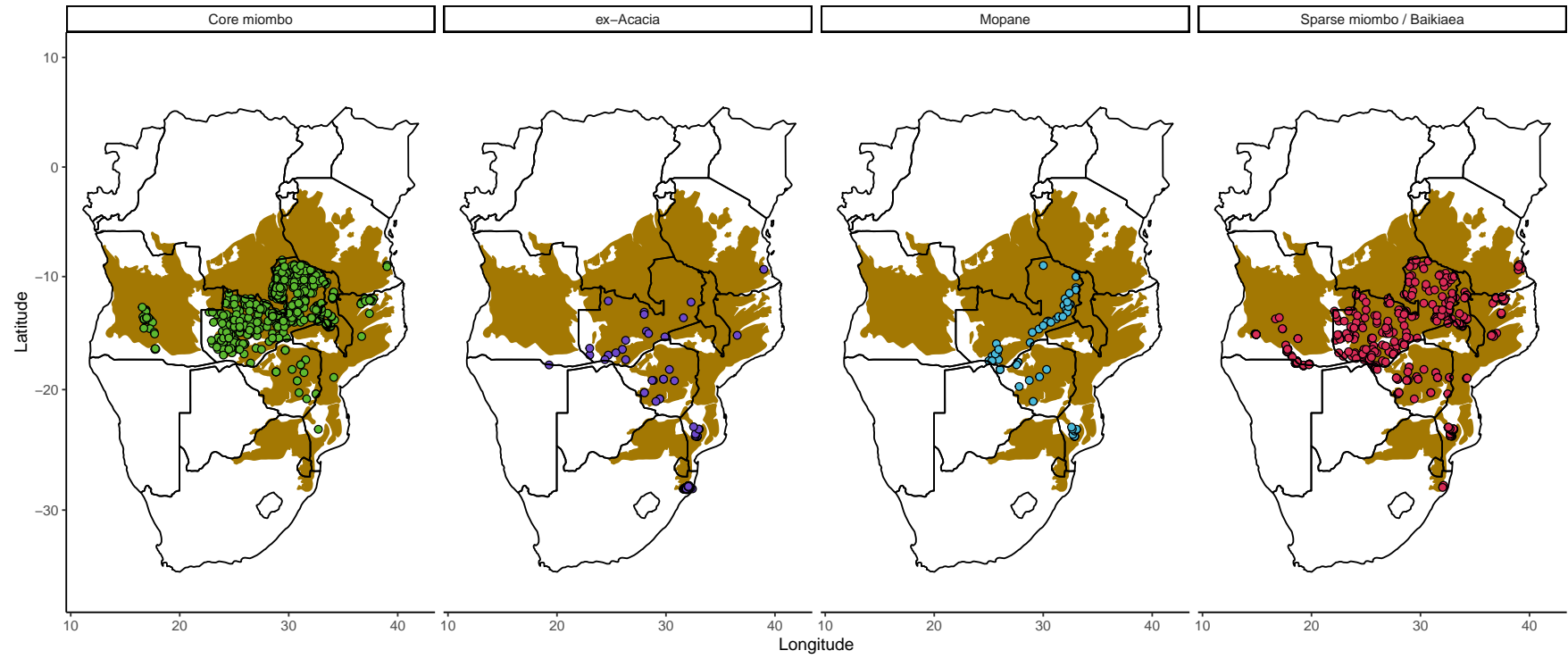
Figure 1: The locations of the 1235 plots used in this study, with respect to the distribution of miombo woodland vegetation according to Hopkins and White (1987). Each panel shows plots categorized by their vegetation type as defined by the vegetation types in Table 1.

5.3.3 Structural Equation Modelling

We used Structural Equation Models (SEM) to investigate 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 attributed to indirect effects, which is challenging in standard multiple regressions. Using SEMs also allowed us to describe latent variables such as "resource availability", "soil fertility", and "disturbance" which have been suggested to act upon biodiversity and biomass/productivity in previous studies despite these factors not having observable measures in our dataset. SEM is also necessary to properly account for potential feedback mechanisms between aspects of ~~climate~~environment and tree species diversity, which could otherwise increase the chances of Type I error and wrongly attribute inference due to the 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, disturbance through fire, tree species diversity, tree structural diversity and stocking density (Figure 2).
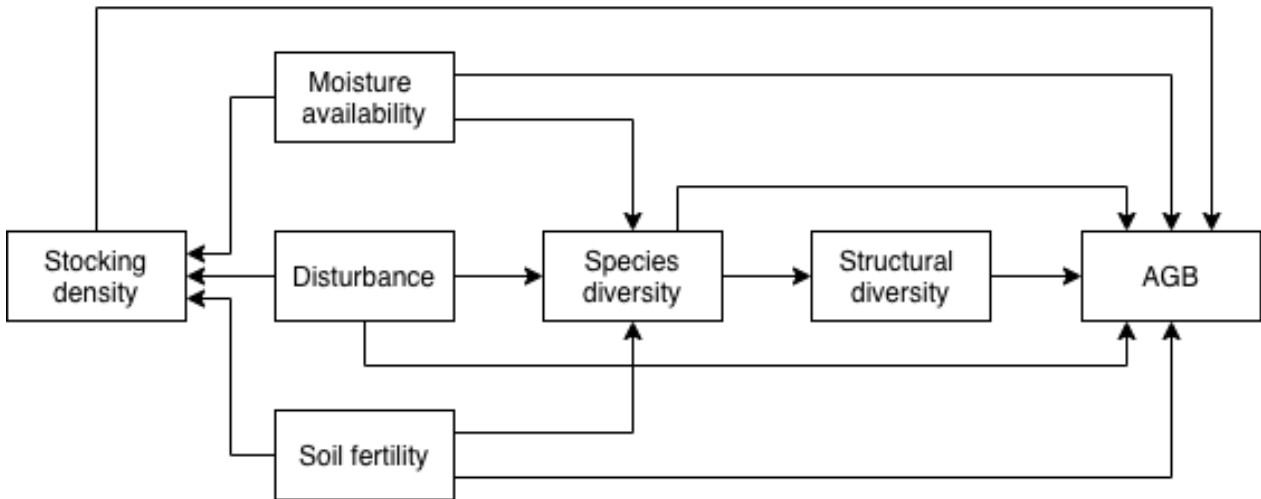

Figure 2: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural diversity, stocking density, and AGB. Hypothesised paths of causation are depicted as arrows from predictor to response.

Observed variables were transformed to achieve normality where necessary and standardised to Z-scores prior to analysis (Appendix A). 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 had their sign reversed. For example, overall moisture availability is expected to decrease as soil sand content increases, therefore sand content was reversed for use in the moisture availability latent variable. Precipitation seasonality, and temperature stress 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 one, 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 one, while ensuring no factor loadings were in

excess of one. We found no significant difference between model specifications (p>0.05). 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).

We assessed the role of tree species diversity and tree structural diversity in determining AGB via a simple mediation model which allowed species diversity to influence AGB both directly and indirectly via structural diversity. To account for variation in stocking density, which may covary with species diversity, we also included it as an observed variable 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, stocking 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 of Approximation (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~~who 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 niche complementarity effects increase in strength as stocking density increases, we repeatedly sub-sampled the available plot dataset to create 50 datasets of similar size with varying median stocking density. We used each of these datasets separately to fit the model including only tree species and structural diversity latent variables to predict AGB. We excluded the effect of stocking density on AGB and the correlation between stocking density and species diversity from this model as we deliberately controlled stocking density in our sub-sampling. We then examined how the unstandardised path coefficients for each path in the SEM varied according to the median stocking density of subsampled datasets.

We incorporated environmental covariates into our model to understand the relative effects of moisture availability, soil fertility and disturbance by fire on AGB both directly and indirectly via species diversity and stocking 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 types were narrow in their climate space, leading to a lack of variance particularly in the moisture availability latent variable.
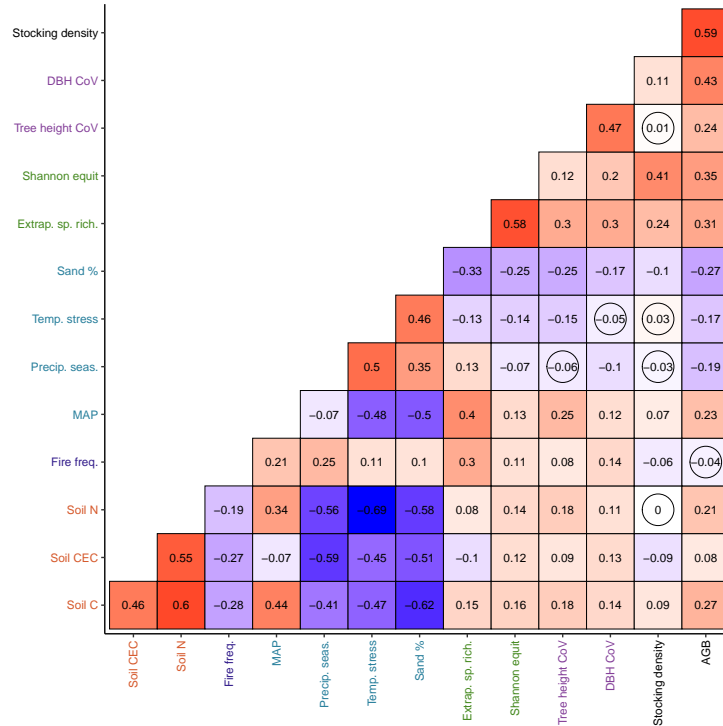
6 Results

Figure 3: Correlation matrix 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. Correlation coefficients marked by a circle indicate that the 95% confidence interval of r overlapped zero. Colours of variable names group them into latent variables used in the SEMs: red = soil fertility, blue = disturbance, turquoise = moisture availability, green = tree species diversity, purple = tree structural diversity. See Appendix B 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. stocking density had the strongest correlation with AGB of all variables considered ($r = 0.59$, p <0.01). Environmental variables had weaker correlations with AGB than diversity variables, with all environmental variables having significant correlations with AGB, except fire frequency.

The direction of these correlations was used as a test of our assumptions for the direction of influence of latent variables later used in the SEMs. As expected, there was a positive correlation between MAP and AGB ($r = 0.23$, p <0.01), and a weak negative correlation between the seasonality of precipitation and AGB ($r = -0.19$, p <0.01). Temperature stress was weakly negatively correlated ~~weakly~~ with AGB ($r = -0.17$, 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 nutrient content and AGB (carbon: $r = 0.27$, p <0.01, nitrogen: $r = 0.21$, p <0.01).

MAP had positive correlations with all tree species diversity and structural diversity variables. Tree species diversity variables had clear positive correlations with stocking density (species richness: $r = 0.24$, p <0.01; Shannon equitability: $r = 0.58$, p <0.01), but structural diversity variables showed weak correlations with stocking density (DBH CoV: $r = 0.11$, p <0.01, Height CoV: $r = 0.01$, p = 0.86).

6.1 Structural and species diversity models

In an SEM describing the effect of tree species diversity on AGB via the mediating effects of tree structural diversity and stocking density (Figure 4), species diversity showed no direct effect on AGB ($\beta = 0.01\pm0.053$, p = 0.88), but did have an indirect positive effect via structural diversity ($\beta = 0.18\pm0.039$, p <0.01) (Figure 4). Model fit was good with high factor loadings for all observed variables. All other path coefficients were significant (p <0.01) (Table 2). The R^2 of AGB was 0.49. The strongest direct effect on AGB was from stocking density ($\beta = 0.5\pm0.033$, p <0.01).
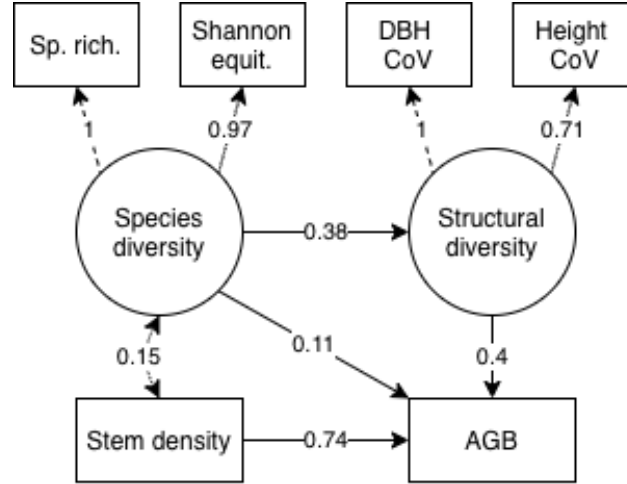

Figure 4: Path diagram with regression coefficients for the tree diversity SEM, including plots from all vegetation clusters. Latent variables are shown as circles while observed variables are shows as rectangles. Standardised path coefficients are shown as solid arrows pointing from predictor to response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

6.2 Variation among vegetation types

When the tree species and structural diversity model (Figure 4) was refitted separately using data from each of the four vegetation types, model fit and the strengths of unstandardised path coefficients varied. The direct effect of tree species diversity on AGB was positive and marginally significant in ex-Acacia ($\beta = 0.16\pm0.121$, p = 0.18) but negligible in Mopane ($\beta = 0.24\pm0.099$, p <0.05), sparse miombo / Baikiaea ($\beta = 0.23\pm0.045$, p <0.01) and Core miombo ($\beta = 0.23\pm0.041$, p <0.01) (Figure 5). Relationships between structural diversity and AGB remained generally similar, with the same sign and overlap between the 95% confidence intervals of path coefficients. The R^2 of AGB was highest in ex-Acacia shrubland ($R^2 = 0.83$) and lowest in sparse miombo / Baikiaea ($R^2 = 0.46$). The total effect of species diversity on AGB remained strongly positive for all vegetation types. All vegetation types 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 ex-Acacia. 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).
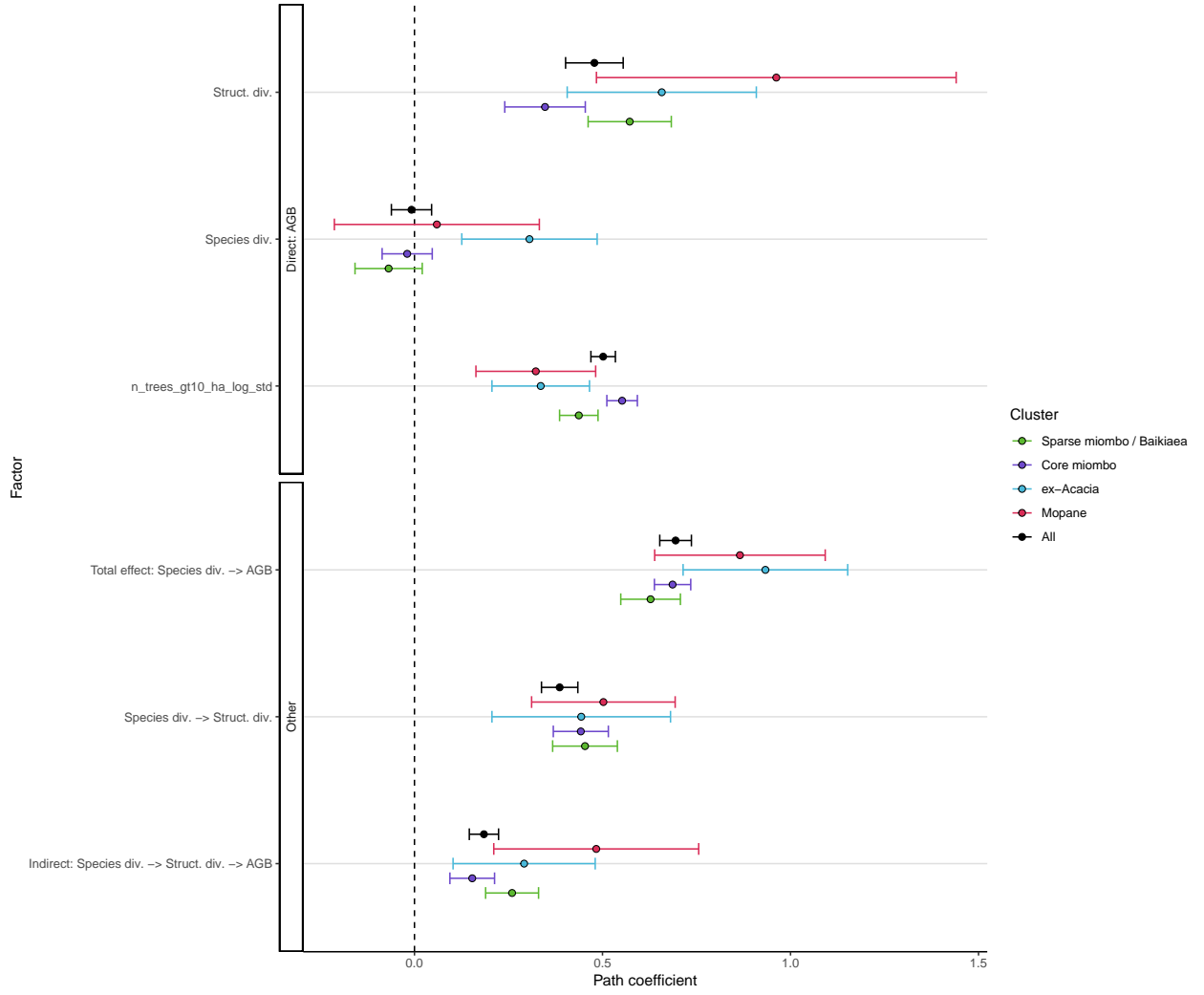
Figure 5: Unstandardised path coefficients for the effects of tree diversity on AGB, mediated by the effect of stand structural diversity. Path coefficients are ±1 standard error. Path coefficients where the standard error does not overlap zero are considered to be significant effects.

Table 2: Model fit statistics for SEMs investigating the effects of tree diversity and stem density on AGB (Figure 4). n = number of plots in cluster, χ^2 = Chi-squared fit statistic, DoF = model degrees of freedom, CFI = Comparative Fit Index, TLI = Tucker-Lewis Index, RMSEA = Root Mean Square Error of Approximation, R^2 AGB = R-squared of AGB.

Cluster	n	χ^2	DoF	CFI	TLI	RMSEA	R^2 AGB
Sparse miombo / Baikiaea	390	43.870	6	0.914	0.784	0.130	0.460
Core miombo	517	78.670	6	0.904	0.759	0.140	0.490
ex-Acacia	28	9.570	6	0.952	0.879	0.130	0.830
Mopane	46	19.880	6	0.834	0.584	0.240	0.510
All	981	91.380	6	0.937	0.843	0.120	0.490

6.3 Moderation of Diversity-AGB relationship by stocking density

In our sub-sampling of the plot dataset by stocking density, we found an increasing positive effect of tree species diversity on AGB as stocking density increased (Figure 6). There appears to be

a minimum stocking density threshold at ~180 trees ha^{-1} below which there appears to be a reasonably constant baseline effect of tree diversity on biomass. The effect of structural diversity on AGB appears to remain constant with increasing stocking density. The indirect effect of species diversity on AGB via structural diversity climbs slightly as stocking density increases.
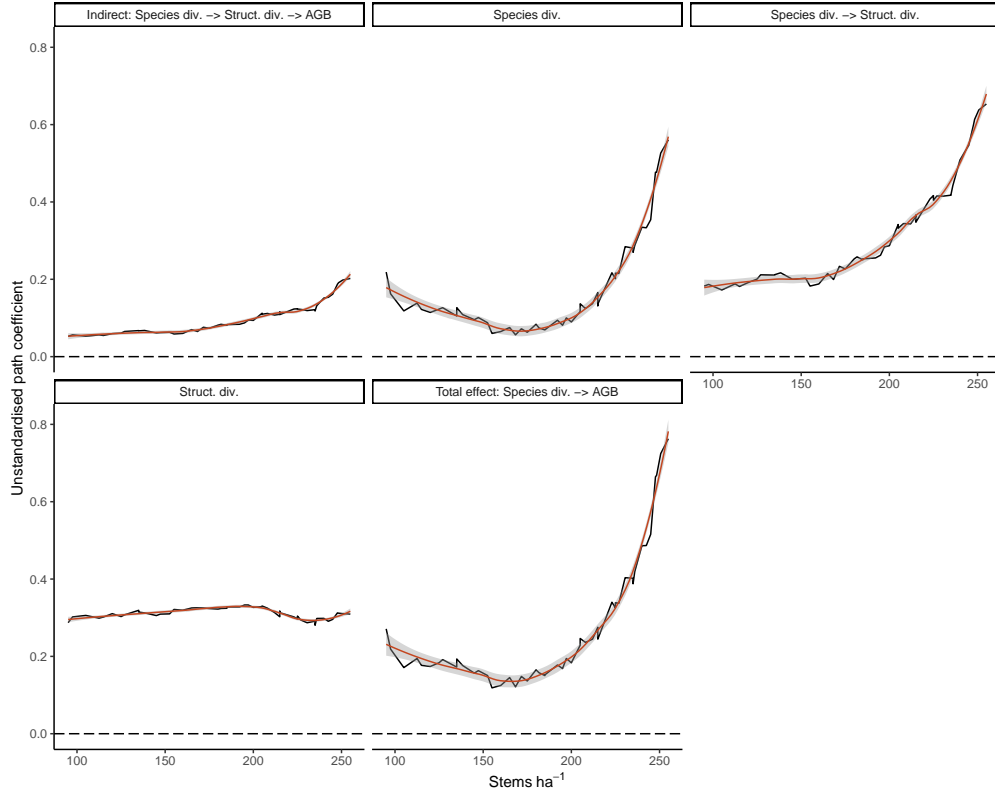

Figure 6: Line plots showing the variation in path coefficients in the SEM, using datasets with different mean stocking density. Smoothed lines are loess curves with standard error shaded bars.

6.4   Environmental covariates and tree diversity

A model incorporating the latent variables of moisture availability, soil fertility and disturbance by fire showed that the total effect of tree species diversity on biomass was similar to that of moisture availability, soil fertility and disturbance (Figure 7, Figure 8). Surprisingly, the direct effects of moisture availability, soil fertility and disturbance on AGB were negligible (moisture, $\beta = 0.1 \pm 0.13$, p = 0.43, soil: $\beta = 0.1 \pm 0.155$, p = 0.51, disturbance: $\beta = -0.04 \pm 0.043$, p = 0.32), with nearly all of their observed effect on AGB coming from the indirect path via stocking density (moisture: $\beta = 0.14 \pm 0.091$, p = 0.12, soil: $\beta = -0.22 \pm 0.109$, p <0.05, disturbance: $\beta = -0.12 \pm 0.03$, p <0.01) and species diversity (moisture: $\beta = 0.62 \pm 0.172$, p <0.01, soil: $\beta = -0.24 \pm 0.209$, p = 0.26, disturbance: $\beta = 0.19 \pm 0.058$, p <0.01). MAP and soil sand content had the greatest contributions to the latent variable of moisture availability. Model fit was acceptable: CFI = 0.925, TLI = 0.900, and RMSEA = 0.153, R^2 of AGB = 0.34.

Similar to the model that 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 ($\beta = 0.19 \pm 0.026$, p <0.01) when environmental covariates were accounted for. Again, the direct effect of species diversity on AGB was negligible ($\beta = -0.05 \pm 0.041$, p = 0.27) The total effect of species diversity on AGB was positive ($\beta = 0.34 \pm 0.044$, p <0.01).

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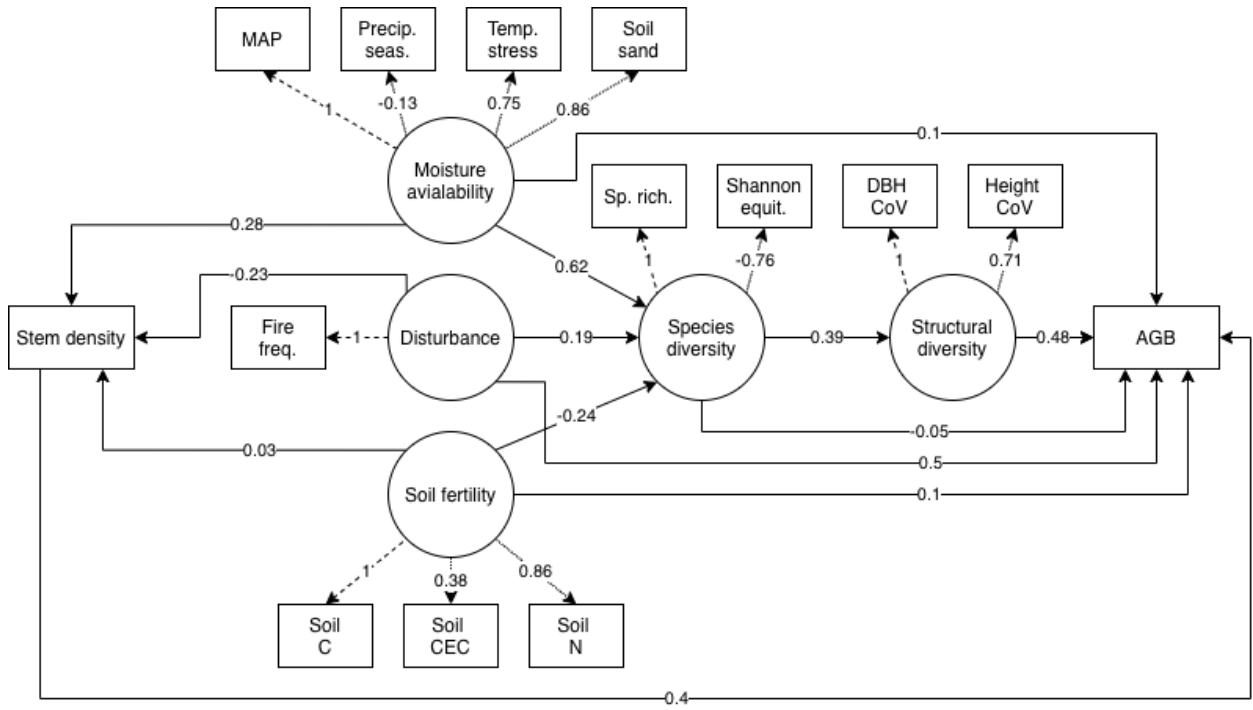
Figure 7: Path diagram with regression coefficients for the SEM incorporating environmental co-variates and tree species and structural diversity across all five vegetation types. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are shown as 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. Observed variables that inform the latent variables are connected by dotted arrows, observed variables with loading set to one are connected by dashed arrows. Measurement errors of exogenous variables are omitted for clarity.
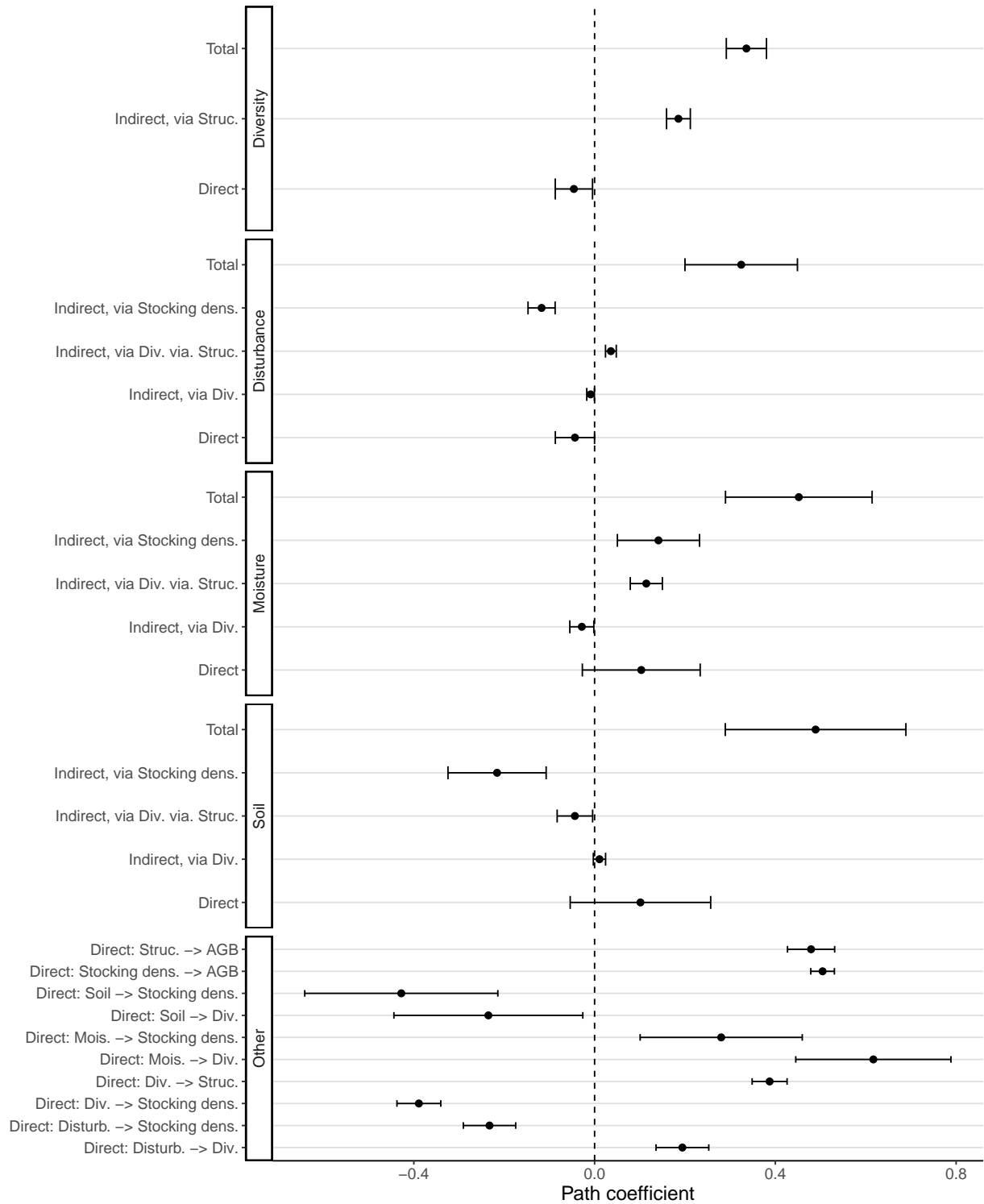
Figure 8: Unstandardised path coefficients for the full model including tree species diversity, environmental covariates and stocking density. Path coefficients are ±1 standard error. Path coefficients where the standard error does not overlap zero are considered significant effects.

7 Discussion

In this study, we assessed the importance of [a] tree species diversity, [b] tree structural diversity, [c] resource availability, [d] disturbance by fire, [e] stocking density and their interactions on above ground woody biomass (AGB) across southern African woodlands, using a network of 1235 woodland plots. Using Structural Equation Modelling (SEM), we found support for a general positive

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relationship between tree species diversity and AGB indirectly via structural diversity (H_1). We found that the effect size of tree species diversity on AGB increased with stocking density (H_2). Tree species diversity, structural diversity and stocking density accounted for 49% of the variation in AGB across the region, while models for specific vegetation types showed even greater explanatory power in some cases (Table 2). The strongest effect on AGB was that of stocking density. When the effects of moisture availability, soil fertility and disturbance by fire were controlled for, the total explanatory power of tree species diversity and structural diversity decreased, but the predictive power of the model increased, suggesting that it is important to control for environmental covariates to understand the true effect of tree species diversity on AGB in regional scale assessments in southern African woodlands.

7.1   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 the current study. Within southern African woodlands we therefore find support for our hypothesis 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 the idea that there is a generalisable positive association between biodiversity and ecosystem function (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 southern African woodlands, a disturbance-structured and poorly studied ecological system.

Much of the total variation in AGB was driven by variation in stocking density. It is possible that within southern African woodlands a higher species diversity allows for a higher stocking density through niche separation, which reduces competition between species occupying varying niche space, leading to an increase in total AGB per unit area. The opposite causation is also plausible however, with increased stocking density causing higher species richness through an increased probability of encountering new species. We attempted to correct for the correlation between species richness and stocking density by estimating the extrapolated species richness. We suggest therefore that an increase in tree species diversity through species richness and evenness produces an assemblage of species which can utilise more available light and moisture, resulting in greater plot-level AGB. This is supported by the moderately strong indirect positive effect of tree species diversity on AGB via structural diversity, and the positive effect of moisture availability on AGB via stocking density in the model which included environmental covariates. However, we found a negative effect of soil fertility on AGB via stocking density.

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 second 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 for niche complementarity, with a highly diverse canopy able to take advantage of a greater proportion of the available light. Although we did not measure them 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. 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 stocking density supports this. In frequently disturbed woodlands such as those studied here however, a woodland 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. Previous studies have found that southern African woodlands with higher species diversity tend to experience less frequent disturbance by fire and tend to form a more closed canopy and a more sparse understorey (Chidumayo, 2013; Mutowo and Murwira, 2012). In our study however, we found a positive effect of disturbance on species diversity, perhaps suggesting that disturbance prevents domination of woodlands by a single dominant species

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(Chidumayo, 2013).

We found a non linear positive effect of stocking density on the relationship between tree species diversity and AGB (Figure 6). At low stocking densities competition between mature trees may not occur, meaning that the niche complementarity effect provided by an increase in tree species richness may not be present, accounting for the low and constant effect of tree species diversity on AGB below ~180 trees ha^{-1}. At very high stem density, there is also increase in the effect of species diversity on structural diversity. This could be because at high stem density, the adaptation of different species to growth form become important. At low stem density, individual trees tend to spread out rather than growing tall, but at high stem density, only certain species ara able to exist in the understory, while others are able to grow tall above the woodland canopy, leading to greater variation in tree height over the plot.

7.2   Effects of moisture availability, soil fertility and disturbance

Moisture availability, soil fertility and disturbance by fire had similar positive total effects on AGB, comparable in size to the total effect of tree species diversity on AGB. 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 stocking 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, we observed weak indirect positive effects on AGB via species diversity and a positive 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~~experience frequent drought. It is surprising that disturbance by fire had a positive total effect on AGB. We found a positive indirect effect of disturbance on AGB via species diversity and structural diversity. It is possible that fire prevents the domination of a woodland by a few highly competitive species, resulting in greater abundance evenness and overall species richness, which in turn increases the effect of niche complementarity. In southern African woodlands moisture availability is linked to 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 fire frequency, which had a negative effect on stocking density, which is expected to decrease AGB. The direct effect of moisture availability on stocking 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 found a positive total effect of soil fertility on AGB in our model. We measured soil fertility using the observed variables of soil carbon, nitrogen and Cation Exchange Capacity (CEC). In wet tropical forests a clear relationship has been observed between these variables and AGB (Slik et al., 2009; de Souza et al., 2019).

7.3   Vegetation type responses

All four vegetation types produced similar results in the simple SEM, with a positive total effect of species diversity on AGB, the majority being indirectly via structural diversity. This demonstrates the robustness of our results, showing they are generalisable across vegetation types in southern Africa. It also demonstrates that similar ecosystem processes are occurring in these vegetation types, despite variation in species composition and overall species richness.

Core miombo and sparse miombo / Baikiaea 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 ex-Acacia

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and Mopane woodlands, miombo woodlands have higher median tree species richness. ex-Acacia and Mopane woodlands are dominated by fewer tree species, notably *Senegalia* spp. in ex-Acacia woodlands and *Colophospermum mopane* in Mopane woodlands which often produce large canopy dominating trees. We postulate that the 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 ex-Acacia 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, while in the species poor Mopane and ex-Acacia woodlands, the addition of extra species may fill a greater proportional niche space, thus increasing total AGB more.

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).

ex-Acacia woodland had the strongest total effect of species diversity on AGB and was the only vegetation type to show a clearly positive direct effect of species diversity on AGB. ex-Acacia 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 ex-Acacia woodlands and their contribution to ecosystem functioning. Unlike mopane woodlands, ex-Acacia woodlands do sometimes contain species other than *Senegalia* spp. which can grow to be high biomass canopy trees, especially in transition zones.

7.4   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 function. 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 trees. We found that the multiple vegetation types which comprise southern African woodlands exhibit similarities in the relationship between species diversity and woody biomass, inferring that similar ecosystem processes occur across the region to determine ecosystem function. 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 tree species and structural diversity.

Southern African woodlands are relied heavily upon for their ecosystem service provision, which is itself affected by ecosystem function. 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 stocking density, and low species diversity, 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. (2019*a*), '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. (2019*b*), '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.

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

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-Yrízar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G. and Vieilledent, G. (2014), 'Improved allometric models to estimate the aboveground biomass of tropical trees', *Global Change Biology* **20**(10), 3177–3190.

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

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., Bebber, 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., Nytch, 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.

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

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.

de Souza, F. C., Dexter, K. G., Phillips, O. L., Pennington, R. T., Neves, D., Sullivan, M. J. P., Alvarez-Davila, E., Alves, Á., Amaral, I., Andrade, A., Aragao, L. E. O. C., Araujo-Murakami, A., Arets, E. J. M. M., Arroyo, L., C., G. A. A., Bánki, O., Baraloto, C., Barroso, J. G., Boot, R. G. A., Brienen, R. J. W., Brown, F., Camargo, J. L. C., Castro, W., Chave, J., Cogollo, A., Comiskey, J. A., Cornejo-Valverde, F., da Costa, A. L., de Camargo, P. B., Fiore, A. D., Feldpausch, T. R., Galbraith, D. R., Gloor, E., Goodman, R. C., Gilpin, M., Herrera, R., Higuchi, N., Coronado, E. N. H., Jimenez-Rojas, E., Killeen, T. J., Laurance, S., Laurance, W. F., Lopez-Gonzalez, G., Lovejoy, T. E., Malhi, Y., Marimon, B. S., Marimon-Junior, B. H., Mendoza, C., Monteagudo-Mendoza, A., Neill, D. A., Vargas, P. N., Mora, M. C. P., Pickavance, G. C., Pipoly, J. J., Pitman, N. C. A., Poorter, L., Prieto, A., Ramirez, F., Roopsind, A., Rudas, A., Salomão, R. P., Silva, N., Silveira, M., Singh, J., Stropp, J., ter Steege, H., Terborgh, J., Thomas-Caesar, R., Umetsu, R. K., Vasquez, R. V., Célia-Vieira, I., Vieira, S. A., Vos, V. A., Zagt, R. J. and Baker, T. R. (2019), 'Evolutionary diversity is associated with wood productivity in amazonian forests', *Nature Ecology & Evolution* **3**(12), 1754–1761.

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

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.

Godlee, J. L., Gonçalves, F. M., Tchamba, J. J., Chisingui, A. V., Muledi, J. I., Shutcha, M. N., Ryan, C. M., Brade, T. K. and Dexter, K. G. (2020), 'Diversity and structure of an arid woodland in southwest angola, with comparison to the wider miombo ecoregion', *Diversity* **12**(4), 1–20.

Grime, J. P. (1979), *Plant strategies and vegetation processes*, John Wiley and Sons, Chichester, UK.

Grime, J. P. and Pierce, S. (2012), *The evolutionary strategies that shape ecosystems*, John Wiley & Sons, Oxford, 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.

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L. and O'Connor, M. I. (2012), 'A global synthesis reveals biodiversity loss as a major driver of ecosystem change', *Nature* **486**(7401), 105–108.

Hopkins, B. and White, F. (1987), 'Vegetation map of Africa. the vegetation of Africa: A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa.', *The Journal of Ecology* **75**(4).

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., H ardtle, W., Raumonen, 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.

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.

Levick, S. R., Asner, G. P., Kennedy-Bowdoin, T. and Knapp, D. E. (2009), 'The relative influence of fire and herbivory on savanna three-dimensional vegetation structure', *Biological Conservation* **142**(8), 1693–1700.

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 southeastern Tanzania', *Ecosystems* **21**, 740–754.

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

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

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

Mukosha, J. and Siampale, A. (2009), *Integrated land use assessment Zambia 2005–2008*, Lusaka, Zambia.

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.

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

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

Poorter, L., van de Sande, M. T., Thompson, J., Arets, E. J. M. M., Alarcòn, A., Àlvarez-Sànchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzmàn, G., Boit, A., Bongers, F., Carvalho, F. A., Casanoves, F., Cornejo-Tenorio, G., Costa, F. R. C., de Castilho, C. V., Duivenvoorden, J. F., Dutrieux, L. P., Enquist, B. J., Fernàndez-Mèndez, F., Finegan, B., Gormley, L. H. L., Healey, J. R., Hoosbeek, M. R., Ibarra-Manrìquez, G., Junqueira, A. B., Levis, C., Licona, J. C., Lisboa, L. S., Magnusson, W. E., Martìnez-Ramos, M., Martìnez-Yrizar, A., Martorano, L. G., Maskell, L. C., Mazzei, L., Meave, J. A., Mora, F., Muñoz, R., Nytch, C., Pansonato, M. P., Parr, T. W., Paz, H., Pèrez-Garcìa, E. A., Renterìa, L. Y., Rodrìguez-Velazquez, J., Rozendaal, D. M. A., Ruschel, A. R., Sakschewski, B., Salgado-Negret, B., Schietti, J., Simões, M., Sinclair, F. L., Souza, P. F., Souza, F. C., Stropp, J., ter Steege, H., Swenson, N. G., Thonicke, K., Toledo, M., Uriarte, M., van der Hout, P., Walker, P., Zamora, N. and Peña-Claros, M. (2015), 'Diversity enhances carbon storage in tropical forests', *Global Ecology and Biogeography* **24**, 1314–1328.

Poorter, L., van der Sande, M. T., Arets, E. J. M. M., Ascarrunz, N., Enquist, B. J., Finegan, B., Licona, J. C., Martínez-Ramos, M., Mazzei, L., Meave, J. A., Muñoz, R., Nytch, C. J., de Oliveira, A. A., Pérez-García, E. A., Prado-Junior, J., Rodríguez-Velázques, J., Ruschel, A. R., Salgado-Negret, B., Schiavini, I., Swenson, N. G., Tenorio, E. A., Thompson, J., Toledo, M., Uriarte, M., van der Hout, P., Zimmerman, J. K. and Peña0-Claros, M. (2017), 'Biodiversity and climate determine the functioning of neotropical forests', *Global Ecology and Biogeography* **26**, 1423–1434.

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

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

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

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

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

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

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

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

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

Sankaran, M., Ratnam, J. and Hanan, N. (2008), 'Woody cover in african savannas: the role of resources, fire and herbivory', *Global Ecology and Biogeography* **17**(2), 236–245.

Seidel, D., Ehbrecht, M., Dorji, Y., Jambay, J., Ammer, C. and Annighöfer, P. (2019), 'Identifying architectural characteristics that determine tree structural complexity', *Trees* **33**(3), 911–919.

Selaya, N. G. and Anten, P. R. (2008), 'Differences in biomass allocation, light interception and mechanical stability between lianas and trees in early secondary tropical forest', *Functional Ecology* **22**, 30–39.

SEOSAW (2019), 'SEOSAW: A Socio-Ecological Observatory for Southern African Woodlands'. [Online; 15-January-2019].

Shapiro, A. (1983), 'Asymptotic distribution theory in the analysis of covariance structures (a unified approach)', *South African Statistical Journal* **17**, 33–81.

Shirima, D. D., Pfeifer, M., Platts, P. J., Totland, Ø. and Moe, S. R. (2015), 'Interactions between canopy structure and herbaceous biomass along environmental gradients in moist forest and dry miombo woodland of tanzania', *PLoS ONE* **10**(11), 1–15.

Slik, J. W. F., Aiba, S.-I., Brearley, F. Q., Cannon, C. H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A. D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E. and van Valkenburg, J. L. C. H. (2009), 'Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in borneo's tropical forests', *Global Ecology and Biogeography* **19**(1), 50–60.

Smith, B. and Wilson, J. B. (1996), 'A consumer's guide to evenness indices', *Oikos* **76**(1), 70–82.

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

Spasojevic, M. J., Grace, J. B., Harrison, S. and Damschen, E. I. (2014), 'Functional diversity supports the physiological tolerance hyopthesis for plant species richness along climatic gradients', *Journal of Ecology* **102**, 447–455.

Stark, S. C., Leitold, V., Wu, J. L., Hunter, M. O., de Castilho, C. V., Costa, F. R. C., McMahon, S. M., Parker, G. G., Shimabukuro, M. T., Lefsky, M. A., Keller, M., Alves, L. F., Schietti, J., Shimabukuro, Y. E., Brandão, D. O., Woodcock, T. K., Higuchi, N., de Camargo, P. B., de Oliveira, R. C. and Saleska, S. R. (2012), 'Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment', *Ecology Letters* **15**, 1406–1414.

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

Stegen, J. C., Swenson, N. G., Enquist, B. J., White, E. P., Phillips, O. L., Jørgensen, P. M., Weiser, M. D., Mendoza, A. M. and Vargas, P. N. (2011), 'Variation in above-ground forest biomass across broad climatic gradients', *Global Ecology and Biogeography* **20**, 744–754.

849 Tilman, D. and Downing, J. A. (1994), 'Biodiversity and stability in grasslands', *Nature* **367**, 363–
850   365.

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

853 Timberlake, J., Chidumayo, E. and Sawadogo, L. (2010), Distribution and characteristics of
854   African dry forests and woodlands, *in* 'The Dry Forests and Woodlands of Africa: Managing
855   for Products and Services', EarthScan, London, United Kingdom, pp. 11–42.

856 Tobner, C. M., Paquette, A., Gravel, D., Reich, P. B., Williams, L. J. and Messier, C. (2016),
857   'Functional identity is the main driver of diversity effects in young tree communities', *Ecology*
858   *Letters* **19**, 638–647.

859 van der Sande, M. T., Poorter, L., Kooistra, L., Balvanera, P., Thonicke, K., Thompson, J., Arets,
860   E. J. M. M., Alaniz, N. G., Jones, L., Mora, F., Mwampamba, T. H., Parr, T. and Peña-Claros,
861   M. (2017), 'Biodiversity in species, traits, and structure determines carbon stocks and uptake in
862   tropical forests', *Biotropica* **49**(5), 593–603.

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

866 Wright, A. J., Wardle, W. D. A., Callaway, W. R. and Gaxiola, A. (2017), 'The overlooked role of
867   facilitation in biodiversity experiments', *Trends in Ecology and Evolution* **32**(5), 383–390.

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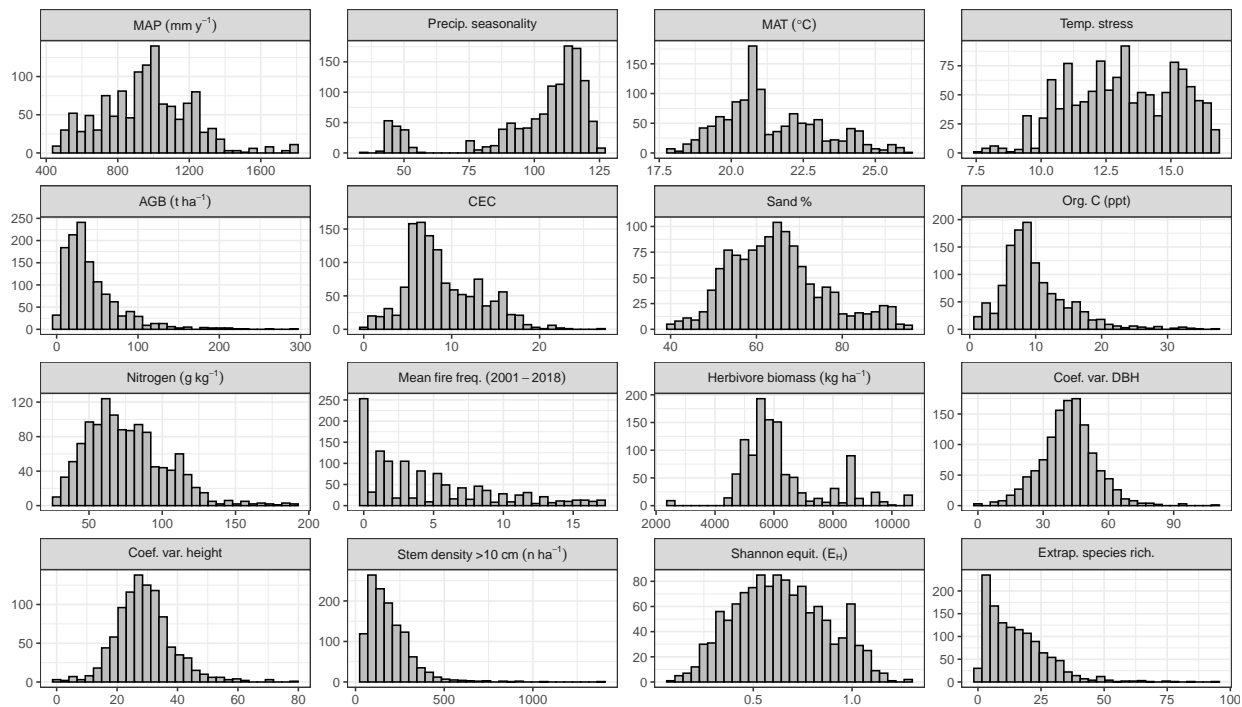870   http://hdl.handle.net/10255/ dryad.235.

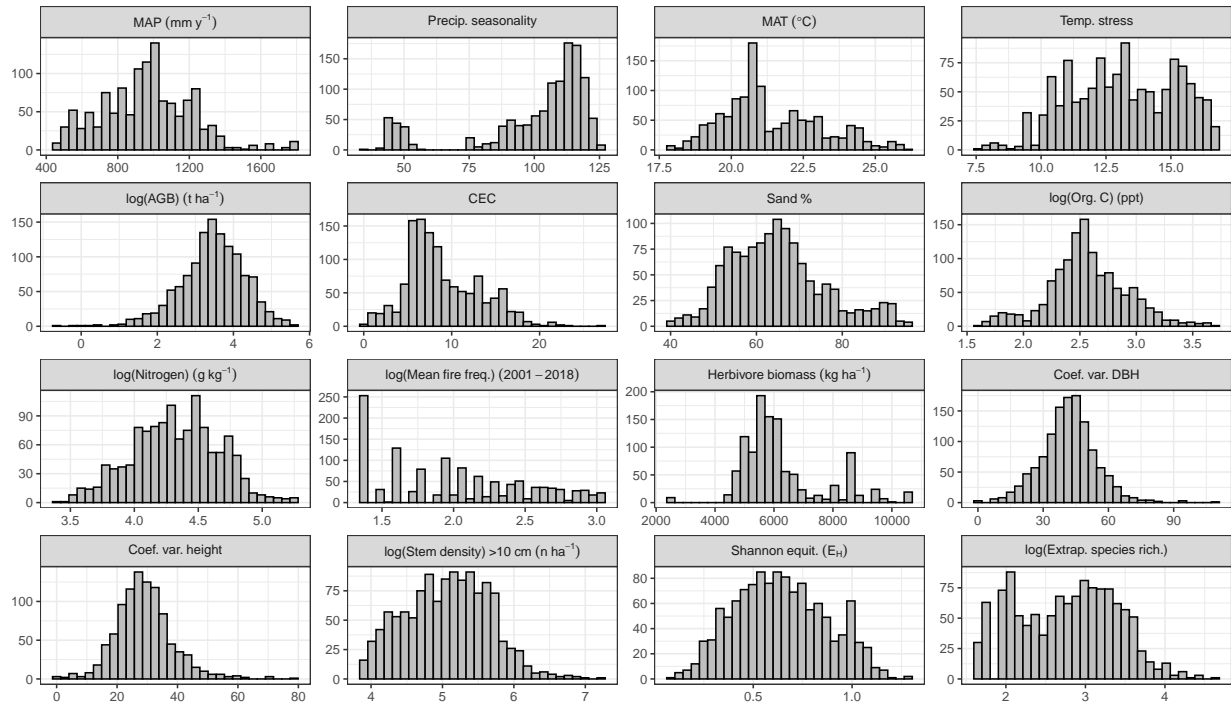Figure 9: Histograms of raw untransformed observed variables used in final analyses.

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

E   Appendix 2 - Table of correlation fit statistics

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

X	Y	r	lower 95% CI	upper 95% CI	n	Prob.
Soil CEC	Soil C	0.460	0.410	0.500	1235	p <0.01
Soil N	Soil C	0.600	0.560	0.630	1235	p <0.01
Fire freq.	Soil C	-0.280	-0.330	-0.220	1235	p <0.01
MAP	Soil C	0.440	0.390	0.480	1235	p <0.01
Precip. seas.	Soil C	-0.410	-0.450	-0.360	1235	p <0.01
Temp. stress	Soil C	-0.470	-0.520	-0.430	1235	p <0.01
Sand %	Soil C	-0.620	-0.650	-0.580	1235	p <0.01
Extrap. sp. rich.	Soil C	0.150	0.090	0.200	1235	p <0.01
Shannon equit	Soil C	0.160	0.110	0.220	1235	p <0.01
Tree height CoV	Soil C	0.180	0.120	0.240	981	p <0.01
DBH CoV	Soil C	0.140	0.080	0.190	1233	p <0.01
Stocking density	Soil C	0.090	0.030	0.140	1235	p <0.01
AGB	Soil C	0.270	0.220	0.320	1235	p <0.01
Soil N	Soil CEC	0.550	0.510	0.580	1235	p <0.01
Fire freq.	Soil CEC	-0.270	-0.320	-0.220	1235	p <0.01
MAP	Soil CEC	-0.070	-0.130	-0.020	1235	p <0.01
Precip. seas.	Soil CEC	-0.590	-0.630	-0.550	1235	p <0.01
Temp. stress	Soil CEC	-0.450	-0.490	-0.410	1235	p <0.01
Sand %	Soil CEC	-0.510	-0.550	-0.470	1235	p <0.01
Extrap. sp. rich.	Soil CEC	-0.100	-0.160	-0.050	1235	p <0.01
Shannon equit	Soil CEC	0.120	0.070	0.180	1235	p <0.01
Tree height CoV	Soil CEC	0.090	0.020	0.150	981	p <0.01

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DBH CoV	Soil CEC	0.130	0.080	0.190	1233	p <0.01
Stocking density	Soil CEC	-0.090	-0.140	-0.030	1235	p <0.01
AGB	Soil CEC	0.080	0.030	0.140	1235	p <0.01
Fire freq.	Soil N	-0.190	-0.240	-0.130	1235	p <0.01
MAP	Soil N	0.340	0.290	0.390	1235	p <0.01
Precip. seas.	Soil N	-0.560	-0.600	-0.520	1235	p <0.01
Temp. stress	Soil N	-0.690	-0.710	-0.650	1235	p <0.01
Sand %	Soil N	-0.580	-0.620	-0.540	1235	p <0.01
Extrap. sp. rich.	Soil N	0.080	0.020	0.130	1235	p <0.01
Shannon equit	Soil N	0.140	0.090	0.200	1235	p <0.01
Tree height CoV	Soil N	0.180	0.120	0.240	981	p <0.01
DBH CoV	Soil N	0.110	0.050	0.160	1233	p <0.01
Stocking density	Soil N	0	-0.060	0.050	1235	p = 0.86
AGB	Soil N	0.210	0.160	0.260	1235	p <0.01
MAP	Fire freq.	0.210	0.160	0.260	1235	p <0.01
Precip. seas.	Fire freq.	0.250	0.190	0.300	1235	p <0.01
Temp. stress	Fire freq.	0.110	0.050	0.170	1235	p <0.01
Sand %	Fire freq.	0.100	0.050	0.160	1235	p <0.01
Extrap. sp. rich.	Fire freq.	0.300	0.250	0.350	1235	p <0.01
Shannon equit	Fire freq.	0.110	0.060	0.170	1235	p <0.01
Tree height CoV	Fire freq.	0.080	0.010	0.140	981	p <0.05
DBH CoV	Fire freq.	0.140	0.090	0.200	1233	p <0.01
Stocking density	Fire freq.	-0.060	-0.110	0	1235	p <0.05
AGB	Fire freq.	-0.040	-0.100	0.010	1235	p = 0.15
Precip. seas.	MAP	-0.070	-0.130	-0.020	1235	p <0.05
Temp. stress	MAP	-0.480	-0.520	-0.440	1235	p <0.01
Sand %	MAP	-0.500	-0.540	-0.460	1235	p <0.01
Extrap. sp. rich.	MAP	0.400	0.350	0.450	1235	p <0.01
Shannon equit	MAP	0.130	0.070	0.180	1235	p <0.01
Tree height CoV	MAP	0.250	0.190	0.310	981	p <0.01
DBH CoV	MAP	0.120	0.060	0.170	1233	p <0.01
Stocking density	MAP	0.070	0.010	0.120	1235	p <0.05
AGB	MAP	0.230	0.180	0.280	1235	p <0.01
Temp. stress	Precip. seas.	0.500	0.460	0.540	1235	p <0.01
Sand %	Precip. seas.	0.350	0.300	0.400	1235	p <0.01
Extrap. sp. rich.	Precip. seas.	0.130	0.070	0.180	1235	p <0.01
Shannon equit	Precip. seas.	-0.070	-0.130	-0.010	1235	p <0.05
Tree height CoV	Precip. seas.	-0.060	-0.120	0.010	981	p = 0.07
DBH CoV	Precip. seas.	-0.100	-0.150	-0.040	1233	p <0.01
Stocking density	Precip. seas.	-0.030	-0.080	0.030	1235	p = 0.33
AGB	Precip. seas.	-0.190	-0.240	-0.130	1235	p <0.01
Sand %	Temp. stress	0.460	0.410	0.500	1235	p <0.01
Extrap. sp. rich.	Temp. stress	-0.130	-0.180	-0.070	1235	p <0.01
Shannon equit	Temp. stress	-0.140	-0.190	-0.080	1235	p <0.01
Tree height CoV	Temp. stress	-0.150	-0.210	-0.090	981	p <0.01
DBH CoV	Temp. stress	-0.050	-0.100	0.010	1233	p = 0.11
Stocking density	Temp. stress	0.030	-0.030	0.090	1235	p = 0.3
AGB	Temp. stress	-0.170	-0.220	-0.120	1235	p <0.01
Extrap. sp. rich.	Sand %	-0.330	-0.370	-0.280	1235	p <0.01
Shannon equit	Sand %	-0.250	-0.300	-0.190	1235	p <0.01
Tree height CoV	Sand %	-0.250	-0.300	-0.190	981	p <0.01
DBH CoV	Sand %	-0.170	-0.230	-0.120	1233	p <0.01
Stocking density	Sand %	-0.100	-0.160	-0.050	1235	p <0.01

AGB	Sand %	-0.270	-0.320	-0.220	1235	p <0.01
Shannon equit	Extrap. sp. rich.	0.580	0.540	0.620	1235	p <0.01
Tree height CoV	Extrap. sp. rich.	0.300	0.250	0.360	981	p <0.01
DBH CoV	Extrap. sp. rich.	0.300	0.250	0.350	1233	p <0.01
Stocking density	Extrap. sp. rich.	0.240	0.190	0.300	1235	p <0.01
AGB	Extrap. sp. rich.	0.310	0.260	0.360	1235	p <0.01
Tree height CoV	Shannon equit	0.120	0.060	0.190	981	p <0.01
DBH CoV	Shannon equit	0.200	0.140	0.250	1233	p <0.01
Stocking density	Shannon equit	0.410	0.360	0.460	1235	p <0.01
AGB	Shannon equit	0.350	0.300	0.400	1235	p <0.01
DBH CoV	Tree height CoV	0.470	0.420	0.520	981	p <0.01
Stocking density	Tree height CoV	0.010	-0.060	0.070	981	p = 0.86
AGB	Tree height CoV	0.240	0.180	0.290	981	p <0.01
Stocking density	DBH CoV	0.110	0.060	0.170	1233	p <0.01
AGB	DBH CoV	0.430	0.390	0.480	1233	p <0.01
AGB	Stocking density	0.590	0.550	0.620	1235	p <0.01

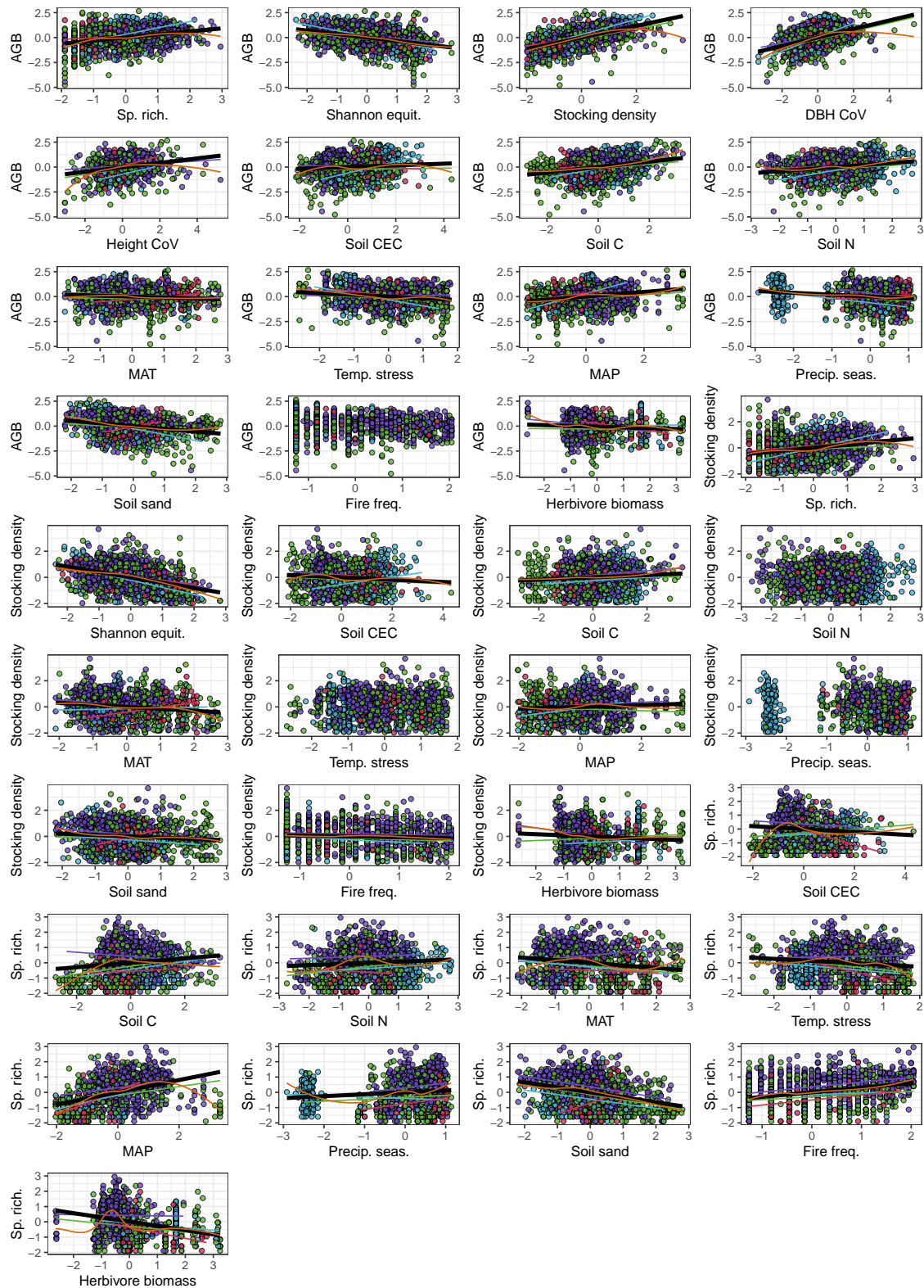# F Appendix 3 - Bivariate relationships of model variables

Figure 11: Bivariate scatter plots for each observed variable used in the SEMs, based on hypothesised paths of causality. Points are coloured according to vegetation type. A single linear regression is presented as a black line, which combines all vegetation types, separate loess trend lines are fitted for each vegetation type. All data is standardised and variables are transformed where it was appropriate for analysis.