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 species diversity and ecosystem function have been widely documented, but the nature of the relationship 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, while controlling for gradients in stem 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/woodland tree plots located across the southern African sub-continent . 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, observed mainly via the increasing effect of 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 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 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 through human actions in southern Africa, may have detrimental outcomes for ecosystem function, specifically woody biomass provision, which is critical in a region that relies on wood fuel as its principal domestic energy source.

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 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 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 ecosystems, 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 nature of biotic activity within an ecosystem (Jax, 2005). This includes 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 relationship between biodiversity and ecosystem function invokes three main mechanisms 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 resource acquisition strategies; 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 forest ecosystems, dry tropical woodlands and savannas are highly structured by disturbance, mainly through fire 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 (Dewees et al., 2010). High levels of disturbance, by fire or otherwise, may weaken the role of competition in determining local species distribution. Disturbance may reduce stem density, reducing competitive interactions between individuals, allowing 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 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). Reduced stem density reduces competition between individuals, possibly weakening the effect of diversity on ecosystem function via niche complementarity. Similarly, more diverse species assemblages may lead to facilitation effects between certain species combinations under limiting environmental conditions such as low water availability. 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' abundances, 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 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, a narrow geographic region (Barthlott et al., 2005). A severe lack of study in dry tropical ecosystems, especially given the potential divergence in BEF relationship mechanisms described above, suggests that a focus on these ecosys-

tems 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.These retain the common features of an open tree canopy and an understorey generally dominated by C4 grasses. Southern African savannas and woodlands are highly diverse, thought to harbour ~8500 plant species of which >300 are 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 (Cardinale et al., 2009). 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, disturbance regime, 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 broad 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. 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). In wet tropical forests in Central America, Condit et al. (2013) found that dry season intensity was the main determinant of tree species distribution and abundance evenness.

Southern African woodlands possess structurally diverse tree canopies, with trees occupying distinct layers of the canopy, depending on their growth stages and species identity Solbrig et al. (1996). 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. Occupancy of multiple canopy layers allows a fuller canopy with 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 a given woodland plant community 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) with path analysis as a preferred method to simultaneously account for environmental and biotic factors, which may have interacting effects on ecosystem structure and therefore biomass. Initially, we posited three hypotheses: (1) water availability and soil fertility will indirectly positively affect woody biomass via an increase in tree species diversity, (2) the strength of the effect of tree species diversity on woody biomass will increase with plot-level stem density (number of stems ha^{-1}), as affected by resource availability and disturbance, due to an increased importance of niche complementarity as stem density and therefore 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 miombo ecoregion (Figure 1, Hopkins and White 1987). The study 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. A 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 (Hopkins and White, 1987), using WorldClim estimates of Mean Annual Temperature (MAT, BIO1) and Mean Annual Precipitation (MAP, BIO12) between 1970 and 2000 with a pixel size of 30 arc seconds (926 m at equator) (Fick and Hijmans, 2017).

Plots were chosen from a larger pool of 5395 plots held in the SEOSAW database (SEOSAW, 2019) 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

221 a stem density >50 trees ha^{-1} (>10 cm stem diameter) were used, to ensure all plots represented
222 woodland rather than "grassy savanna", which is considered a separate biome with very different
223 species composition (Parr et al., 2014).

224 Many plots provided by the 2005-2008 Zambian Integrated Land Use Assessment (Mukosha and
225 Siampale, 2009) were arranged in clusters of up to four 20x50 m plots, 20 metres apart. Plots
226 within each cluster were aggregated before the plot dataset filtering described above and treated
227 as a single plot in analyses.

5.2 Data collection

229 We considered only trees and shrubs in our calculations of Above-Ground woody Biomass (AGB),
230 including woody species such as palms and cycads which are functionally tree-like. Woody lianas
231 are scarce in our study plots and were not measured. Only stems >10 cm DBH (Diameter at Breast
232 Height, 1.3 m) were included in analyses. Many plots in the dataset did not include data on stems
233 <10 cm DBH. For those plots which contained stem measurements <10 cm DBH, small stems
234 only accounted for a median of 2.1% of the plot level AGB.

235 All stems >10 cm DBH were measured within each plot resulting in a total of 66,758 stems with
236 measurements. A tree may be comprised of multiple stems and so tree-level diversity estimates,
237 rather than stem-level estimates, were used to prevent bias from species which readily coppice.
238 For each tree, we recorded species, DBH and tree height to the top of the highest branch material.
239 Height was measured through a variety of means including laser rangefinders, manual clinometers
240 and measuring sticks. When DBH could not be measured at 1.3 m due to trunk abnormalities, it
241 was measured at the closest regular portion of the trunk to 1.3 m. The height of this measurement
242 was recorded and used to estimate the DBH$_e$ at 1.3 m using a cubic polynomial regression, with
243 parameters estimated using a test dataset from Ryan C., (unpublished), see Godlee et al. (2020).

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

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

245 where ρ is the species level mean wood density, D is the DBH$_e$ at 1.3 m, and H is the tree height.
246 Wood density estimates were taken from the global wood density database for each species where
247 possible (Chave et al., 2009; Zanne et al., 2009). Wood density for species without species level
248 estimates was estimated from the means of their respective genera. For stems where tree height
249 was unknown, the plots' climatic parameters, estimated from plot location, were used to estimate
250 tree height, according to Chave et al. (2014).

251 Climatic data were taken from the WorldClim database, using the BioClim variables (Fick and
252 Hijmans, 2017). In addition to MAT and MAP, temperature stress was calculated as the mean
253 diurnal temperature range (BIO2) and precipitation seasonality was calculated as the mean of the
254 coefficient of variation of monthly mean precipitation (BIO15). Soil fertility data were extracted
255 from the ISRIC gridded soil information data product at 250 m resolution, taking the grid cell
256 value for each plot centre (Hengl et al., 2017). We extracted Cation Exchange Capacity (CEC),
257 soil organic carbon stocks (kg m^{-2}) soil sand content by volume (Sand g kg^{-1}) and soil nitrogen
258 content (g kg^{-1}). These data are a modelled product derived from various remotely sensed and
259 directly measured data sources. The degree of fire disturbance was calculated using the MODIS
260 monthly burned area product at 0.01 degree resolution, 1.11 km at the equator (MCD64A1, Giglio
261 et al. 2015), as the number of observed fires between 2001 and 2018.

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 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 esti- mated species richness. Abundance evenness allows for greater niche complementarity at small scales due to potentially increased heterogeneity of functional traits. We quantified tree struc- tural 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 de- fined in Fayolle et al. (2018) in an Africa-wide analysis of floristic units using plot data in savan- nas and woodlands with tree species diversity and relative abundance data. Group identification was conducted using unconstrained correspondence analysis, followed by hierarchical clustering based on dominant ordination axes. Plot data used in this study occurred in four compositional vegetation types. See Table 1 for a description of each vegetation cluster and Figure 1 for the spa- tial 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	*Brachystegia spiciformis* *Julbernardia paniculata* *Brachystegia boehmii*	*Parinari curatellifolia* *Uapaca kirkiana* *Brachystegia spiciformis*	523	20(16.9)	204(142.5)	44.2(36.11)
ex-Acacia	Spirostachys africana *Senegalia burkei* *Senegalia nigrescens*	*Euclea racemosa* *Vachellia nilotica* *Spirostachys africana*	188	12(10.3)	181(166.5)	54.5(61.33)
Mopane	*Colophospermum mopane* *Androstachys johnsonii* *Kirkia acuminata*	*Colophospermum mopane* *Psuedolachnostylis maprouneifolia* *Lannea discolor*	58	10(10.2)	186(125.6)	42.7(32.83)
Sparse miombo / Baikiaea	*Baikiaea plurijuga* *Burkea africana* *Pterocarpus angolensis*	*Burkea africana* *Baikiaea plurijuga* *Pterocarpus angolensis*	466	12(13.7)	178(129.5)	36.9(26.98)
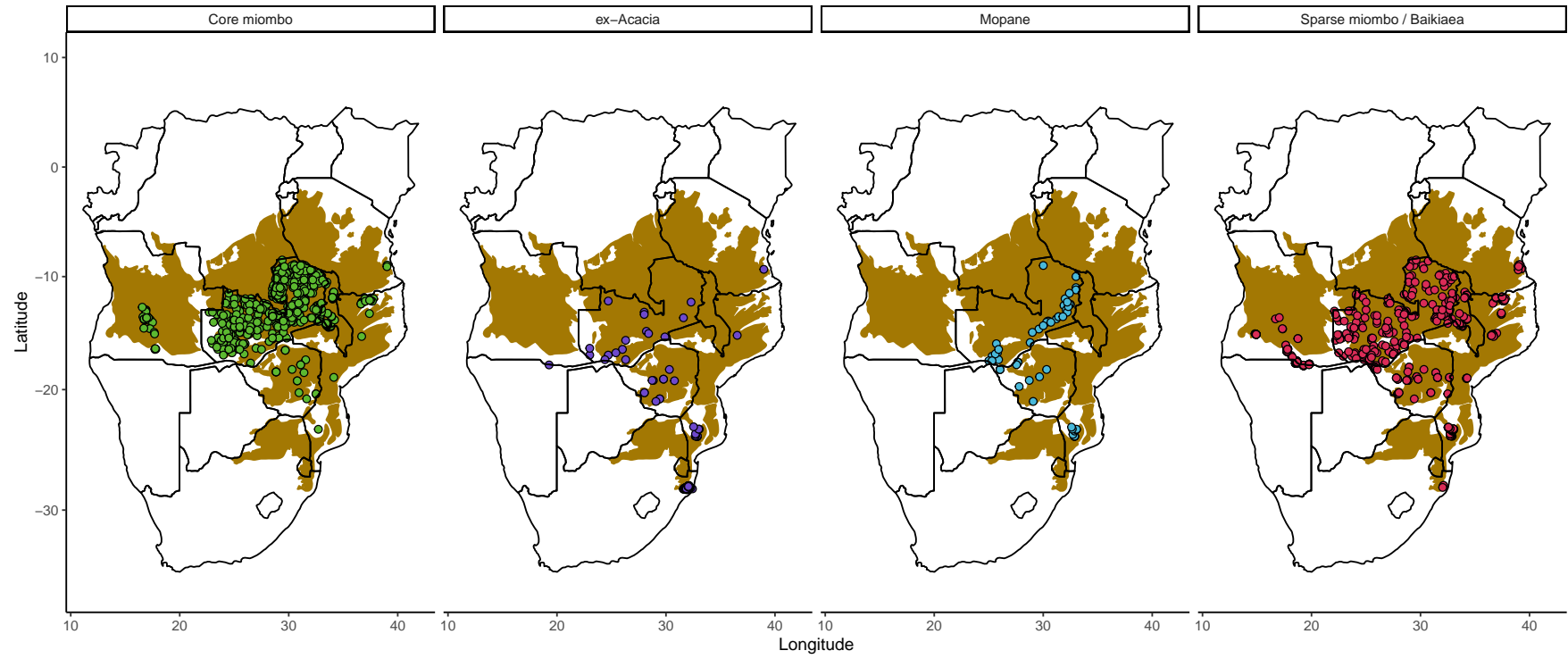
Figure 1: The locations of the 1235 plots used in this study, with respect to the distribution of miombo woodland vegetation according to Hopkins and White (1987). Each panel shows plots categorized by their vegetation type as defined by the vegetation types in Table 1.

5.3.3 Structural Equation Modelling

We used Structural Equation Modelling (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 SEM 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 "water availability", "soil fertility", and "disturbance" which have been suggested to act upon biodiversity and biomass/productivity in previous studies despite these factors not having directly observable measures in our dataset. SEM is also necessary to properly account for potential feedback mechanisms between aspects of 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: water availability, soil fertility, disturbance, tree species diversity, tree structural diversity and stem density (Figure 2).
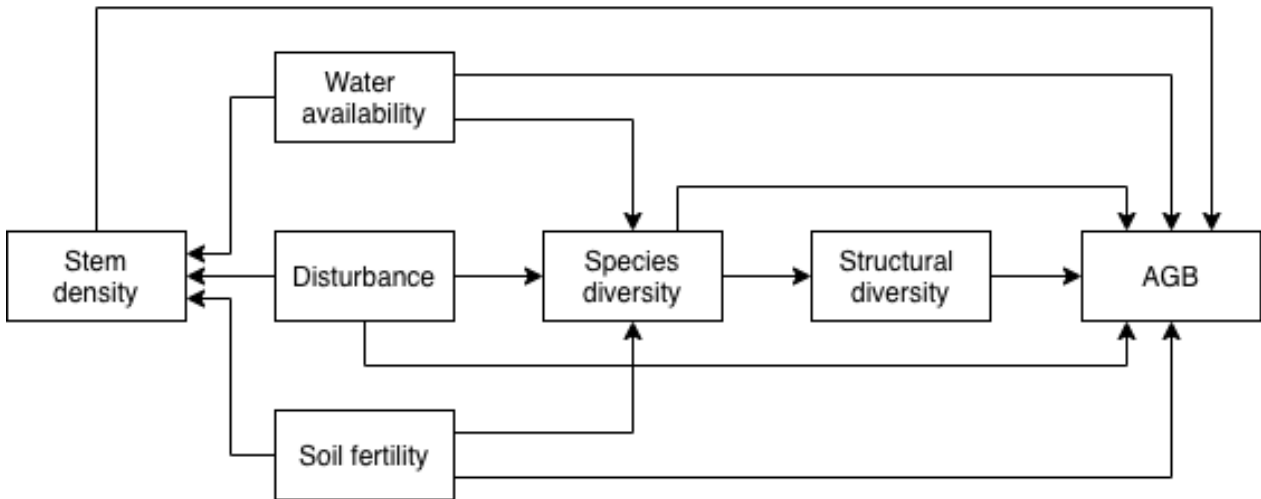

Figure 2: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural diversity, stem density, and AGB. Hypothesised paths of causation are depicted as arrows from predictor to response.

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 variation across 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 water availability is expected to decrease as soil sand content increases, therefore sand content was reversed for use in the water availability latent variable. Precipitation seasonality, and temperature stress were also reversed in this way to account for the direction of their effect on water 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 combi-

nations 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 Maximum 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. Structural diversity can also directly influence AGB in this model, without an effect of species diversity. To account for variation in stem density, which may covary with species diversity, we 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 type separately. We compared unstandardised path coefficients among the models for different vegetation types 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 given path with other paths 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 assessed model fit in each case, taking into consideration the recommendations of Hu and Bentler (1999) 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 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 deliberately controlled 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. Preliminary analyses that included herbivore biomass (Hempson et al., 2017) did not converge, possibly due to the spatially coarse nature of the available data, we therefore did not include herbivory in our final model. We incorporated environmental covariates into our model to understand the relative effects of water availability, soil fertility and disturbance 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 types were narrow in their climate space, leading to a lack of environmental variation, particularly in the water availability latent variable.
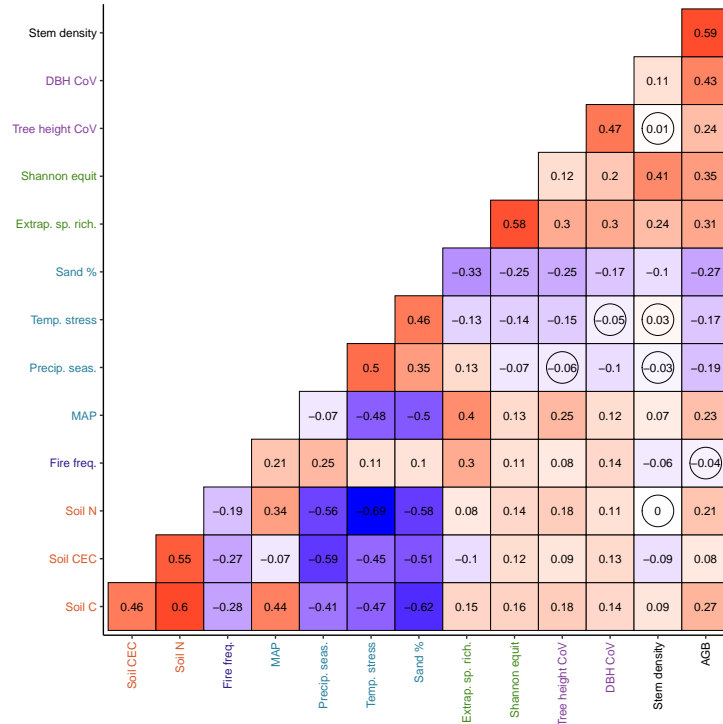
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6 Results

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 = water 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 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 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 stem 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 stem 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 stem 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 stem density ($\beta = 0.5\pm0.033$, p <0.01).
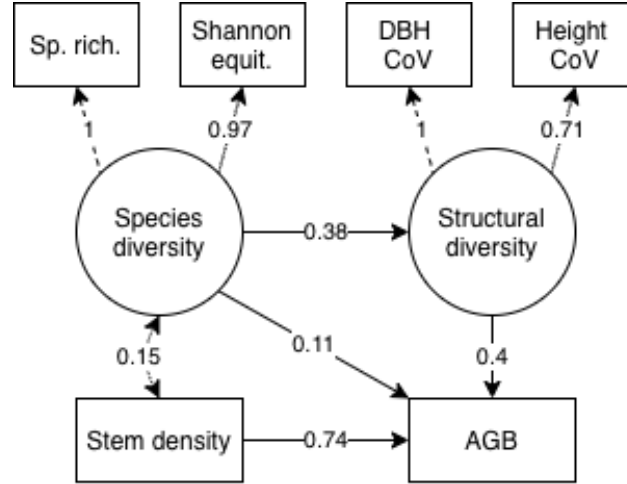

Figure 4: Path diagram with regression coefficients for the tree diversity SEM, including plots from all vegetation clusters. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are shown as solid arrows pointing from predictor to response with the effect size of the path coefficient expressed in terms of standard deviations on the latent variable response scale. 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).
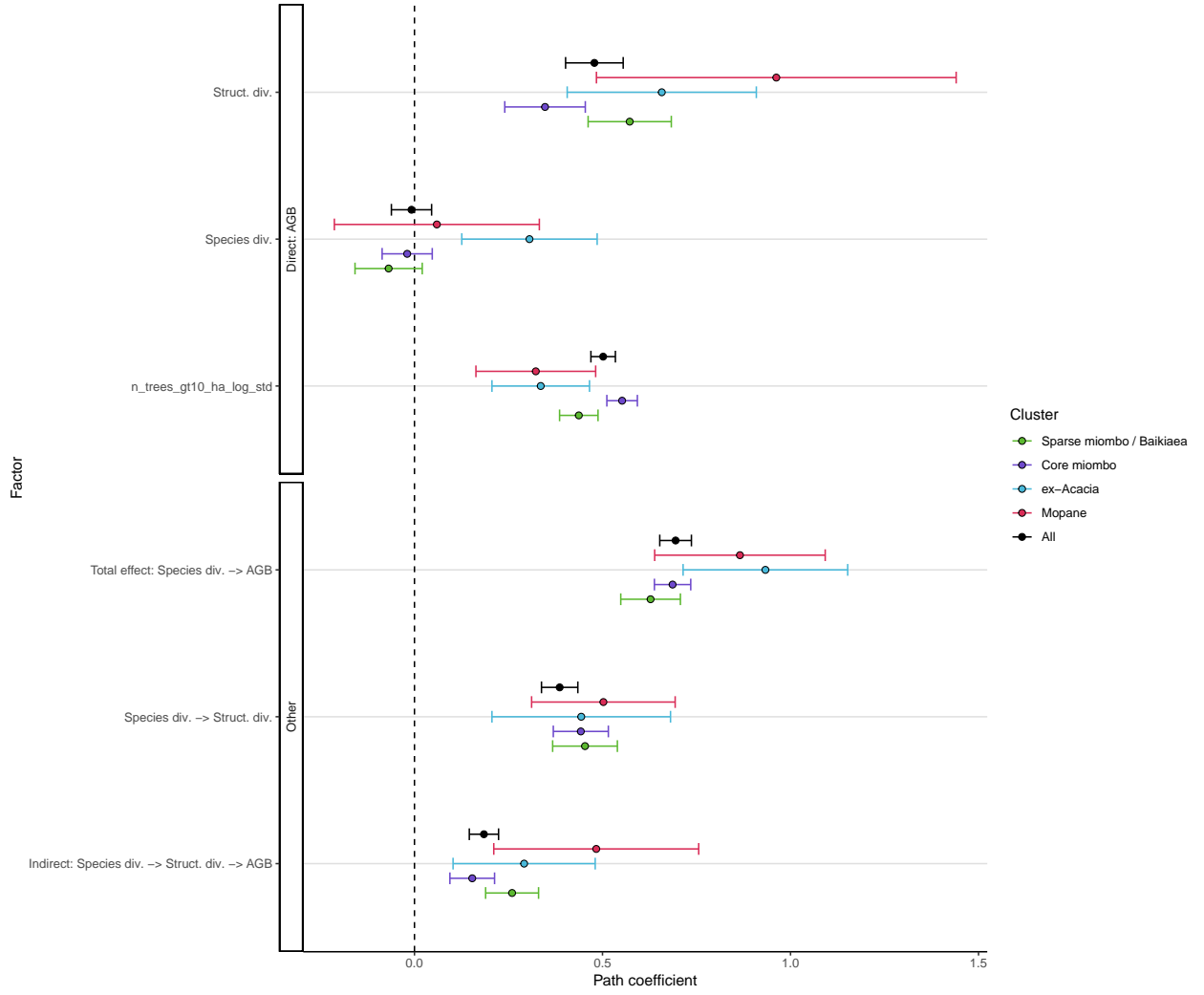
Figure 5: Unstandardised path coefficients for the effects of tree diversity on AGB, mediated by the effect of stand structural diversity. Path coefficients are ±1 standard error. Path coefficients where the standard error does not overlap zero are considered to be significant effects.

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	466	43.870	6	0.914	0.784	0.130	0.580
Core miombo	523	78.670	6	0.904	0.759	0.140	0.490
ex-Acacia	188	9.570	6	0.952	0.879	0.130	0.830
Mopane	58	19.880	6	0.834	0.584	0.240	0.510
All	1235	91.380	6	0.937	0.843	0.120	0.490

6.3 Moderation of Diversity-AGB relationship by stem density

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

mum stem density threshold at ~180 trees ha⁻¹ below which there appears to be a reasonably con-
stant, small baseline effect of tree diversity on biomass. The effect of structural diversity on AGB
appears to remain constant with increasing stem density. The indirect effect of species diversity on
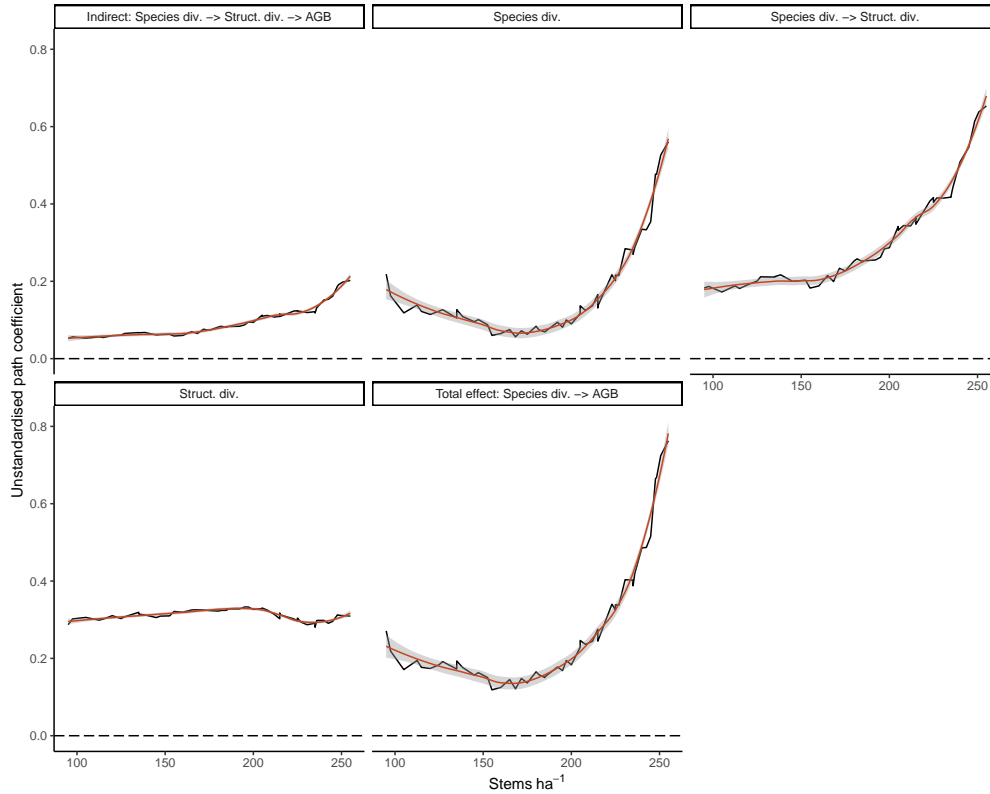AGB via structural diversity climbs as stem density increases.

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.

6.4 Environmental covariates and tree diversity

A model incorporating the latent variables of water availability, soil fertility and disturbance by
fire showed that the total effect of tree species diversity on biomass was similar to that of water
availability, soil fertility and disturbance (Figure 7, Figure 8). The direct effects of water availabil-
ity, soil fertility and disturbance on AGB were negligible (water: $\beta = 0.1 \pm 0.13$, 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 paths via stem density (water: $\beta = 0.14 \pm 0.091$, 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 (wa-
ter: $\beta = 0.62 \pm 0.172$, 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 wa-
ter 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 di-
rect 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 ac-
counted 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).
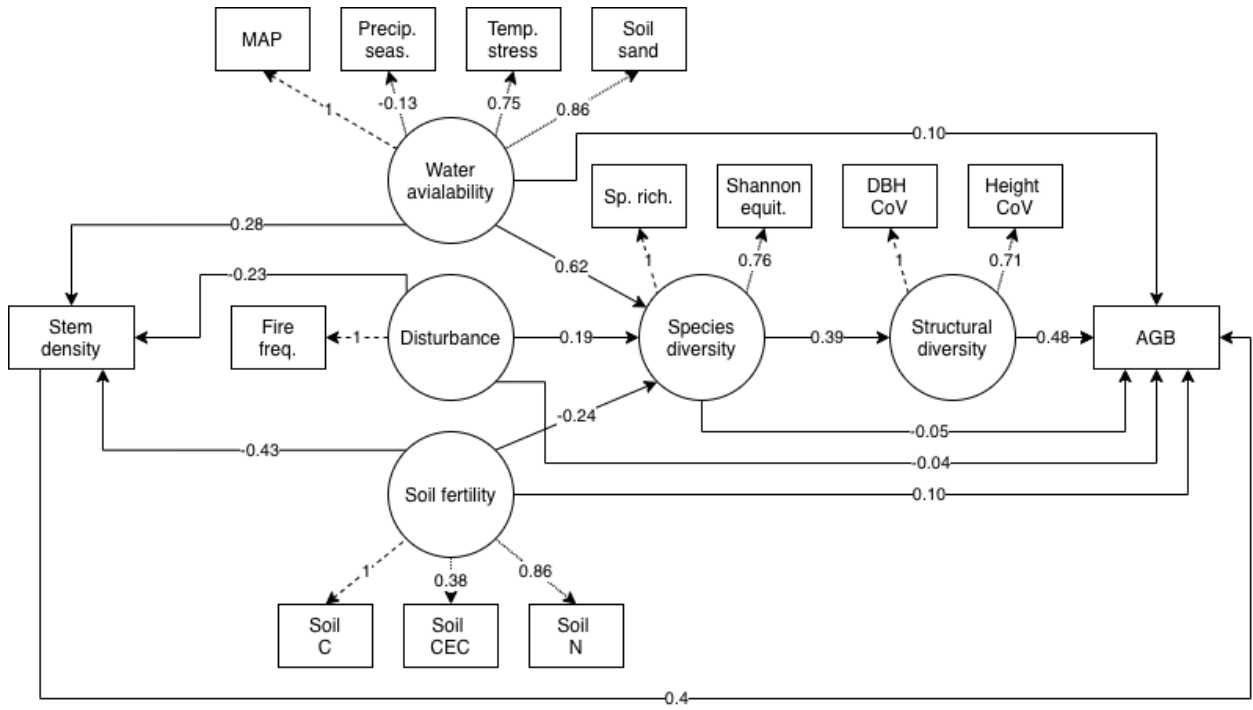
Figure 7: Path diagram with regression coefficients for the SEM incorporating environmental covariates and tree species and structural diversity across all five vegetation types. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are 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 one are connected by dashed arrows. Measurement errors of exogenous variables are omitted for clarity.
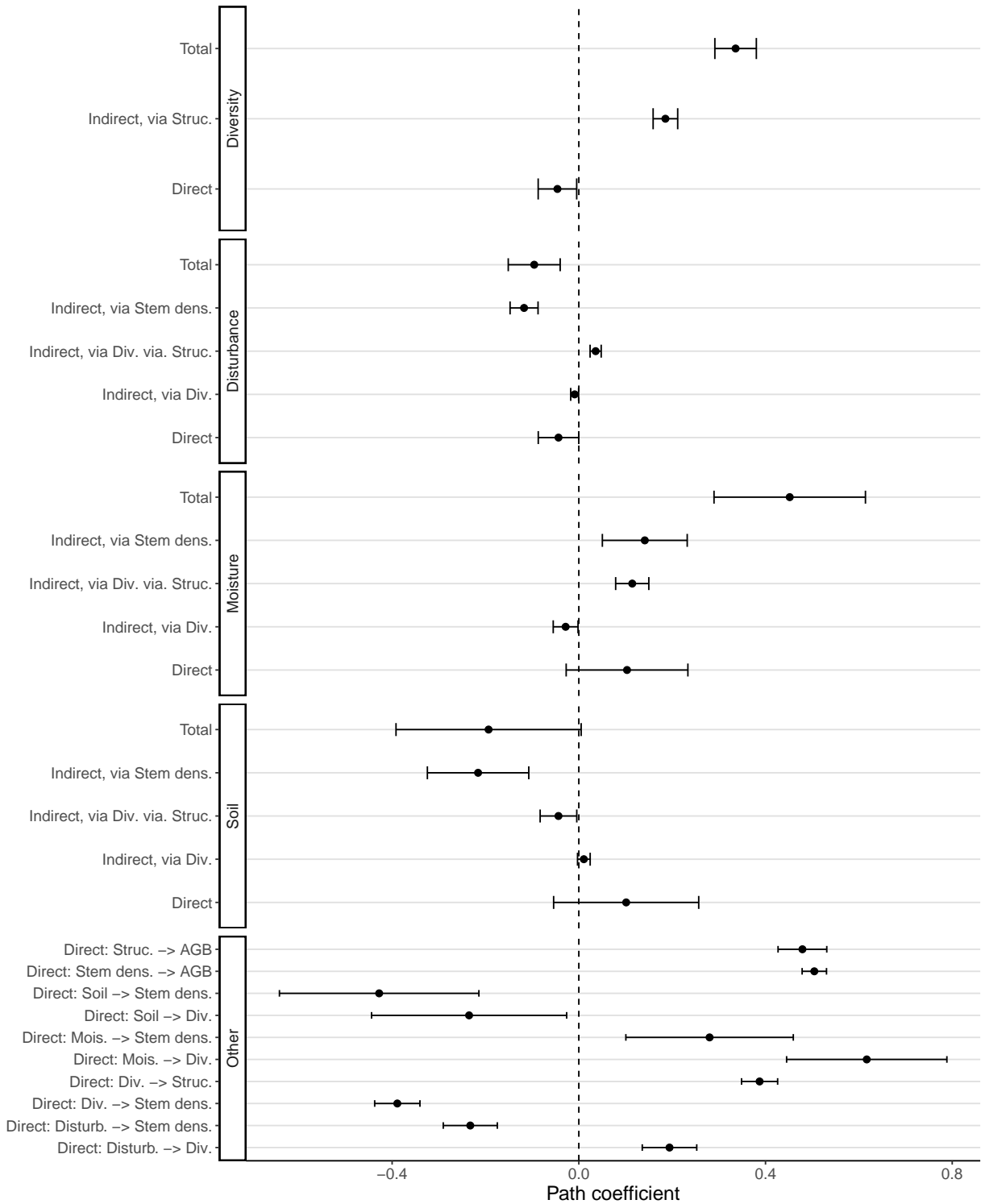
Figure 8: Unstandardised path coefficients for the full model including tree species diversity, environmental covariates and stem density. Path coefficients are ±1 standard error. Path coefficients where the standard error does not overlap zero are considered significant effects.

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] stem 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, operating indirectly via structural diversity (H_1). We found that the effect size of tree species diversity on AGB increased with stem density (H_2). Tree species 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. When the effects of water 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 leads to 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 stem density. It is possible that within southern African woodlands a higher species diversity allows for a higher stem 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 stem density causing higher species richness through an increased probability of encountering new species. We attempted to correct for the correlation between species richness and stem density by estimating, and using in models, 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 water availability on AGB via stem density in the model which included environmental covariates.

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 canopy of diversely sized trees 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; broad flat crowns vs. narrow deep crowns, 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 stem density supports this mechanism. 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 (Chidumayo, 2013).

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 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 small effect of tree species diversity on AGB below ~180 trees ha^{-1}. At very high stem density, there is also an 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 water availability, soil fertility and disturbance

Water availability had a positive total effect on AGB, comparable in size to the total effect of tree species diversity on AGB, while soil fertility had a negative total effect. We expected that higher water 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 water 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 indirect positive effects of water availability on AGB via species diversity and a positive but only marginally significant direct effect on AGB. Compared to moist tropical forests, water availability is more of a limiting factor to tree growth in southern African woodlands, which experience frequent drought. The negative total effect of soil fertility on AGB was driven mostly by an indirect negative effect via stem density, however, the direct effect on AGB remained positive and marginally significant, as expected. Disturbance by fire had a negative total effect on AGB. We found negligible indirect effects of disturbance on AGB via species diversity and structural diversity.

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, overall species richness and mean biomass.

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 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 slight 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 top level of 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. In other words, 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 not lead to niche partitioning, 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 and 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 woodlands showed 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 woodlands also had 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* and *Vachellia* 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 ecosystem function, quantified as above-ground woody biomass (AGB). Additionally, we found that much of this effect of species diversity on biomass exists as an indirect effect by increasing the structural diversity of trees. We found that the multiple vegetation types which comprise southern African woodlands exhibit similarities in the relationship between species diversity and woody biomass, suggesting that similar ecosystem processes occur across the region to determine ecosystem function. In contrast to previous studies, we found, at the scale of our study region, that the direct effects of water availability and soil fertility on woody biomass were negligible, with most of their effect being indirectly through their effects on tree species and structural diversity. This strongly suggests that data on tree species diversity be included into models predicting ecosystem functionality in this region. We also advocate for explicit inclusion of environmental covariates in regional scale models of biodiversity and ecosystem function, generally.

Southern African woodlands are relied heavily upon for their ecosystem service provision, which is itself related to 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 low species diversity, which are those areas 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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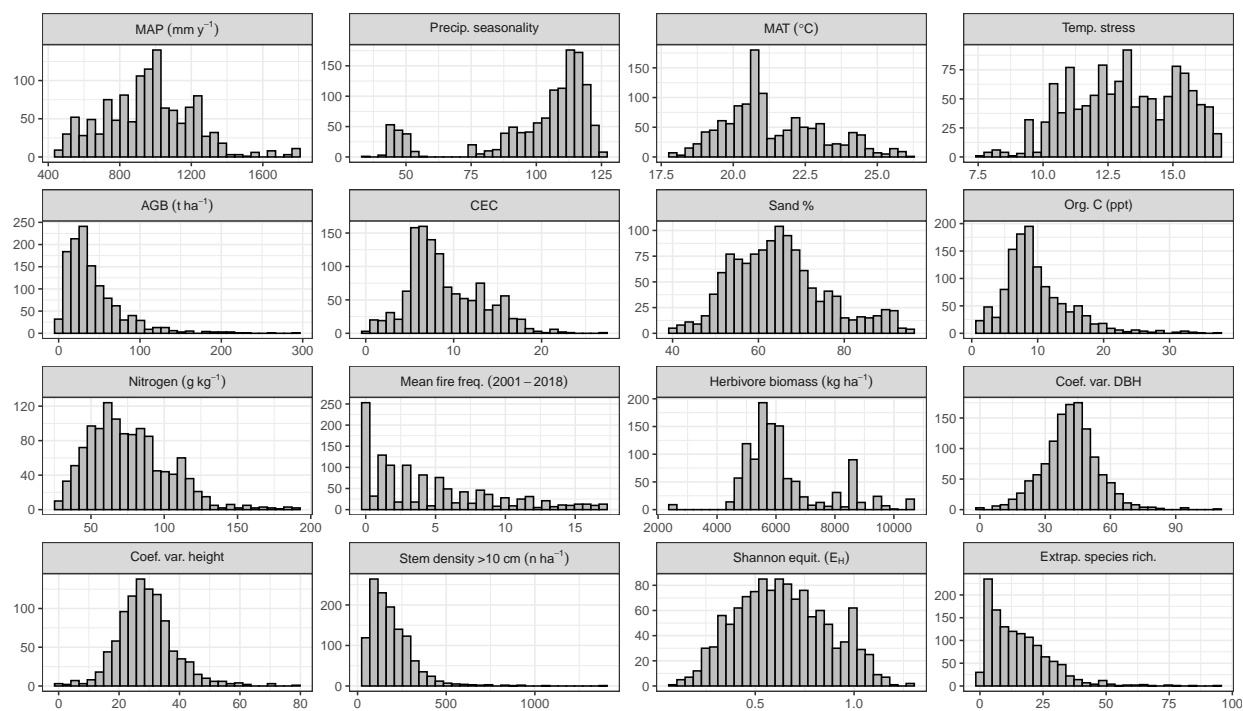
Figure 9: Histograms of raw untransformed observed variables used in final analyses.
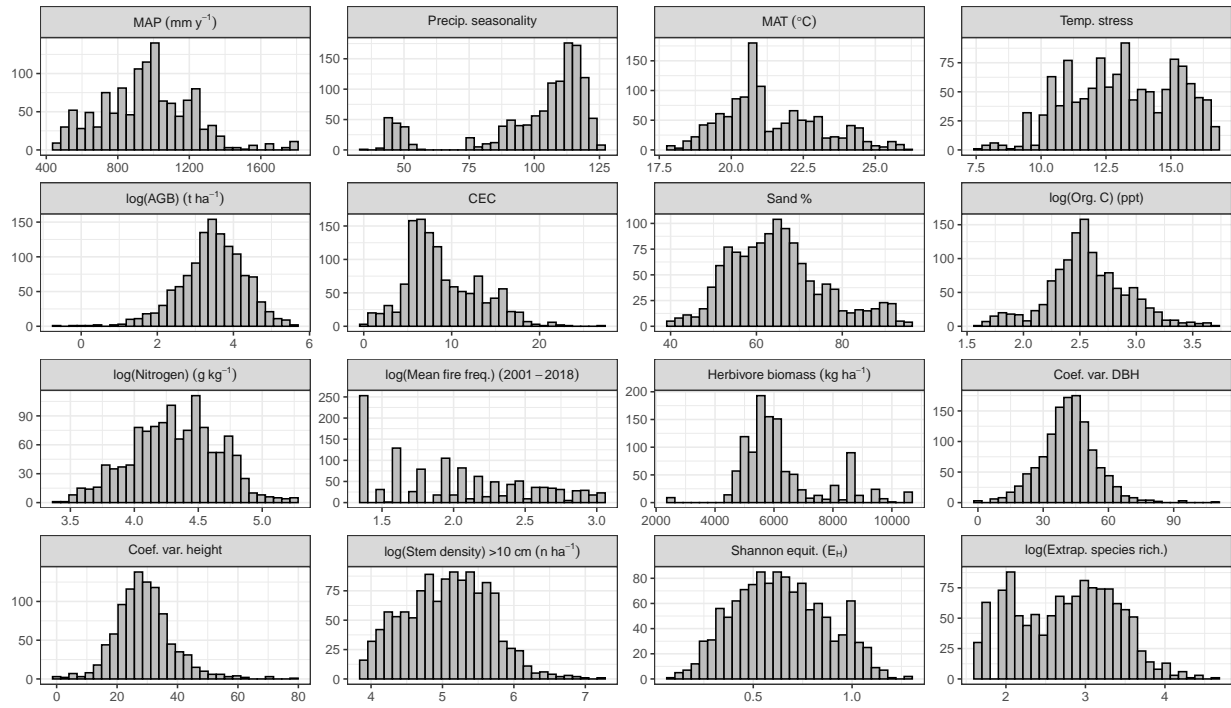
Figure 10: Histograms of observed variables transformed to achieve a normal frequency distribution.

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
Stem 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
Stem 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
Stem 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
Stem 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
Stem 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
Stem 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
Stem 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
Stem 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
Stem 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
Stem 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
Stem 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
Stem 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	Stem density	0.590	0.550	0.620	1235	p $<$0.01

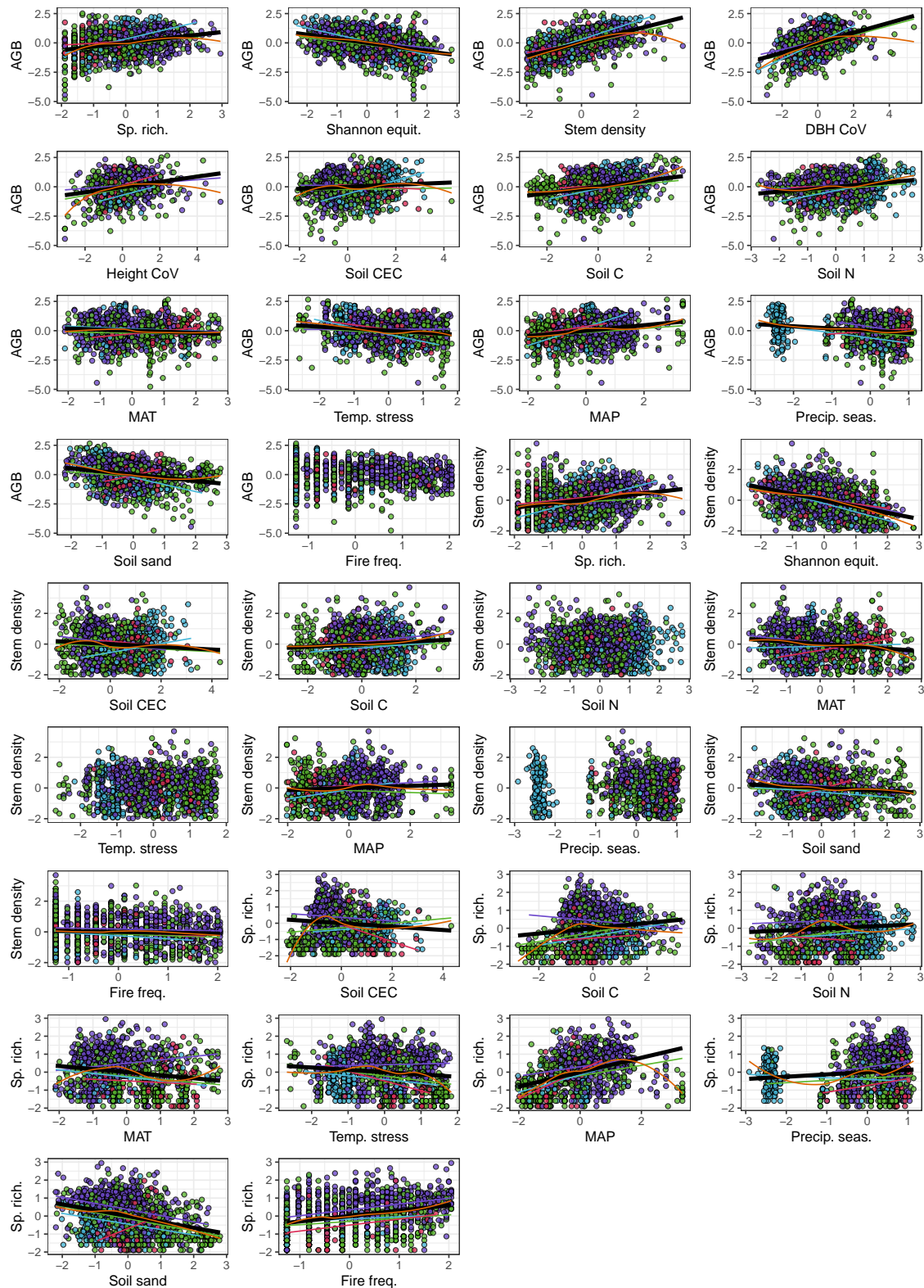# F   Appendix 3 - Bivariate relationships of model variables

Figure 11: Bivariate scatter plots for each observed variable used in the SEMs, based on hypoth-esised 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.