

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

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16 providers and the field assistance they received when collecting plot data.

## 17 2 Biosketch

18 SEOSAW (A Socio-Ecological Observatory for Southern African Woodlands, [https://seosaw.](https://seosaw.github.io)  
19 [github.io](https://seosaw.github.io)) aims to understand the response of southern African woodlands to global change.

20 The goal of SEOSAW is to produce novel analyses of the determinants of ecosystem structure and  
21 function for the southern Africa region, based on syntheses of plot data. Additionally the group  
22 hopes to develop infrastructure for a long-term regional plan for plot remeasurement in the south-  
23 ern African region. While working on a multitude of diverse projects in the dry tropics at large,  
24 all authors have a broad interest in community ecology and ecosystem assemblage in southern  
25 African woodlands.

## Blinded Main Text File

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 ecophysiolegically 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 stem density, resource availability, disturbance through fire and herbivory, 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 woodlands~~ 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 stem 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 stem 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 Baikiaea woodlands, which showed the strongest biodiversity - ecosystem function relationship.

### 4 Introduction

Scientific interest in the relationship between species diversity and ecosystem function springs from both an interest in the factors which structure ecological communities (), and a more applied interest in determining the effect of global biodiversity loss on ecosystem form and function (). 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

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 function (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 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).

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 BEFR between dry tropical woodlands and other forested ecosystems demands further investigation ~~in order to characterise if we are to derive~~ a generalisable BEFR.

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, es-

pecially given the potential mismatch in BEFR mechanisms 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<sup>2</sup> (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-speciesgrasses. Southern African savannas and woodlands (SAWs) are highly diverse, thought to harbour ~8500 plant species of which there-are >300 are tree-speciestrees (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 SAWs, 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 BEFR 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 highly variable environmental conditions within which SAWs 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 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 SAWs 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. OccupationOccupancy of multiple canopy layers allows a more-fullfuller 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 (?).

High levels of disturbance in SAWs may moderate the observable BEFR through its effect on ecosystem composition. Fire disturbance in forests has been linked to abundance-dependent mortal-

ity among smaller tree stems (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 (SAWs), 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 deposited 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 stem stocking 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.

## 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 spaces the core climate space of the region, with a precipitation gradient from  $\sim 460$  mm  $y^{-1}$  in southern Mozambique and southern Zimbabwe to  $\sim 1700$  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 (SAWs) (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 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[appendix~~

## 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 66,758.080,027,926,1 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~~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<sub>e</sub> at 1.3 m using a cubic polynomial regression, with parameters estimated using a test dataset from Ryan C., (unpublished), see ?.

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

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

where  $\rho$  is the species level mean wood density,  $D$  is the DBH<sub>e</sub> 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.

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 seasonality (TS) and precipitation seasonality (PS) were both calculated as the mean of the coefficient of variation of daily mean temperature and precipitation, respectively, for each of the 18 years of available data. Soil fertility data was extracted from the ISRIC gridded soil information data product at 250 m resolution, taking the grid cell value for each plot centre (Hengl et al., 2017). We extracted Cation Exchange Capacity (CEC), percentage soil organic carbon by volume (Org. C %), and percentage soil sand content by volume (Sand %). These data are a modelled product derived from various remotely sensed and directly measured data sources.

## 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 .

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<sup>-1</sup> and AGB are medians and interquartile ranges (75th percentile - 25th percentile).

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



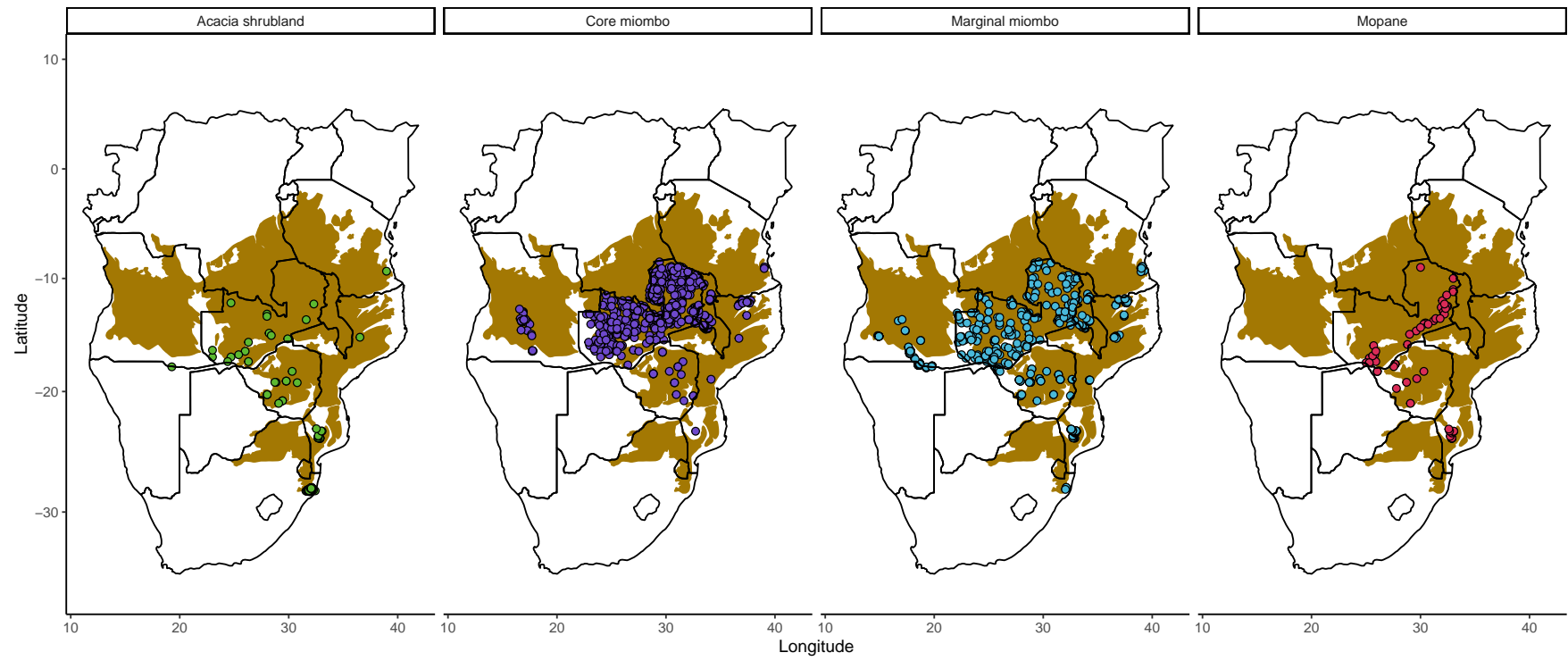


Figure 1: The locations of the 1235 plots used in this study, with respect to the distribution of miombo woodland vegetation according to Hopkins and White (1987). Each panel shows plots categorized by their vegetation type as defined by the vegetation types in Table 1.

### 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” 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. Structural equation modelling is also necessary to properly account for potential feedback mechanisms between aspects of climate and tree species diversity, which could otherwise increase the chances of Type I error and wrongly attribute inference due to covariance of explanatory variables when using conventional regression analyses (Nachtigall et al., 2003).

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

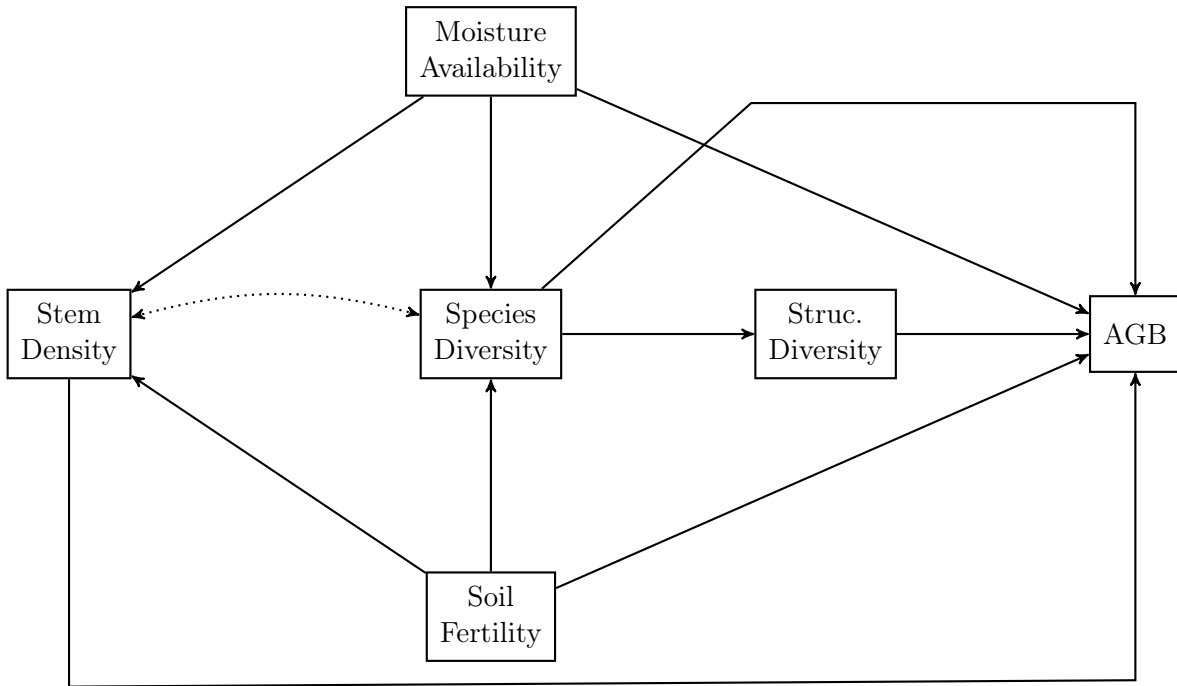


Figure 2: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural diversity, tree stem density, and AGB. Hypothesised paths of causation are depicted as arrows from predictor to response. Correlations are depicted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

Observed variables were transformed to achieve normality where necessary and standardised to Z-scores prior to analysis (Appendix 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 were reversed by multiplying by -1. For example, soil fertility is expected to decrease as soil sand content increases, so soil percentage sand content was reversed

for model fitting. Precipitation seasonality (PS), temperature seasonality (TS), and mean annual temperature (MAT) were also reversed in this way to account for the direction of their effect on moisture availability.

The factor loadings of the observed variable assumed to contribute most to each latent variable were set to 1 as per convention, with other observed variables being allowed to vary (Beaujean, 2014). We tested the robustness of our assumptions with a chi-squared test of all possible combinations of observed variable factor loadings set to 1, while ensuring no factor loadings were in excess of 1. We found no significant difference between model specifications ( $p > 0.05$ ). 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 structural diversity and species 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 stem density, which may covary with species diversity, we also included it as a 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 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 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 separately 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 as we were deliberately controlling stem density in our subsampling. We then examined how the unstandardised path coefficients for each path in the SEM varied according to the median stem density of subsampled datasets.

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.

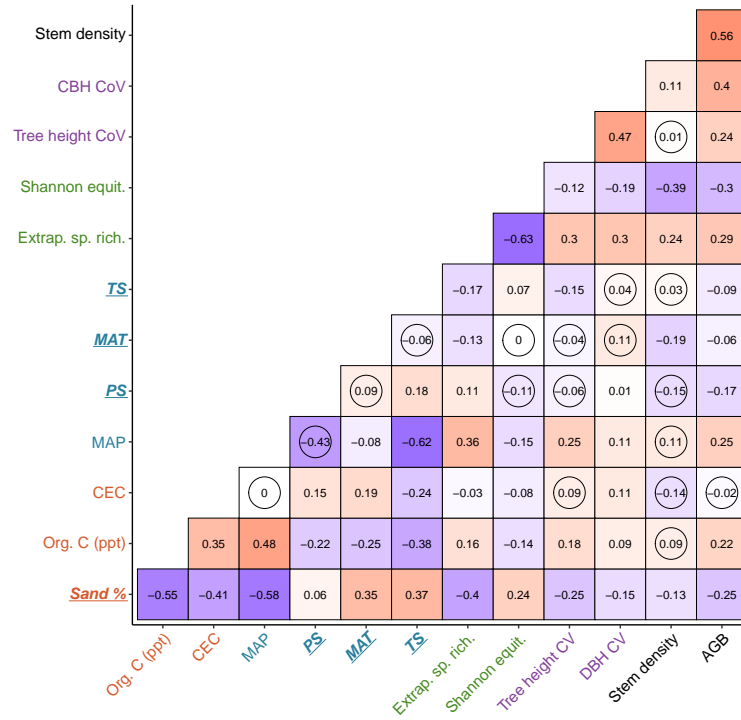


Figure 3: Correlation matrix of standardised observed variables used in the SEMs, with Pearson correlation coefficients ( $r$ ) coloured according to sign (+ve red, -ve blue) and shaded by strength of correlation. Variables in bold and underlined on the axis labels had their signs later reversed for 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 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. Stem 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 CEC and MAT.

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 ( $r = -0.19$ ,  $p < 0.01$ ). MAT and temperature seasonality (TS) were weakly negatively correlated weakly with AGB (MAT:  $r = -0.09$ ,  $p < 0.01$ ; TS:  $r = -0.17$ ,  $p < 0.01$ ). 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 organic carbon and AGB ( $r = 0.27$ ,  $p < 0.01$ ).

MAP had positive correlations with tree species richness ( $r = 0.4$ ,  $p < 0.01$ ), evenness ( $r = -0.13$ ,  $p < 0.01$ ), tree height diversity ( $r = 0.25$ ,  $p < 0.01$ ) and tree stem density ( $r = 0.07$ ,  $p < 0.05$ ). MAT had weak correlations with tree species and structural diversity variables. Tree species diversity variables had clear positive correlations with stem density (Species richness:  $r = 0.24$ ,  $p < 0.01$ ; Shannon equitability:  $r = -0.58$ ,  $p < 0.01$ ).



394 tation types (Table 1). The  $R^2$  of AGB was highest in Marginal miombo ( $R^2 = 0.46$ ) and lowest  
395 in the Core miombo ( $R^2 = 0.49$ ).

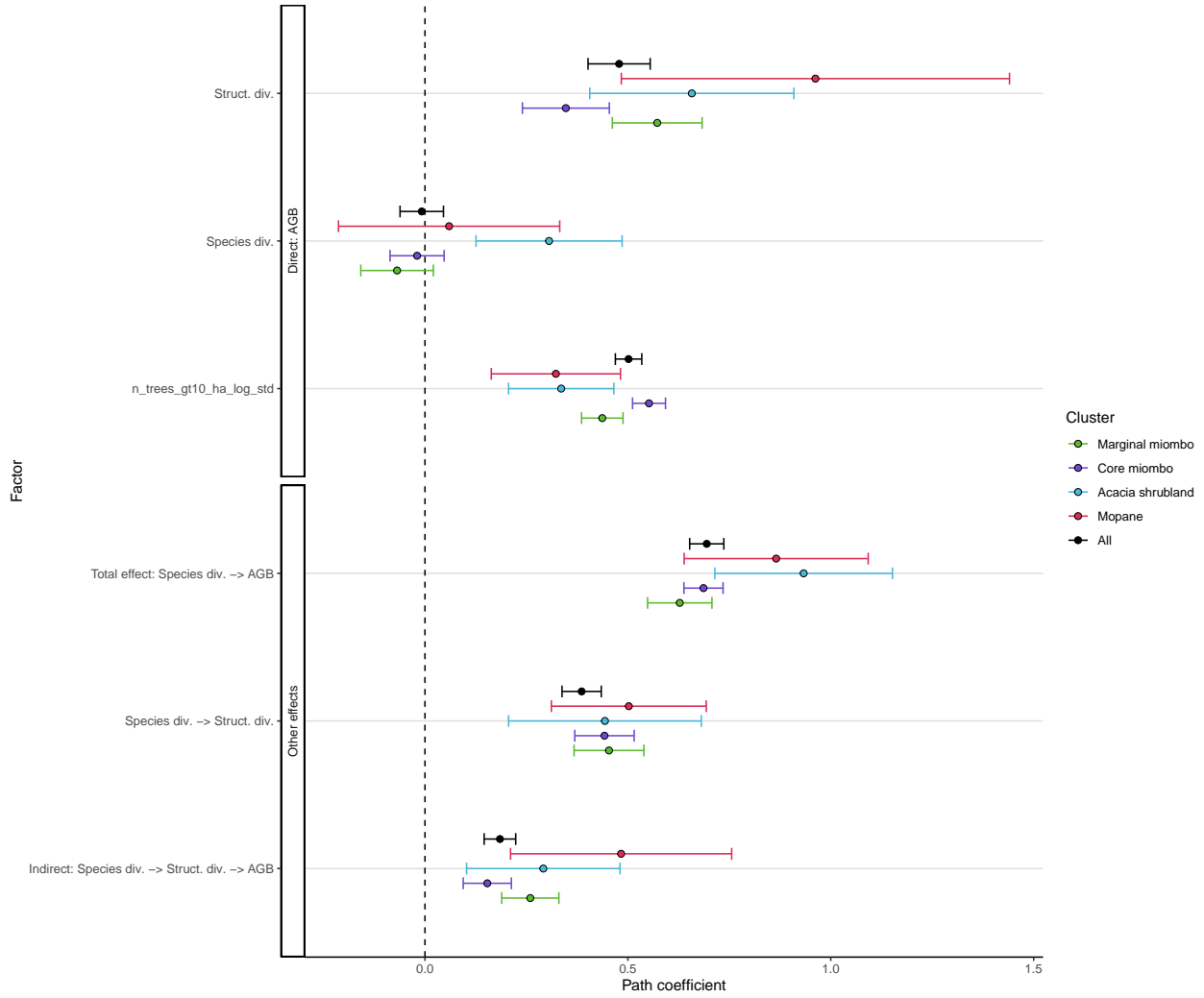


Figure 5: Unstandardised path coefficients for the effects of tree diversity on AGB, mediated by the effect of stand structural diversity. Path coefficients are  $\pm 1$  standard error. Path coefficients where the standard error does not overlap zero are considered to be significant effects.

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

Cluster	n	$\chi^2$	DoF	CFI	TLI	LogLik	RMSEA	$R^2$ AGB
Marginal miombo	390	43.870	6	0.914	0.784	-3111	0.130	0.460
Core miombo	517	78.670	6	0.904	0.759	-3710.000	0.140	0.490
Acacia shrubland	28	9.570	6	0.952	0.879	-180.900	0.130	0.830
Mopane	46	19.880	6	0.834	0.584	-336.500	0.240	0.510
All	981	91.380	6	0.937	0.843	-7517.000	0.120	0.490

### 396 6.3 Moderation of Diversity-AGB relationship by stem density

397 In our sub-sampling of the plot dataset by mean stem density, we found an increasing positive ef-  
398 fect of tree species diversity on AGB as stem density increased (Figure 6). There appears to be a



399 minimum stem density threshold at  $\sim 180$  stems  $\text{ha}^{-1}$  below which there appears to be a reasonably  
 400 constant low baseline effect of tree diversity on biomass. The effect of structural diversity on AGB  
 401 appears to remain constant with increasing stem density. The indirect effect of species diversity on  
 402 AGB via structural diversity climbs slightly as stem density increases.

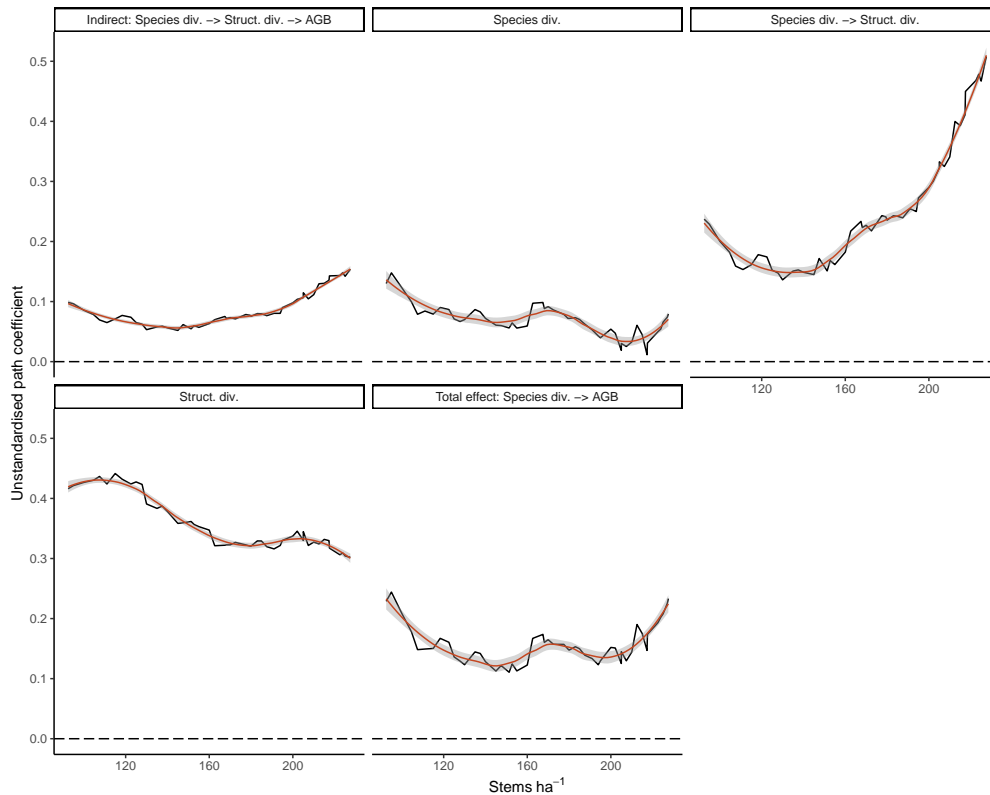


Figure 6: Line plots showing the variation in path coefficients in the SEM, using datasets with different mean stem density. Smoothed lines are loess curves with standard error shaded bars.

#### 403 6.4 Environmental covariates and tree diversity

404 A model incorporating the latent variables of moisture availability and soil fertility showed that  
 405 the total effect of tree species diversity on biomass was greater than that of both moisture avail-  
 406 ability and soil fertility (Figure 7). Surprisingly, the direct effects of moisture availability and  
 407 soil fertility on biomass were negligible, with nearly all of their observed effect on AGB coming  
 408 from the indirect path via species diversity (moisture:  $\beta = -0.01 \pm 0.007$ ,  $p = 0.25$ , soil:  $\beta = -$   
 409  $0.01 \pm 0.012$ ,  $p = 0.24$ ). MAP and temperature seasonality (TS) had the greatest contributions to  
 410 the latent variable of moisture availability. Moisture availability and soil fertility also had neg-  
 411 ligible direct effects on stem density. Model fit was acceptable: CFI = 0.924, TLI = 0.905, and  
 412 RMSEA = 0.16,  $R^2$  of AGB = 0.5.

413 Similar to the model that only considered tree species and structural diversity (Figure 4), the di-  
 414 rect effect of species diversity on structural diversity was positive, while structural diversity itself  
 415 had a positive effect on AGB, leading to a strong positive indirect effect of species diversity on  
 416 AGB via structural diversity ( $\beta = 0.18 \pm 0.037$ ,  $p < 0.01$ ). The total effect of species diversity on  
 417 AGB was positive ( $\beta = 0.26 \pm 0.04$ ,  $p < 0.01$ ).

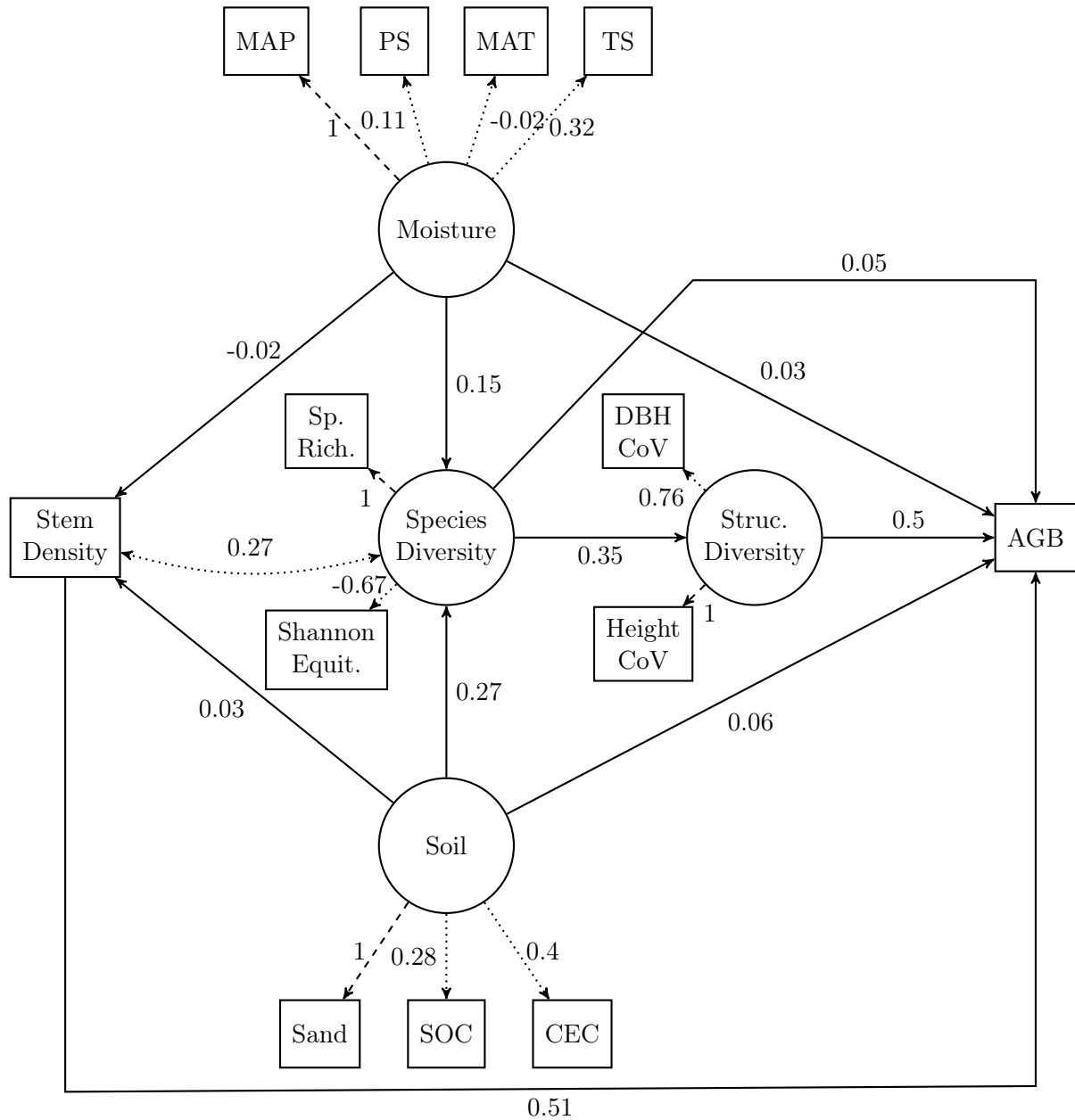


Figure 7: Path diagram with regression coefficients for the SEM incorporating environmental covariates and tree species and structural diversity across all five vegetation types. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are 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 1 are connected by dashed arrows. Correlations between variables are depicted as dotted curved arrows. Measurement errors of exogenous variables are omitted for clarity.

## 7 Discussion

In this study, we assessed the importance of [a] tree species diversity, [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 SAWs, using a network of 1235 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 influ-

ence 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 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 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, either in the form of moisture or soil fertility, on AGB ( $H_3$ ).

## 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 this study. Within SAWs 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 SAWs, a disturbance-structured and poorly studied ecological system.

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 SAWs 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 indirect positive effect of tree species diversity on AGB via structural 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 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 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 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. 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 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. While we did not have access to adequate data on disturbance history in our plots, previous studies have found that SAWs 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  $\sim 180$  stems  $\text{ha}^{-1}$ .

## 7.2 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 of moisture availability on AGB. Compared to moist tropical forests, moisture availability is more of a limiting factor to tree growth in SAWs, which ~~are frequently droughted~~ experience frequent drought. It is possible that the range of observed moisture availability in this study ( $\sim 460\text{--}1700\text{ mm y}^{-1}$ ) may not have been able to capture variation in AGB. 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 along the moisture gradient may have obscured a direct relationship being observed between moisture availability and AGB.

In SAWs 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 (Slik et al., 2009; de Souza et al., 2019).

## 7.3 Vegetation type 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 tree 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.

## 7.4 Conclusion

In this study we found that across southern African woodlands (SAWs), 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 tree canopies. We found that the multiple vegetation types which comprise SAWs 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 SAWs.

SAWs 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 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.

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846 A Data accessibility statement

847 B Tables

848 C Figure legends and embedded figures

849 D Appendix 1 - Frequency distribution of observed variables

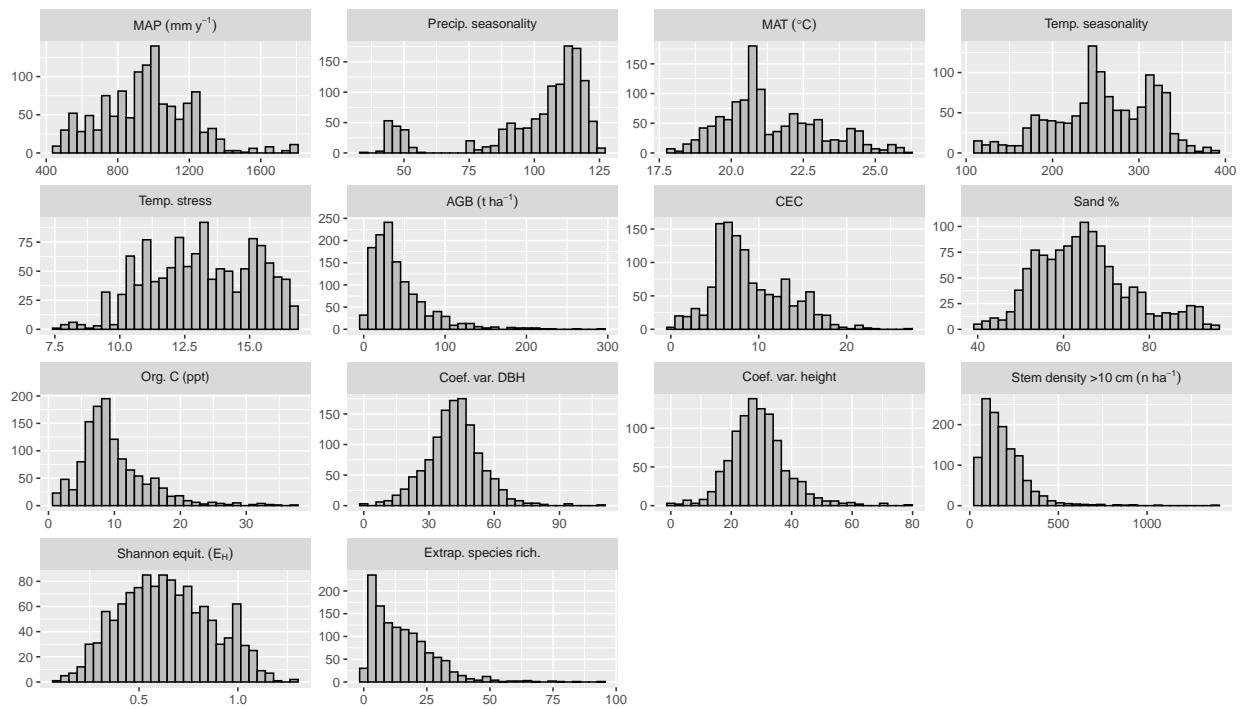


Figure 8: Histograms of raw untransformed observed variables used in final analyses.

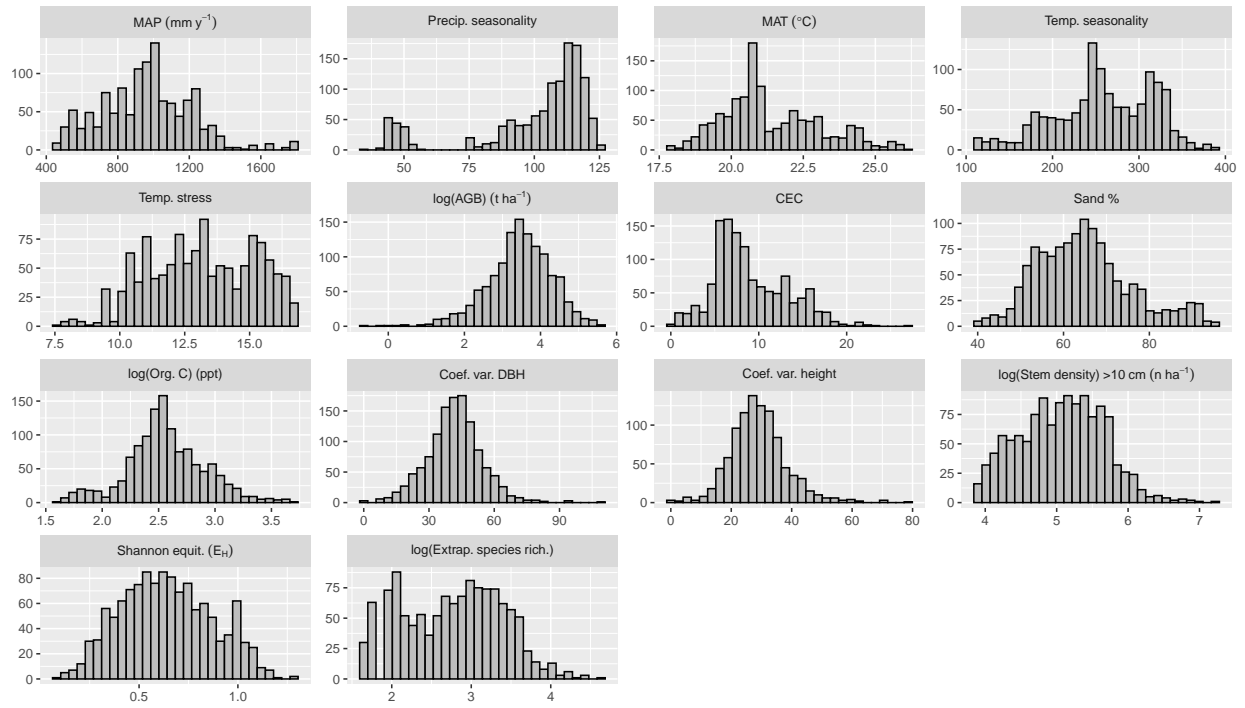


Figure 9: Histograms of observed variables transformed to achieve a normal frequency distribution.

## 850 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.
Sand %	Org. C (ppt)	-0.620	-0.650	-0.580	1235	p <0.01
Sand %	CEC	-0.510	-0.550	-0.470	1235	p <0.01
Sand %	MAP	-0.500	-0.540	-0.460	1235	p <0.01
Sand %	PS	0.350	0.300	0.400	1235	p <0.01
Sand %	MAT	0.340	0.280	0.380	1235	p <0.01
Sand %	TS	0.460	0.410	0.500	1235	p <0.01
Sand %	Sp. rich.	-0.330	-0.370	-0.280	1235	p <0.01
Sand %	Shannon equit.	0.250	0.190	0.300	1235	p <0.01
Sand %	Tree height CV	-0.250	-0.300	-0.190	981	p <0.01
Sand %	DBH CV	-0.170	-0.230	-0.120	1233	p <0.01
Sand %	Stems ha	-0.100	-0.160	-0.050	1235	p <0.01
Sand %	AGB	-0.270	-0.320	-0.220	1235	p <0.01
Org. C (ppt)	CEC	0.460	0.410	0.500	1235	p <0.01
Org. C (ppt)	MAP	0.440	0.390	0.480	1235	p <0.01
Org. C (ppt)	PS	-0.410	-0.450	-0.360	1235	p <0.01
Org. C (ppt)	MAT	-0.280	-0.330	-0.230	1235	p <0.01
Org. C (ppt)	TS	-0.470	-0.520	-0.430	1235	p <0.01
Org. C (ppt)	Sp. rich.	0.150	0.090	0.200	1235	p <0.01
Org. C (ppt)	Shannon equit.	-0.160	-0.220	-0.110	1235	p <0.01
Org. C (ppt)	Tree height CV	0.180	0.120	0.240	981	p <0.01
Org. C (ppt)	DBH CV	0.140	0.080	0.190	1233	p <0.01
Org. C (ppt)	Stems ha	0.090	0.030	0.140	1235	p <0.01

Org. C (ppt)	AGB	0.270	0.220	0.320	1235	p < 0.01
CEC	MAP	-0.070	-0.130	-0.020	1235	p < 0.01
CEC	PS	-0.590	-0.630	-0.550	1235	p < 0.01
CEC	MAT	0.170	0.120	0.220	1235	p < 0.01
CEC	TS	-0.450	-0.490	-0.410	1235	p < 0.01
CEC	Sp. rich.	-0.100	-0.160	-0.050	1235	p < 0.01
CEC	Shannon equit.	-0.120	-0.180	-0.070	1235	p < 0.01
CEC	Tree height CV	0.090	0.020	0.150	981	p < 0.01
CEC	DBH CV	0.130	0.080	0.190	1233	p < 0.01
CEC	Stems ha	-0.090	-0.140	-0.030	1235	p < 0.01
CEC	AGB	0.080	0.030	0.140	1235	p < 0.01
MAP	PS	-0.070	-0.130	-0.020	1235	p < 0.05
MAP	MAT	-0.200	-0.260	-0.150	1235	p < 0.01
MAP	TS	-0.480	-0.520	-0.440	1235	p < 0.01
MAP	Sp. rich.	0.400	0.350	0.450	1235	p < 0.01
MAP	Shannon equit.	-0.130	-0.180	-0.070	1235	p < 0.01
MAP	Tree height CV	0.250	0.190	0.310	981	p < 0.01
MAP	DBH CV	0.120	0.060	0.170	1233	p < 0.01
MAP	Stems ha	0.070	0.010	0.120	1235	p < 0.05
MAP	AGB	0.230	0.180	0.280	1235	p < 0.01
PS	MAT	0	-0.050	0.060	1235	p = 0.95
PS	TS	0.500	0.460	0.540	1235	p < 0.01
PS	Sp. rich.	0.130	0.070	0.180	1235	p < 0.01
PS	Shannon equit.	0.070	0.010	0.130	1235	p < 0.05
PS	Tree height CV	-0.060	-0.120	0.010	981	p = 0.07
PS	DBH CV	-0.100	-0.150	-0.040	1233	p < 0.01
PS	Stems ha	-0.030	-0.080	0.030	1235	p = 0.33
PS	AGB	-0.190	-0.240	-0.130	1235	p < 0.01
MAT	TS	-0.070	-0.130	-0.020	1235	p < 0.05
MAT	Sp. rich.	-0.170	-0.220	-0.120	1235	p < 0.01
MAT	Shannon equit.	0	-0.060	0.060	1235	p = 0.98
MAT	Tree height CV	-0.040	-0.100	0.020	981	p = 0.2
MAT	DBH CV	0.060	0.010	0.120	1233	p < 0.05
MAT	Stems ha	-0.150	-0.210	-0.100	1235	p < 0.01
MAT	AGB	-0.090	-0.150	-0.040	1235	p < 0.01
TS	Sp. rich.	-0.130	-0.180	-0.070	1235	p < 0.01
TS	Shannon equit.	0.140	0.080	0.190	1235	p < 0.01
TS	Tree height CV	-0.150	-0.210	-0.090	981	p < 0.01
TS	DBH CV	-0.050	-0.100	0.010	1233	p = 0.11
TS	Stems ha	0.030	-0.030	0.090	1235	p = 0.3
TS	AGB	-0.170	-0.220	-0.120	1235	p < 0.01
Sp. rich.	Shannon equit.	-0.580	-0.620	-0.540	1235	p < 0.01
Sp. rich.	Tree height CV	0.300	0.250	0.360	981	p < 0.01
Sp. rich.	DBH CV	0.300	0.250	0.350	1233	p < 0.01
Sp. rich.	Stems ha	0.240	0.190	0.300	1235	p < 0.01
Sp. rich.	AGB	0.310	0.260	0.360	1235	p < 0.01
Shannon equit.	Tree height CV	-0.120	-0.190	-0.060	981	p < 0.01
Shannon equit.	DBH CV	-0.200	-0.250	-0.140	1233	p < 0.01
Shannon equit.	Stems ha	-0.410	-0.460	-0.360	1235	p < 0.01
Shannon equit.	AGB	-0.350	-0.400	-0.300	1235	p < 0.01
Tree height CV	DBH CV	0.470	0.420	0.520	981	p < 0.01
Tree height CV	Stems ha	0.010	-0.060	0.070	981	p = 0.86
Tree height CV	AGB	0.240	0.180	0.290	981	p < 0.01

DBH CV	Stems ha	0.110	0.060	0.170	1233	$p < 0.01$
DBH CV	AGB	0.430	0.390	0.480	1233	$p < 0.01$
Stems ha	AGB	0.590	0.550	0.620	1235	$p < 0.01$

851 **F Appendix 3 - Bivariate relationships of model variables**

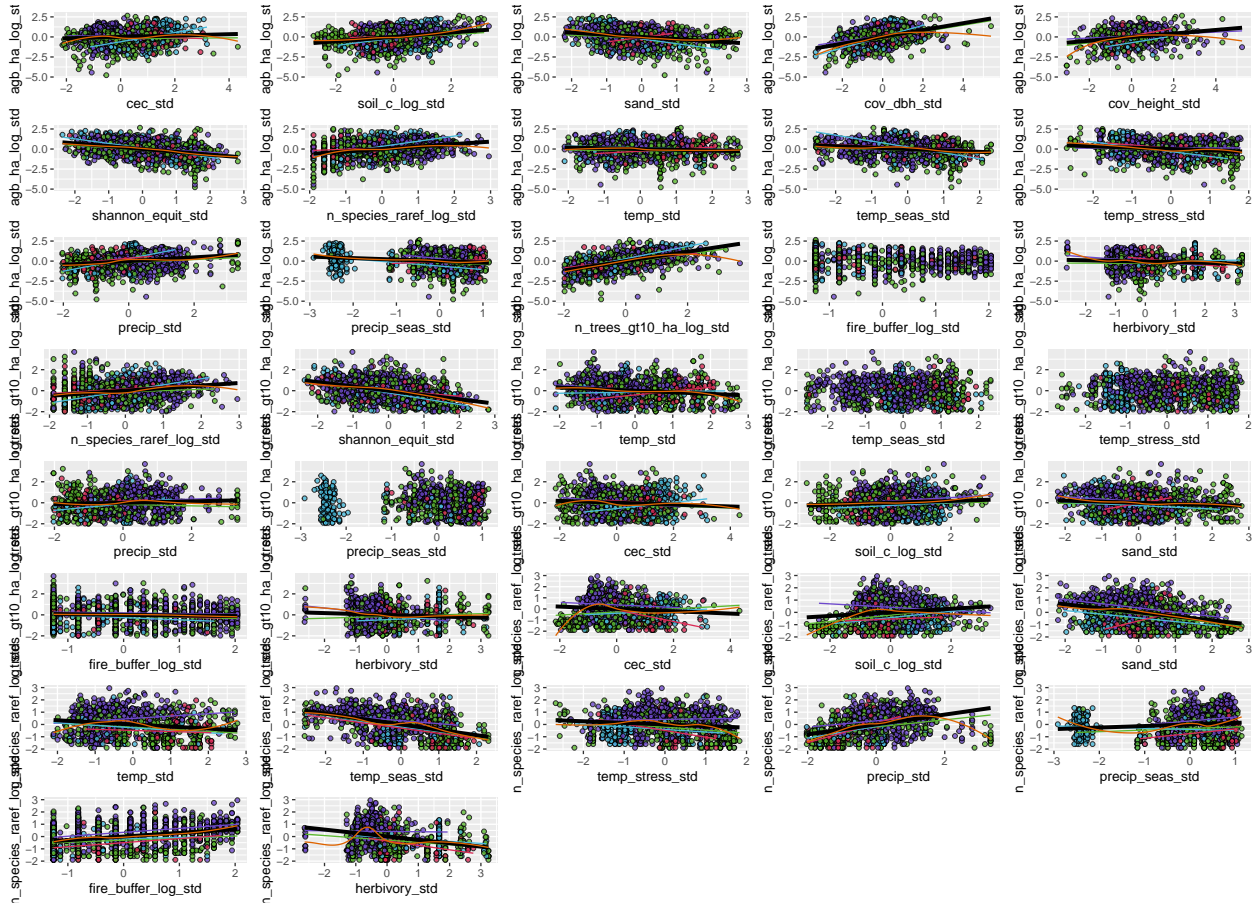


Figure 10