Title: Tree species and structural diversity are important determinants of ecosystem function across southern African woodlands

Authors: John L. Godlee[1], Casey M. Ryan[1], David Bauman[2,3], Samuel J. Bowers[1], Joao M. B. Carreiras[4], Antonio Valter Chisingui[5], Joris P. G. M. Cromsigt[6,7,8], Dave J. Druce[9,10], Manfred Finkch[11], Francisco Maiato Gonçalves[5], Ricardo M. Holdo[12], Steve Makungwa[13], Iain M. McNicol[1], Edward T. A. Mitchard[1], Anderson Muchawona[14], Rasmus Revermann[11,15], Natasha Sofia Ribeiro[16], Abel Siampale[17], Stephen Syampungani[18], José João Tchamba[5], Hemant G. Tripathi[19], Johannes Wallenfang[11], Mariska te Beest[20,21,22], Mathew Williams[1], Kyle G. Dexter[1,23]

1: School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3FF, United Kingdom

2: Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, United Kingdom

3: Laboratoire d'Écologie Végétale et Biogéochimie, CP 244, Université Libre de Bruxelles, Brussels, Belgium

4: National Centre for Earth Observation (NCEO), University of Sheffield, Hicks Building, Hounsfield Road, Sheffield, S3 7RH, United Kingdom

5: Herbarium of Lubango, ISCED Huíla, Sarmento Rodrigues Str. No. 2, CP. 230, Lubango, Angola

6: Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

7: Department of Zoology, Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, South Africa

8: Copernicus Institute of Sustainable Development, Utrecht University, 3584CS Utrecht, the Netherlands

9: Ecological Advice, Ezemvelo KZN Wildlife, Hluhluwe-iMfolozi Park, South Africa

10: School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa

11: Biodiversity, Evolution and Ecology of Plants, Institute of Plant Sciences and Microbiology, University of Hamburg, Ohnhorststr. 18, 22609 Hamburg, Germany

12: Odum School of Ecology, University of Georgia, 140 E. Green St., Athens, GA 30602, USA

13: Lilongwe University of Agriculture and Natural Resources (LUANAR), Lilongwe, Malawi

14: Forest Research Center, 1 Orange Groove Highlands, Harare, Zimbabwe

15: Faculty of Natural Resources and Spatial Sciences, Namibia University of Science and Technology, Windhoek, Namibia

16: Department of Forest Engineering, Faculty of Agronomy and Forest Engineering, UEM Av. Julius Nyerere, 3453, Campus Universitario, Maputo, Mozambique

17: Forestry Department Headquarters - MLNR, Cairo Road, Lusaka, Zambia

18: School of Natural Resources, Copperbelt University, Kitwe, Zambia

19: Faculty of Biological Sciences, University of Leeds, LS2 9JT, United Kingdom

20: Copernicus Institute of Sustainable Development, Utrecht University, 3508 TC Utrecht, The Netherlands

21: Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, 6031, South Africa

22: South African Environmental Observation Network, Grasslands-Forests-Wetlands Node, Montrose, 3201, South Africa

23: Royal Botanic Garden Edinburgh, Edinburgh, EH3 5LR, United Kingdom

Corresponding author:

John L. Godlee

johngodlee@gmail.com

School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3FF, United Kingdom

1 Acknowledgements

This work is funded by a NERC E3 Doctoral Training Partnership PhD studentship at the University of Edinburgh (John L. Godlee, Grant No. NE/L002558/1). The data for this study was contributed by a number of independently funded projects and was assembled and prepared by SEOSAW (A Socio-Ecological Observatory for Southern African Woodlands, https://seosaw.github.io), an activity of the Miombo Network and a NERC-funded project (Grant No. NE/P008755/1). Revisions of the SEOSAW dataset were funded by SavannaChange, a GCRF/University of Edinburgh funded project. We thank all data providers and the field assistance they received when collecting plot data. JMBC was supported by the Natural Environment Research Council (Agreement PR140015 between NERC and the National Centre for Earth Observation).

2 Conflict of interest statement

All authors declare no conflict of interest regarding this study.

3 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.

Blinded Main Text File

Title: Tree species and structural diversity are important determinants of ecosystem function across southern African woodlands

Running title: Diversity - ecosystem function in southern African woodlands

4 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. It is posited that high levels of disturbance moderate the effects of competition in savannas, weakening the correlation between biodiversity and niche complementarity that drives ecosystem function. Here, we explore the relationship between tree species diversity and aboveground biomass across southern African savannas and woodlands, while controlling for variation in stem density, resource availability, disturbance through fire, and 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, stem density and vegetation type.

Results: We found a positive effect of tree species diversity on aboveground biomass, across vegetation types, 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, with a minimum threshold of ~180 stems ha^{-1}. Finally, we found that resource availability affects biomass in southern African woodlands mainly indirectly, via its effect on species diversity, suggesting that tree diversity may have been under-appreciated as a determinant of savanna structure.

Main conclusions: The study underlines the close association between tree diversity and ecosystem structure and 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.

Keywords: biodiversity, ecosystem function, woodland, miombo, biomass, structural equation modelling, forest structure.

5 Introduction

In order to understand the effects of global biodiversity change, it is necessary to explore the relationship between biodiversity and ecosystem function (Tilman, Isbell & Cowles, 2014). 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 & 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 (Cardinale et al., 2009; D. U. Hooper et al., 2012; 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, Hill, Ohlemüller, Roy & Thomas, 2011), which follow from early small-scale experimental studies conducted predominantly in artificial grassland mesocosms (Tilman & 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 aggregate properties of ecosystems that describe the nature of biotic activity within those ecosystems (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 resilience of productivity to disturbance, and further to ecosystem properties which themselves influence process, such as trophic complexity and total vegetative biomass. The frequently reported BEF relationship invokes three main mechanisms to explain it (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.

Savannas and woodlands are the dominant vegetation type across southern Africa, spanning >4 million km^2 (Hopkins & 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, Hall & Goetz, 2009; Mayaux, Eva, Brink, Achard & Belward, 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 international efforts to reduced deforestation and degradation (REDD+) (Hinsley, Entwistle & Pio, 2015). Despite these efforts however, human actions are driving rapid changes in biodiversity, with largely unquantified consequences for ecosystem structure and function.

Compared to forest ecosystems, southern African dry tropical woodlands and savannas are highly structured by disturbance, through fire (Lehmann et al., 2014), herbivory (Levick, Asner, Kennedy-Bowdoin & Knapp, 2009; Sankaran, Ratnam & Hanan, 2008), and human activities such as shifting cultivation agriculture (Heinimann et al., 2017), timber extraction and charcoal processing (Dewees et al., 2010; McNicol, Ryan & Mitchard, 2018). High levels of disturbance, by fire or otherwise, may weaken the role of competition in determining local species distribution. Disturbance reduces stem density and woody biomass, 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 (Poorter et al., 2015; van der Sande et al., 2017; Wright, Wardle, Callaway & Gaxiola, 2017), may not be as important in dry woodland/savanna ecosystems, thus weakening the BEF relationship. Instead, stress tolerance and the functional contribution of particular species (selection effects) may be the predominant forces influencing ecosystem function (Lasky et al., 2014; Tobner et al., 2016). A threshold stem density may exist below which the effects of tree species diversity on ecosystem function are not detectable, with potential consequences for our classification of ecosystems limited by biodiversity and those limited by other factors.

More diverse species assemblages may lead to facilitation effects between certain species combinations under the limiting environmental conditions prevalent across African savannas, 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, York, Rasheed and Northfield (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, Mutke, Rafiqpoor, Kier & Kreft, 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 the BEF in southern African woodlands could greatly strengthen our understanding of a global BEF relationship and its environmental determinants. A small number of studies in southern African woodlands, all of which were restricted in spatial scope to a small region of miombo woodland, found that above-ground woody carbon/biomass stocks correlate positively with tree species richness (McNicol, Ryan, Dexter, Ball & Williams, 2018; Mutowo & Murwira, 2012; Shirima, Pfeifer, Platts, Totland & Moe, 2015). 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 spatial scales (<1 ha), biodiversity shows a strong effect on ecosystem function, but at broad spatial scales (>10000s ha) biodiversity effects pale in significance compared to abiotic factors such as climate (Pasari, Levi, Zavaleta & Tilman, 2013).

Environmental heterogeneity is known to affect both woody biomass and tree species diversity independently, in a number of different biomes (Michaletz, Cheng, Kerkhoff & Enquist, 2014; Michaletz, Kerkhoff & Enquist, 2018; Spasojevic, Grace, Harrison & Damschen, 2014). Southern African woodlands particularly, occur over a wide range of precipitation, diurnal and annual temperature, and disturbance regimes (Frost, 1996). It is important therefore to account for this environmental heterogeneity and understand how it influences both biomass and biodiversity to effectively model and correctly attribute the effects of biodiversity on woody biomass. Sankaran et al. (2005) and Lehmann et al. (2014) both report independently that total precipitation sets the upper limit for woody biomass in African savannas. Lehmann et al. (2014) also report complex indirect relationships between climate, disturbance by fire and woody biomass, demonstrating the need for directional multi-facetted modelling techniques to properly account for the effects of climate.

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 (Bond & Keeley, 2005; Roques, O'Connor & Watkinson, 2001; Staver, Bond, Stock, van Rensburg & Waldram, 2009). 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.

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, Medina & Silva, 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, Bohrer, Gough, Vogel & Curtis, 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 & Pierce, 2012).

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 spanning broad 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 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 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 effect of tree species diversity on woody biomass will increase with plot-level stem density (number of stems ha^{-1}), due to an increased importance of niche complementarity as stem density and therefore competition increases. In addition, we expect that an increase in disturbance by fire will decrease stem density and therefore competition, weakening the effect of tree species diversity on woody biomass. Finally, we expect that (3) tree species diversity will increase tree structural diversity (i.e. physiognomic diversity), providing an indirect path by which tree diversity increases woody biomass.

6 Materials and methods

6.1 Study location

The study used 1235 woodland monitoring plots from the larger SEOSAW network (SEOSAW, n.d.) located across 10 countries within southern Africa in the miombo ecoregion (Figure 1; Hopkins & 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 & 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 & Hijmans, 2017).

Plots were chosen from a larger pool of 5395 plots held in the SEOSAW database (SEOSAW, n.d.) 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 (Hill & Hanan, 2011; Ratnam et al., 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 analyses, 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

>50 trees ha^{-1} (>10 cm stem diameter) were used, to ensure all plots represented woodland rather than "grassy savanna", which is considered a separate biome with very different species composition (Parr, Lehmann, Bond, Hoffmann & Andersen, 2014).

3760 plots provided by the 2005-2008 Zambian Integrated Land Use Assessment (Mukosha & Siampale, 2009; Pelletier et al., 2018) were arranged in clusters of four 20x50 m plots, 20 metres apart. Data from each plot within a cluster were combined and treated as a single plot in analyses, resulting in 940 aggregate plots which were then subject to the plot filtering process described above.

6.2 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. Woody lianas are scarce in our study plots and were not measured. Only stems >10 cm DBH (Diameter at Breast Height, 1.3 m) were included in analyses. Many plots in the dataset did not include data on stems <10 cm DBH. For those plots which contained stem measurements <10 cm DBH, small stems only accounted for a median of 2.1% of the plot level AGB.

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

AGB for each plot (t ha^{-1}) was calculated using Equation 1, taken from Chave et al. (2014):

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

where ρ is the species mean wood density (g cm^{-3}), D is the DBH$_e$ (cm) at 1.3 m, and H is the tree height (m). 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 genera. For stems where tree height was unknown, the plots' climatic parameters, estimated from plot location, were used to estimate tree height, according to Chave et al. (2014).

Climatic data were taken from the WorldClim database, using the BioClim variables (Fick & Hijmans, 2017). In addition to MAT and MAP, temperature stress was calculated as the mean diurnal temperature range (BIO2) and precipitation seasonality was calculated as the mean of the coefficient of variation of monthly mean precipitation (BIO15). Soil fertility data were 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) (cmolc kg^{-1}), soil organic carbon stocks (kg m^{-2}) percentage soil sand content (0.05-2 mm) by weight and soil nitrogen content (g kg^{-1}). These data are a modelled product derived from various remotely sensed and directly measured data sources. The degree of fire disturbance was calculated using the MODIS monthly burned area product at 500 m resolution (MCD64A1; Giglio, Justice, Boschetti and Roy 2015), counting the total number of times the plot pixel was classified as burning, between 2001 and 2018. We initially aimed to include disturbance by herbivory in our model, including total herbivore biomass from the Hempson, Archibald and Bond (2017) modelled herbivory product, but this inclusion prevented models from converging due to its collinearity with other observed variables, notably MAP and disturbance by fire.

6.3 Data analysis

6.3.1 Species diversity and structural diversity metrics

Estimated tree species richness was calculated for each plot using 'ChaoRichness()' from the 'iNEXT' package in R (Hsieh, Ma & Chao, 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 & 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 potentially increased heterogeneity of functional traits. We quantified tree structural diversity for each plot by calculating the coefficient of variation of DBH (DBH CoV) and tree height (Height CoV).

6.3.2 Vegetation clusters

Plots were assigned to vegetation type groups based on tree species composition. Groups were defined in a manner adapted from 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, 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 spatial distribution of plots from each of these clusters. Cluster names were assigned post-hoc based on the dominant and indicator species in each cluster.

6.3.3 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, Kroehne, Funke & Steyer, 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).

Observed variables were transformed to achieve normality where necessary and standardised to Z-scores prior to analysis (Appendix A). 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 combinations of observed variable factor loadings set to one, while ensuring no factor loadings were in excess of one. We found no significant difference between model specifications ($p>0.05$). Full Information Maximum Likelihood (FIML) was used in each model to estimate the values of missing data in each latent variable (Cham, Reshetnyak, Rosenfeld & Breitbart, 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, separate to the effect of 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.

7 Results

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. 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).

7.1 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 (β = 0.01±0.053, p = 0.88), but did have an indirect positive effect via structural diversity (β = 0.18±0.039, 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 (β = 0.5±0.033, p <0.01).

7.2 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, we found that the effect sizes of each latent variable remained largely similar, though model fit varied. The direct effect of tree species diversity on AGB was positive and marginally significant in ex-Acacia (β = 0.16±0.121, p = 0.18) but negligible in Mopane (β = 0.24±0.099, p <0.05), sparse miombo / *Baikiaea* (β = 0.23±0.045, p <0.01) and Core miombo (β = 0.23±0.041, 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 (D. Hooper, Coughlan & Mullen, 2008).

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

7.4 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, Appendix D). The direct effects of water availability, soil fertility and disturbance on AGB were negligible (water: β = 0.1±0.13, p = 0.43, soil: β = 0.1±0.155, p = 0.51, disturbance: β = -0.04±0.043, p = 0.32), with nearly all of their observed effect on AGB coming from the indirect paths via stem density (water: β = 0.14±0.091, p = 0.12, soil: β = -0.22±0.109, p <0.05, disturbance: β = -0.12±0.03, p <0.01) and species diversity (water: β = 0.62±0.172, p <0.01, soil: β = -0.24±0.209, p = 0.26, disturbance: β = 0.19±0.058, p <0.01). MAP and soil sand content had the greatest contributions to the latent variable of water availability. Model fit was acceptable: CFI = 0.925, TLI = 0.900, and RMSEA = 0.153, R^2 of AGB = 0.34.

Similar to the model that only considered tree species and structural diversity (Figure 4), the direct effect of species diversity on structural diversity was positive, while structural diversity itself had a positive effect on AGB, leading to a strong positive indirect effect of species diversity on AGB via structural diversity (β = 0.19±0.026, p <0.01) when environmental covariates were accounted for. Again, the direct effect of species diversity on AGB was negligible (β = -0.05±0.041, p = 0.27). The total effect of species diversity on AGB was positive (β = 0.34±0.044, p <0.01). Compared to the simple model with no environmental covariates, the total explanatory power of tree species diversity and structural diversity in this model decreased, but the predictive power of the model as a whole increased.

8 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 relationship between tree species diversity and AGB, operating indirectly via structural diversity (H_1). 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). We found that the effect of tree species diversity on AGB increased with stem density (H_2), with an apparent threshold of 180 stems ha^{-1} below which the effect of species diversity on AGB remained at a low baseline level. 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.

8.1 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 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 (Cardinale et al., 2009; Liang et al., 2016). 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 using extrapolated species richness, which extrapolates a rarefaction curve to its predicted asymptote, thus estimating the total landscape-level species richness which is unaffected by plot size and stem density. 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 (Pretzsch, 2014), 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, Bagnato, Sidari & Mercurio, 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 & 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 are able to exist in the understorey, while others are able to grow tall above the woodland canopy, leading to greater variation in tree height over the plot.

8.2 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 & 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, 2019b; 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. 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.

A negative total effect of soil fertility on AGB is in contrast to other studies in the region and against general ecological theory, which predicts a positive effect of soil nutrients on biomass. The negative total effect of soil fertility on AGB was driven mostly by an indirect negative effect via stem density. The direct effect on AGB however, remained positive and marginally significant, as expected. Model estimates of the effect of soil on AGB were poorly constrained compared with other latent variables. This wide standard error on the model predictions is possibly due to the coarseness and nature of the soil data we used. SoilGrids provides modelled data at 250 m resolution, while soil structure and nutrient content varies at much finer scales (Bucini & Hanan, 2007; Muledi et al., 2017) in southern African woodlands, often being further structured by the vegetation overlying it, an aspect which SoilGrids does not model precisely. Due to the plots used in this study often being situated non-randomly in the landscape, coupled with the coarseness of the SoilGrids data, it is not surprising that this model path is poorly constrained. Soil data is time-consuming to collect and difficult to compare across studies when different protocols are used, though this study prompts the need for further effort in this regard, which may reveal interesting findings about the complex interactions between soil, disturbance and tree diversity in southern African woodlands. Lehmann et al. (2014) similarly found weak and poorly constrained relationships for soil in a Structural Equation Model including precipitation, temperature, soil, fire and tree basal area.

8.3 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 and suppressing the few species which tend to create high biomass, such as *Julbernadia* and *Brachystegia* spp.. In the species poor Mopane and ex-Acacia woodlands however, 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, Chidumayo & Sawadogo, 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 & 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 significant 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 contain a wider variety of species which can grow to large canopy trees, albeit at low densities, especially in transition zones with miombo woodlands.

8.4 Conclusion

In this study we found that even in highly disturbed southern African woodlands, there exists a generalisable positive association between tree species diversity and ecosystem function, quantified as above-ground woody biomass (AGB). Additionally, we found that much of the 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 small, 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.

The presence of a stem density threshold above which the effect of tree species diversity on AGB increases clearly implies the presence of niche complementarity effects in southern African woodlands, an aspect which has often been overlooked in favour of disturbance effects. On a practical note, 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.

References

Ali, A., Lin, S., He, J., Kong, F., Yu, J. & Jiang, H. (2019a). Big-sized trees overrule remaining trees' attributes and species richness as determinants of aboveground biomass in tropical forests. *Global Change Biology*, *25*, 2810–2824. doi: 10.1111/gcb.14707

Ali, A., Lin, S., He, J., Kong, F., Yu, J. & Jiang, H. (2019b). Climate and soils determine above-ground biomass indirectly via species diversity and stand structural complexity in tropical forests. *Forest Ecology and Management*, *432*, 823–831. doi: 10.1016/j.foreco.2018.10.024

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

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

Bond, W. J. & Keeley, J. E. (2005). Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, *20*, 387–394. doi: 10.1016/j.tree.2005.04.025

Bucini, G. & Hanan, N. P. (2007). A continental-scale analysis of tree cover in African savannas. *Global Ecology and Biogeography*, *16*, 593–605. doi: 10.1111/j.1466-8238.2007.00325.x

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

Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M., ... Loreau, M. (2009). Effects of biodiversity on the functioning of ecosystems: a summary of

164 experimental manipulations of species richness. *Ecology*, *90*, 854–854. doi: 10.1890/08-1584.1
Cham, H., Reshetnyak, E., Rosenfeld, B. & Breitbart, W. (2017). Full information maximum likelihood estimation for latent variable interactions with incomplete indicators. *Multivariate Behavioural Research*, *52*, 12–30. doi: 10.1080/00273171.2016.1245600
Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G. & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*, 351–366. doi: 10.1111/j.1461-0248.2009.01285.x
Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., ... Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, *20*, 3177–3190. doi: 10.1111/gcb.12629
Chen, I., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. (2011). Rapid range of species associated with high levels of climate warming. *Science*, *333*, 1024–1026. doi: 10.1126/science.1206432
Chidumayo, E. N. (2013). Forest degradation and recovery in a miombo woodland landscape in Zambia: 22 years of observations on permanent sample plots. *Forest Ecology and Management*, *291*, 154–161. doi: 10.1016/j.foreco.2012.11.031
Clarke, D. A., York, P. H., Rasheed, M. A. & Northfield, T. D. (2017). Does biodiversity - ecosystem function literature neglect tropical ecosystems. *Trends in Ecology & Evolution*, *32*, 320–323. doi: 10.1016/j.tree.2017.02.012
Dengler, J. (2009). Which function describes the species-area relationship best? A review and empirical evaluation. *Journal of Biogeography*, *36*, 728–744. doi: 10.1111/j.1365-2699.2008.02038.x
Dewees, P. A., Campbell, B. M., Katerere, Y., Sitoe, A., Cunningham, A. B., Angelsen, A. & Wunder, S. (2010). Managing the miombo woodlands of southern Africa: Policies, incentives and options for the rural poor. *Journal of Natural Resources Policy Research*, *2*, 57–73. doi: 10.1080/19390450903350846
Dufrêne, M. & Legendre, P. (1997). Species assemblage and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, *67*, 345–366. doi: 10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2
Fayolle, A., Swaine, M. D., Aleman, J., Azihou, A. F., Bauman, D., te Beest, M., ... Woollen, E. (2018). A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas. *Journal of Biogeography*, *46*, 1–12. doi: 10.1111/jbi.13475
Fick, S. E. & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302–4315. doi: 10.1002/joc.5086
Frost, P. (1996). The ecology of miombo woodlands. In B. Campbell (Ed.), *The miombo in transition: woodlands and welfare in Africa* (pp. 11–55). Bogor, Indonesia: Center for International Forestry Research.
Giglio, L., Justice, C., Boschetti, L. & Roy, D. (2015). MCD64A1 MODIS/Terra+Aqua Burned Area Monthly L3 Global 500m SIN Grid V006 [data set] [Computer software manual]. NASA EOSDIS Land Processes DAAC. [Accessed 2020-04-20].
Godlee, J. L., Gonçalves, F. M., Tchamba, J. J., Chisingui, A. V., Muledi, J. I., Shutcha, M. N., ... Dexter, K. G. (2020). Diversity and structure of an arid woodland in southwest Angola, with comparison to the wider miombo ecoregion. *Diversity*, *12*, 1–20. doi: 10.3390/d12040140
Grime, J. P. (1979). *Plant strategies and vegetation processes.* Chichester, UK: John Wiley and Sons.
Grime, J. P. & Pierce, S. (2012). *The evolutionary strategies that shape ecosystems.* Oxford, UK: John Wiley & Sons.
Hardiman, B. S., Bohrer, G., Gough, C. M., Vogel, C. S. & Curtis, P. S. (2011). The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. *Ecology*, *92*, 1818–1827. doi: 10.1890/10-2192.1

Hector, A. & Bagchi, R. (2007). Biodiversity and ecosystem multifunctionality. *Nature*, *448*, 188–190. doi: 10.1038/nature05947

Heinimann, A., Mertz, O., Frolking, S., Christensen, A. E., Hurni, K., Sedano, F., ... Hurtt, G. (2017). A global view of shifting cultivation: Recent, current, and future extent. *PLOS ONE*, *12*, e0184479. doi: 10.1371/journal.pone.0184479

Hempson, G. P., Archibald, S. & Bond, W. J. (2017). The consequences of replacing wildlife with livestock in Africa. *Scientific Reports*, *7*. doi: 10.1038/s41598-017-17348-4

Hengl, T., Mendes de Jesus, J., Heuvelink, G. B. M., Gonzalez, M. R., Kilibarda, M., Blagotić, A., ... Kempen, B. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLoS ONE*, *12*, 1–40. doi: 10.1371/journal.pone.0169748

Hill, M. J. & Hanan, N. P. (Eds.). (2011). *Ecosystem function in savannas.* Boca Raton FL, USA: CRC Press. doi: 10.1201/b10275

Hinsley, A., Entwistle, A. & Pio, D. V. (2015). Does the long-term success of REDD+ also depend on biodiversity. *Oryx*, *49*, 216–221. doi: 10.1017/S0030605314000507

Hooper, D., Coughlan, J. & Mullen, M. R. (2008). Structural equation modelling: guidelines for determining model fit. *Electronic Journal of Business Research Methods*, *6*, 53–60.

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., ... O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, *486*, 105–108. doi: 10.1038/nature11118

Hopkins, B. & White, F. (1987). Vegetation map of Africa. The vegetation of Africa: A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. *The Journal of Ecology*, *75*. doi: 10.2307/2260340

Houghton, R. A., Hall, F. & Goetz, S. J. (2009). Importance of biomass in the global carbon cycle. *Journal of Geophysical Research*, *114*, 1–13. doi: 10.1029/2009JG000935

Hsieh, T. C., Ma, K. H. & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*, 1451–1456. doi: 10.1111/2041-210X.12613

Hu, L. & Bentler, P. M. (1999). Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives. *Structural Equation Modeling*, *6*, 1–55. doi: 10.1080/10705519909540118

Jax, K. (2005). Function and "functioning" in ecology: what does it mean? *Oikos*, *111*, 641–648. doi: 10.1111/j.1600-0706.2005.13851.x

Keddy, P. A. (1990). Competitive hierarchies and centrifugal organization in plant communities. In J. B. Grace & D. Tilman (Eds.), *Perspectives on plant competition* (pp. 266–287). San Diego CA, USA: Academic Press.

Kraaij, T. & Ward, D. (2006). Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology*, *186*, 235–246. doi: 10.1007/s11258-006-9125-4

Kunz, M., Fichtner, A., Härdtle, W., Raumonen, P., Bruelheide, H. & von Oheimb, G. (2019). Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees. *Ecology Letters*, 1–11. doi: 10.1111/ele.13400

Lasky, J. R., Uriarte, M., Boukili, V. K., Erickson, D. L., Kress, W. J. & Chazdon, R. L. (2014). The relationship between tree biodiversity and biomass dynamic changes with tropical forest succession. *Ecology Letters*, *17*, 1158–1167. doi: 10.1111/ele.12322

Lee, S. Y. (2007). *Structural equation modeling: A bayesian approach.* New York, USA: Wiley.

Lehmann, C. E. R., Anderson, T. M., Sankaran, M., Higgins, S. I., Archibald, S., Hoffmann, W. A., ... Bond, W. J. (2014). Savanna vegetation-fire-climate relationships differ among continents. *Science*, *343*, 548–552. doi: 10.1126/science.1247355

Levick, S. R., Asner, G. P., Kennedy-Bowdoin, T. & Knapp, D. E. (2009). The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. *Biological Conservation*, *142*, 1693–1700. doi: 10.1016/j.biocon.2009.03.004

Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., ... Reich, P. B. (2016).

Positive biodiversity-productivity relationship predominant in global forests. *Science*, *354*, aaf8957-aaf8957. doi: 10.1126/science.aaf8957

Mayaux, P., Eva, H., Brink, A., Achard, F. & Belward, A. (2008). Remote sensing of land-cover and land-use dynamics. In *Earth observation of global change: The role of satellite remote sensing in monitoring the global environment* (pp. 85–108). Berlin, Germany: Springer-Verlag. doi: 10.1007/978-1-4020-6358-9_5

McNicol, I. M., Ryan, C. M., Dexter, K. G., Ball, S. M. J. & Williams, M. (2018). Aboveground carbon storage and its links to stand structure, tree diversity and floristic composition in south-eastern Tanzania. *Ecosystems*, *21*, 740–754. doi: 10.1007/s10021-017-0180-6

McNicol, I. M., Ryan, C. M. & Mitchard, E. T. A. (2018). Carbon losses from deforestation and widespread degradation offset by extensive growth in African woodlands. *Nature Communications*, *9*. doi: 10.1038/s41467-018-05386-z

Michaletz, S. T., Cheng, D., Kerkhoff, A. J. & Enquist, B. J. (2014). Convergence of terrestrial plant production across global climate gradients. *Nature*, *512*, 39–43. doi: 10.1038/nature13470

Michaletz, S. T., Kerkhoff, A. J. & Enquist, B. J. (2018). Drivers of terrestrial plant production across broad geographical gradients. *Global Ecology and Biogeography*, *27*, 166–174. doi: 10.1111/geb.12685

Mittermeier, R. A., Mittermeier, C. G., Brooks, T. M., Pilgrim, J. D., Konstant, W. R., da Fonseca, G. A. B. & Kormos, C. (2003). Wilderness and biodiversity conservation. *Proceedings of the National Academy of Sciences*, *100*, 10309–10313. doi: 10.1073/pnas.1732458100

Mukosha, J. & Siampale, A. (2009). Integrated land use assessment zambia 2005–2008 [Computer software manual]. Lusaka, Zambia: Ministry of Tourism, Environment and Natural Resources, Forestry Department, and Food and Agriculture Organization of the United Nations.

Muledi, J. I., Bauman, D., Drouet, T., Vleminckx, J., Jacobs, A., Lejoly, J., . . . Shutcha, M. N. (2017). Fine-scale habitats influence tree species assemblage in a miombo forest. *Journal of Plant Ecology*, *10*, 958–969. doi: 10.1093/jpe/rtw104

Muscolo, A., Bagnato, S., Sidari, M. & Mercurio, R. (2014). A review of the roles of forest canopy gaps. *Journal of Forestry Research*, *25*, 725–736. doi: 10.1007/s11676-014-0521-7

Mutowo, G. & Murwira, A. (2012). Relationship between remotely sensed variables and tree species diversity in savanna woodlands of southern Africa. *International Journal of Remote Sensing*, *33*, 6378–6402. doi: 10.1080/01431161.2012.687472

Nachtigall, C., Kroehne, U., Funke, F. & Steyer, R. (2003). (Why) should we use SEM? Pros and cons of Structural Equation Modeling. *Methods of Psychological Research*, *8*, 1–22.

Parr, C. L., Lehmann, C. E. R., Bond, W. J., Hoffmann, W. A. & Andersen, A. N. (2014). Tropical grassy biomes: misunderstood, neglected, and under threat. *Trends in Ecology and Evolution*, *29*, 205–213. doi: 10.1016/j.tree.2014.02.004Âă

Pasari, J. R., Levi, T., Zavaleta, E. S. & Tilman, D. (2013). Several scales of biodiversity affect ecosystem multifunctionality. *Proceedings of the National Academy of Sciences*, *110*, 10219–10222. doi: 10.1073/pnas.1220333110

Pelletier, J., Paquette, A., Mbindo, K., Zimba, N., Siampale, A., Chendauka, B., . . . Roberts, J. W. (2018). Carbon sink despite large deforestation in African tropical dry forests (miombo woodlands). *Environmental Research Letters*, *13*, 094017. doi: 10.1088/1748-9326/aadc9a

Poorter, L., van de Sande, M. T., Thompson, J., Arets, E. J. M. M., Alarcòn, A., Àlvarez-Sànchez, J., . . . Peña-Claros, M. (2015). Diversity enhances carbon storage in tropical forests. *Global Ecology and Biogeography*, *24*, 1314–1328. doi: 10.1111/geb.12364

Poorter, L., van der Sande, M. T., Arets, E. J. M. M., Ascarrunz, N., Enquist, B. J., Finegan, B., . . . Peña-Claros, M. (2017). Biodiversity and climate determine the functioning of neotropical forests. *Global Ecology and Biogeography*, *26*, 1423–1434. doi: 10.1111/geb.12668

Pretzsch, H. (2014). Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *Forest Ecology and Management*, *327*, 251–264. doi: 10.1016/

j.foreco.2014.04.027

R Core Team. (2019). R: A language and environment for statistical computing [Computer software manual]. Vienna, Austria. Retrieved from https://www.R-project.org/

Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., ... Baeten, L. (2017). Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology Letters*, *20*, 1414–1426. doi: 10.1111/ele.12849

Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. A., Archibald, S., Lehmann, C. E. R., ... Sankaran, M. (2011). When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography*, *20*, 653–660. doi: 10.1111/j.1466-8238.2010.00634.x

Roberts, D. W. (2019). labdsv: Ordination and multivariate analysis for ecology [Computer software manual]. Retrieved from https://CRAN.R-project.org/package=labdsv (R package version 2.0-1)

Roques, K. G., O'Connor, T. G. & Watkinson, A. R. (2001). Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, *38*, 268–280. doi: 10.1046/j.1365-2664.2001.00567.x

Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, *48*, 1–36. Retrieved from http://www.jstatsoft.org/v48/i02/

Ryan, C. M., Pritchard, R., McNicol, I., Owen, M., Fisher, J. A. & Lehmann, C. (2016). Ecosystem services from southern African woodlands and their future under global change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 1–16. doi: 10.1098/rstb.2015.0312

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., ... Zambatis, N. (2005). Determinants of woody cover in African savannas. *Nature*, *438*, 846–849. doi: 10.1038/nature04070

Sankaran, M., Ratnam, J. & Hanan, N. (2008). Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography*, *17*, 236–245. doi: 10.1111/j.1466-8238.2007.00360.x

Seidel, D., Ehbrecht, M., Dorji, Y., Jambay, J., Ammer, C. & Annighöfer, P. (2019). Identifying architectural characteristics that determine tree structural complexity. *Trees*, *33*, 911–919. doi: 10.1007/s00468-019-01827-4

SEOSAW. (n.d.). *SEOSAW: A Socio-Ecological Observatory for Southern African woodlands.*

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

Shirima, D. D., Pfeifer, M., Platts, P. J., Totland, Ø. & Moe, S. R. (2015). Interactions between canopy structure and herbaceous biomass along environmental gradients in moist forest and dry miombo woodland of tanzania. *PLoS ONE*, *10*, 1–15. doi: 10.1371/journal.pone.0142784

Smith, B. & Wilson, J. B. (1996). A consumer's guide to evenness indices. *Oikos*, *76*, 70–82. doi: 10.2307/3545749

Solbrig, O. T., Medina, E. & Silva, J. F. (1996). *Biodiversity and savanna ecosystem processes.* Berlin, Germany: Springer-Verlag.

Spasojevic, M. J., Grace, J. B., Harrison, S. & Damschen, E. I. (2014). Functional diversity supports the physiological tolerance hyopthesis for plant species richness along climatic gradients. *Journal of Ecology*, *102*, 447–455. doi: 10.1111/1365-2745.12204

Stark, S. C., Leitold, V., Wu, J. L., Hunter, M. O., de Castilho, C. V., Costa, F. R. C., ... Saleska, S. R. (2012). Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment. *Ecology Letters*, *15*, 1406–1414. doi: 10.1111/j.1461-0248.2012.01864.x

Staver, A. C., Bond, W. J., Stock, W. D., van Rensburg, S. J. & Waldram, M. S. (2009). Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications*, *19*, 1909–1919. doi: 10.1890/08-1907.1

Stegen, J. C., Swenson, N. G., Enquist, B. J., White, E. P., Phillips, O. L., Jørgensen, P. M., ... Vargas, P. N. (2011). Variation in above-ground forest biomass across broad climatic gradients. *Global Ecology and Biogeography*, *20*, 744–754. doi: 10.1111/j.1466-8238.2010.00645.x

Tilman, D. & Downing, J. A. (1994). Biodiversity and stability in grasslands. *Nature*, *367*, 363–365. doi: 10.1038/367363a0

Tilman, D., Isbell, F. & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 471-493. doi: 10.1146/annurev-ecolsys-120213-091917

Timberlake, J., Chidumayo, E. & Sawadogo, L. (2010). Distribution and characteristics of African dry forests and woodlands. In *The dry forests and woodlands of Africa: Managing for products and services* (pp. 11–42). London, United Kingdom: EarthScan.

Tobner, C. M., Paquette, A., Gravel, D., Reich, P. B., Williams, L. J. & Messier, C. (2016). Functional identity is the main driver of diversity effects in young tree communities. *Ecology Letters*, *19*, 638–647. doi: 10.1111/ele.12600

van der Sande, M. T., Poorter, L., Kooistra, L., Balvanera, P., Thonicke, K., Thompson, J., ... Peña-Claros, M. (2017). Biodiversity in species, traits, and structure determines carbon stocks and uptake in tropical forests. *Biotropica*, *49*, 593–603. doi: 10.1111/btp.12453

Vilà, M., Inchausti, P., Vayreda, J., Barrantes, O., Gracia, C., Ibàñez, J. J. & Mata, T. (2005). Confounding factors in the observational productivity-diversity relationship in forests. *Ecological Studies*, *176*, 65–86.

Wright, A. J., Wardle, W. D. A., Callaway, W. R. & Gaxiola, A. (2017). The overlooked role of facilitation in biodiversity experiments. *Trends in Ecology and Evolution*, *32*, 383–390. doi: 10.1016/j.tree.2017.02.011

Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S. L., ... Chave, J. (2009). Global wood density database [Computer software manual]. Dryad. (http://hdl.handle.net/10255/dryad.235)

9 Author contribution statement

JG and KD conceived the study. JG conducted data analysis, data management for further versions of the SEOSAW dataset, and wrote the manuscript. CR conceived the SEOSAW database and conducted data management for earlier versions of the SEOSAW dataset. JG, CR, DB, JMBC, MF, RH, EM, SS, HT, HT, MB, MW, and KD contributed to manuscript revisions. JG, CR, SB, VC, JPGMC, DD, MF, FG, SM, IM, AM, RR, NR, AS, SS, JT, JW, MB, and MW contributed to experimental design, field data collection, data preparation and data management of parts of the dataset used in this study.

10 Tables

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 & 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 Richness	Stem density (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)

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

11 Figure legends and embedded figures

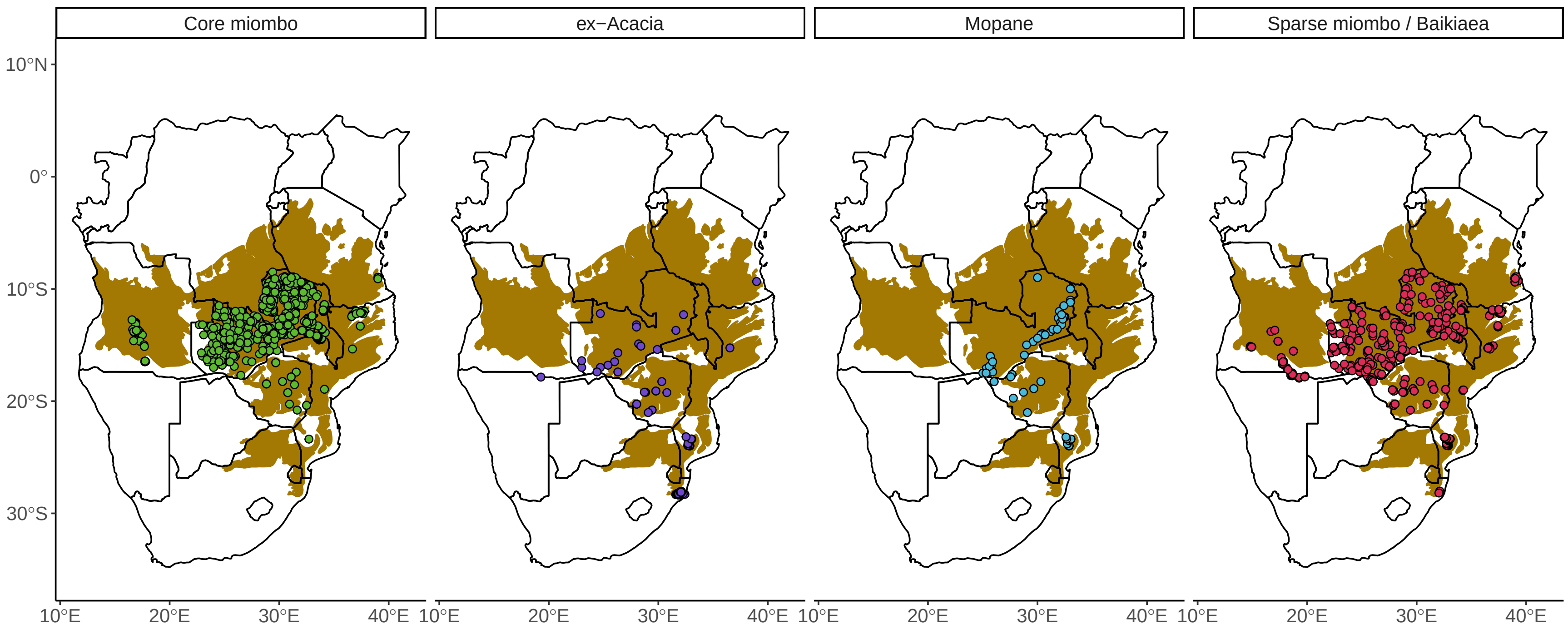

Figure 1: The locations of the 1235 plots used in this study, with respect to the distribution of miombo woodland vegetation according to Hopkins and White (1987). Each panel shows plots categorized by their vegetation type as defined by the vegetation types in Table 1.

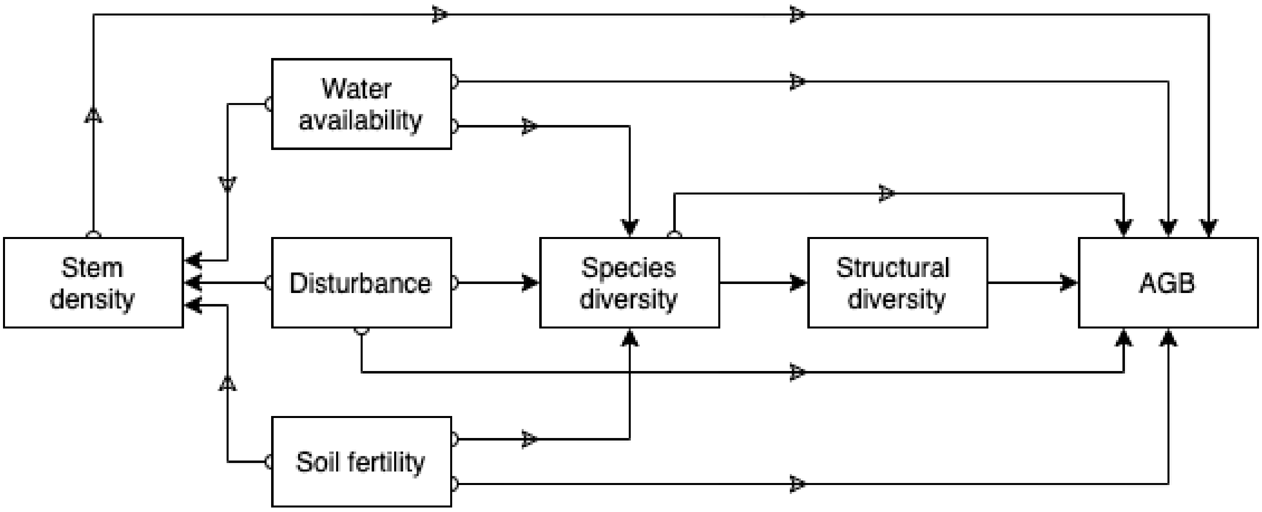

Figure 2: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural diversity, stem density, and AGB. Hypothesised paths of causation are depicted as arrows from predictor to response.

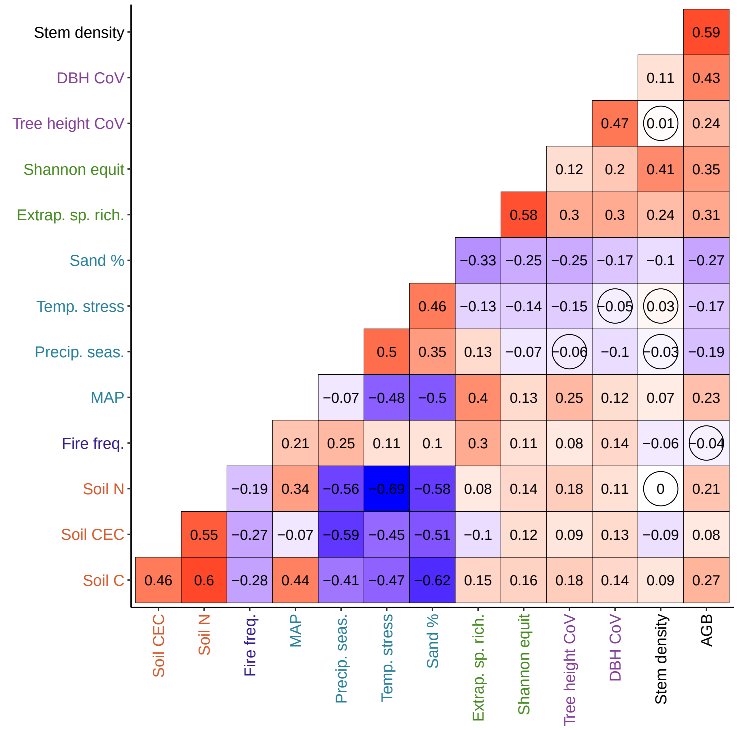

Figure 3: Correlation matrix of standardised observed variables used in the SEMs, with Pearson correlation coefficients (r) coloured according to sign (+ve red, −ve blue) and shaded by strength of correlation. Correlation coefficients marked by a circle indicate that the 95% confidence interval of r 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.

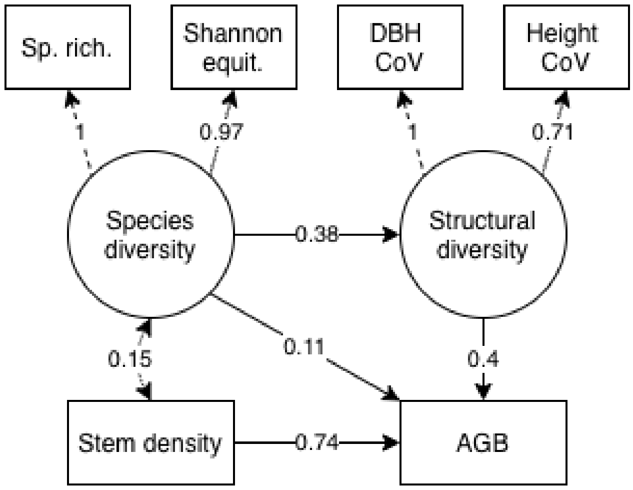

Figure 4: Path diagram with regression coefficients for the tree diversity SEM, including plots from all vegetation clusters. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are shown as solid arrows pointing from predictor to response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

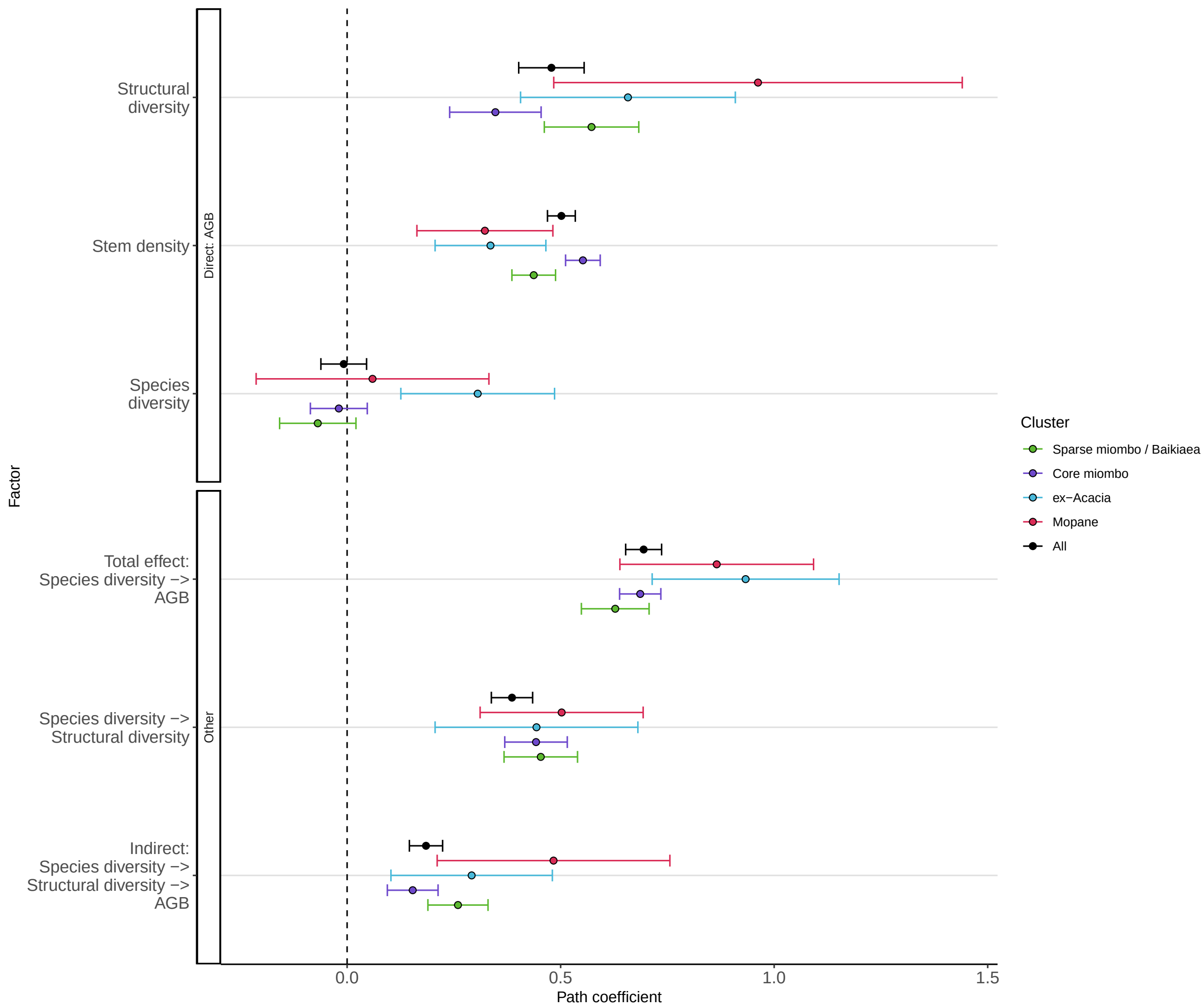

Figure 5: Unstandardised path coefficients for the effects of tree diversity on AGB, mediated by the effect of stand structural diversity. Path coefficients are ±1 standard error. Path coefficients where the interval (standard error) does not overlap zero are considered to be significant effects.

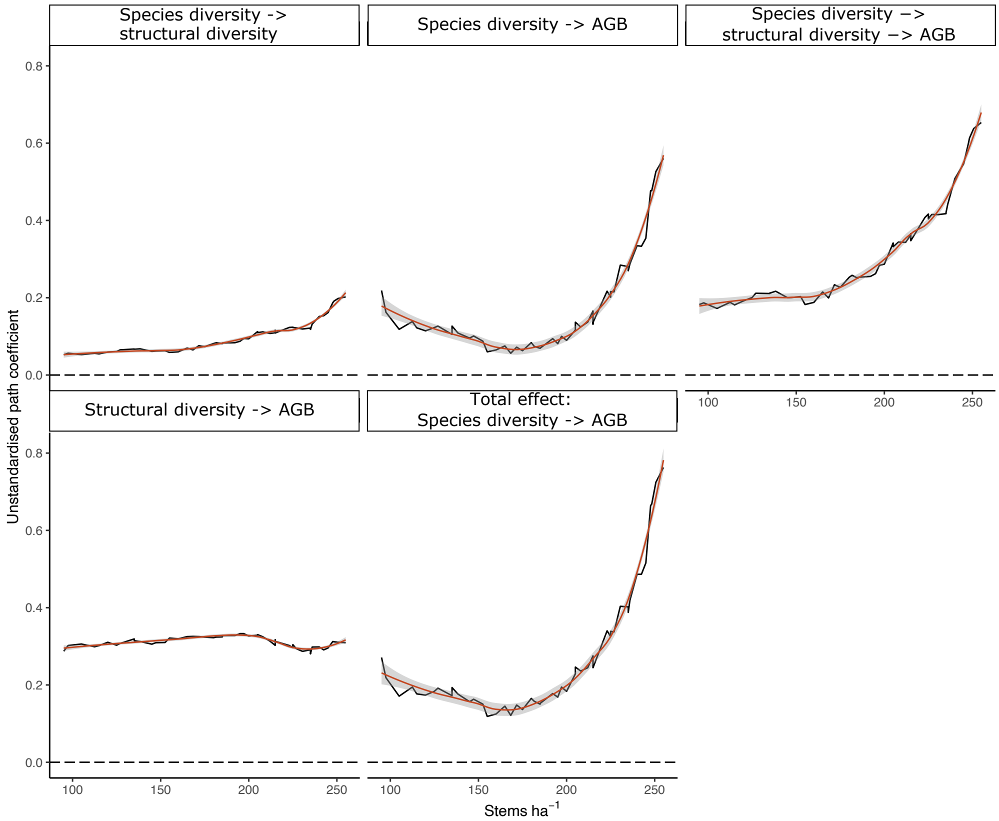

Figure 6: Line plots showing the variation in path coefficients in the SEM, using datasets with different mean stem density. Smoothed lines are loess curves with standard error shaded bars.

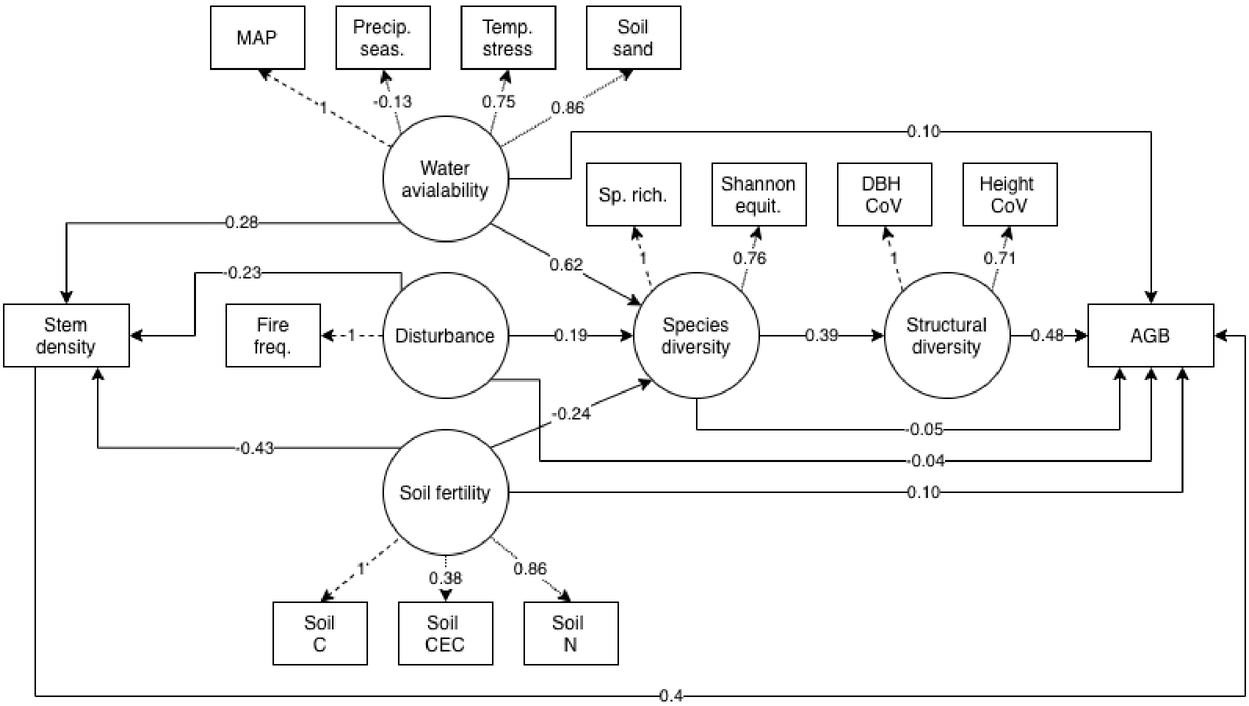

Figure 7: Path diagram with regression coefficients for the SEM incorporating environmental covariates and tree species and structural diversity across all five vegetation types. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are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

12 Appendix 1 - Frequency distribution of observed variables

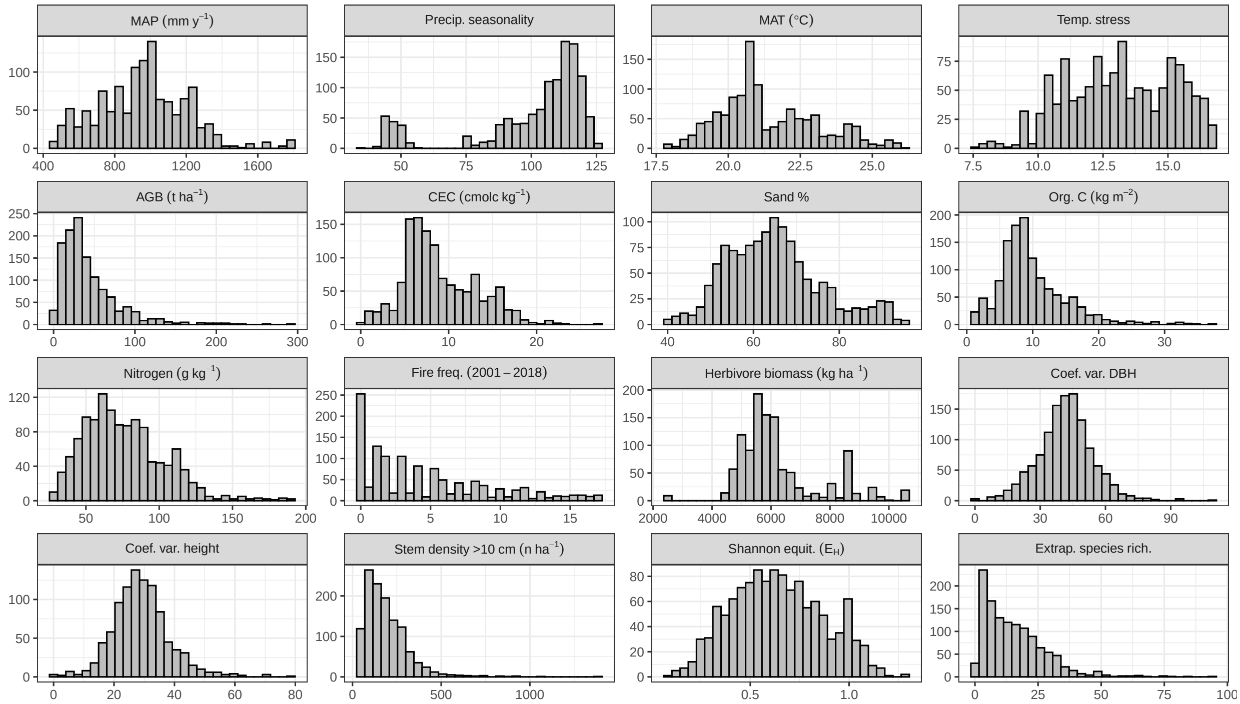

Figure 8: Histograms of raw untransformed observed variables used in final analyses.

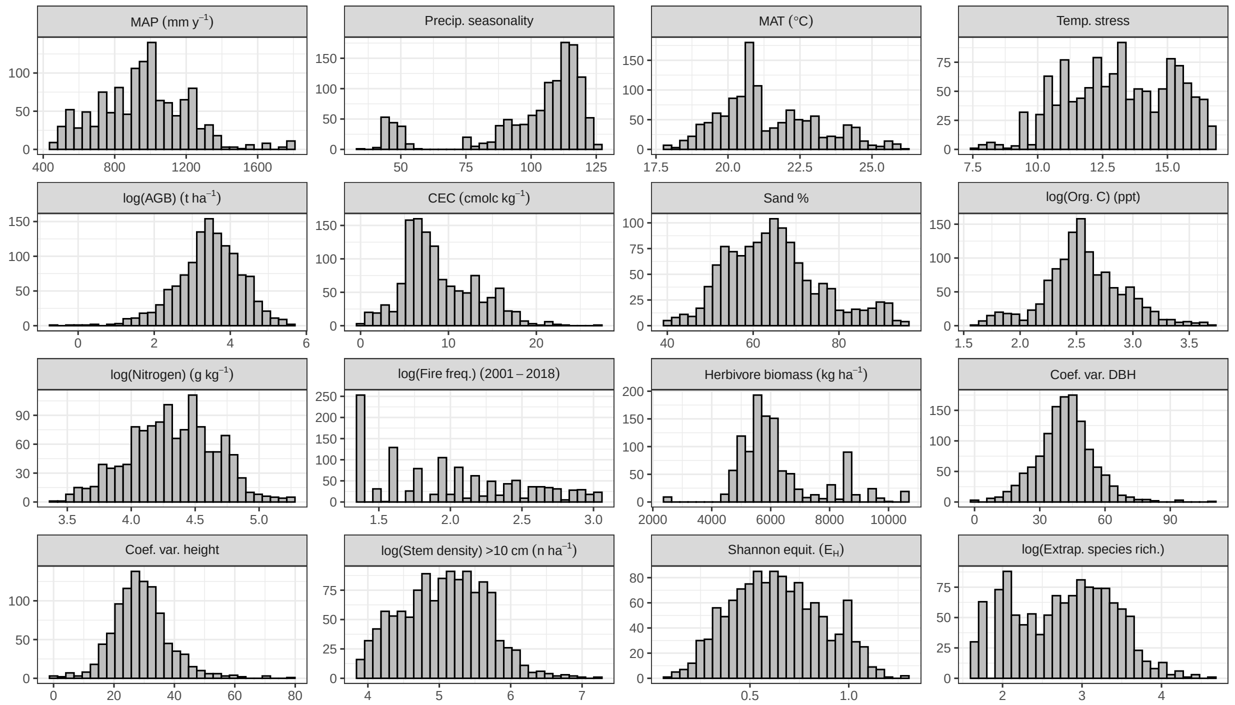

Figure 9: Histograms of observed variables transformed to achieve a normal frequency distribution.

A 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	$p < 0.01$
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

B Appendix 3 - Bivariate relationships of model variables

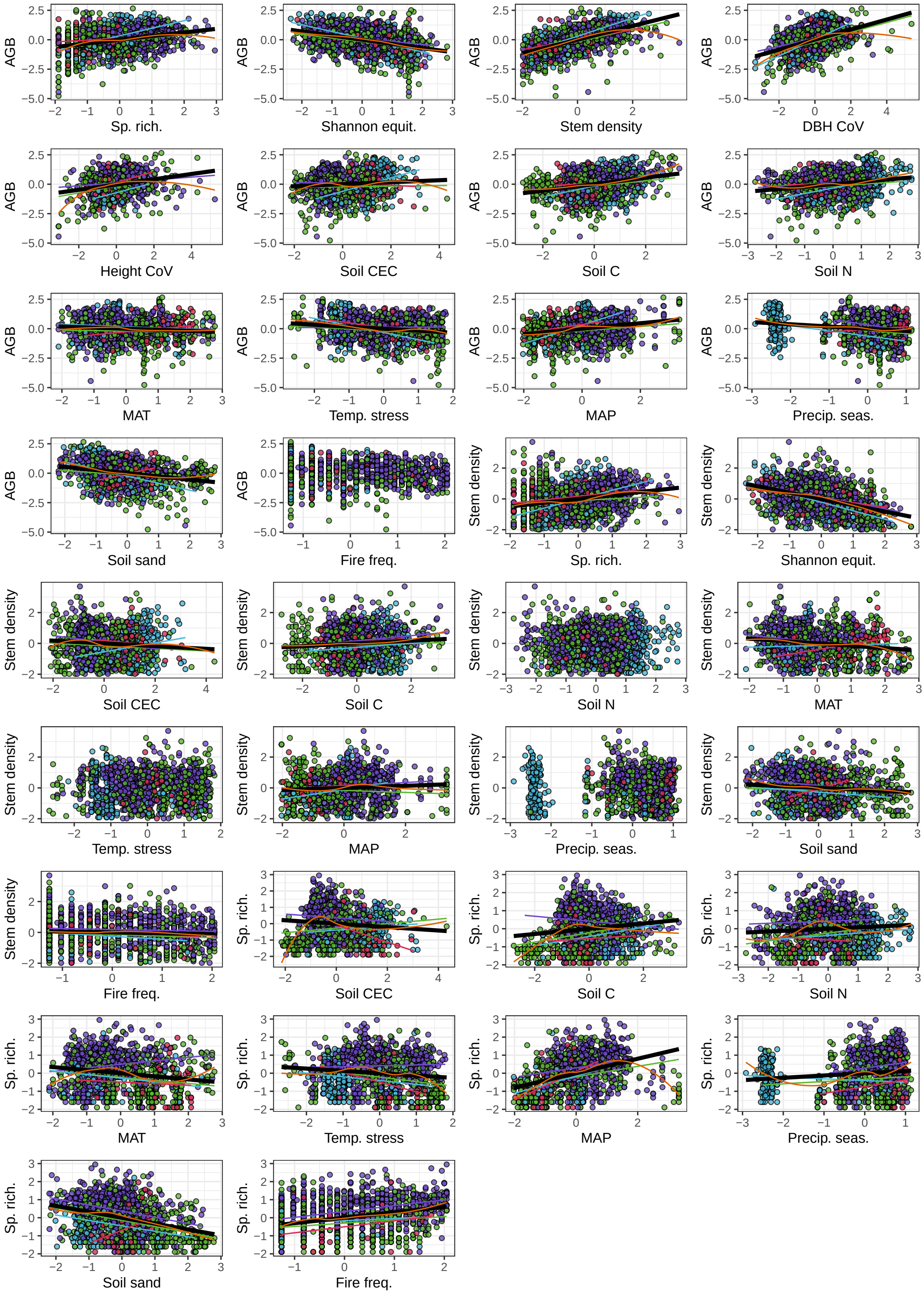

Figure 10: Bivariate scatter plots for each observed variable used in the SEMs, based on hypothesised paths of causality. Points are coloured according to vegetation type. A single linear regression is presented as a black line, which combines all vegetation types, separate loess trend lines are fitted for each vegetation type. An orange loess trend line is fitted for all the data. All data is standardised and variables are transformed where it was appropriate for analysis.

C Appendix 4 - Path coefficients for model incorporating environmental covariates

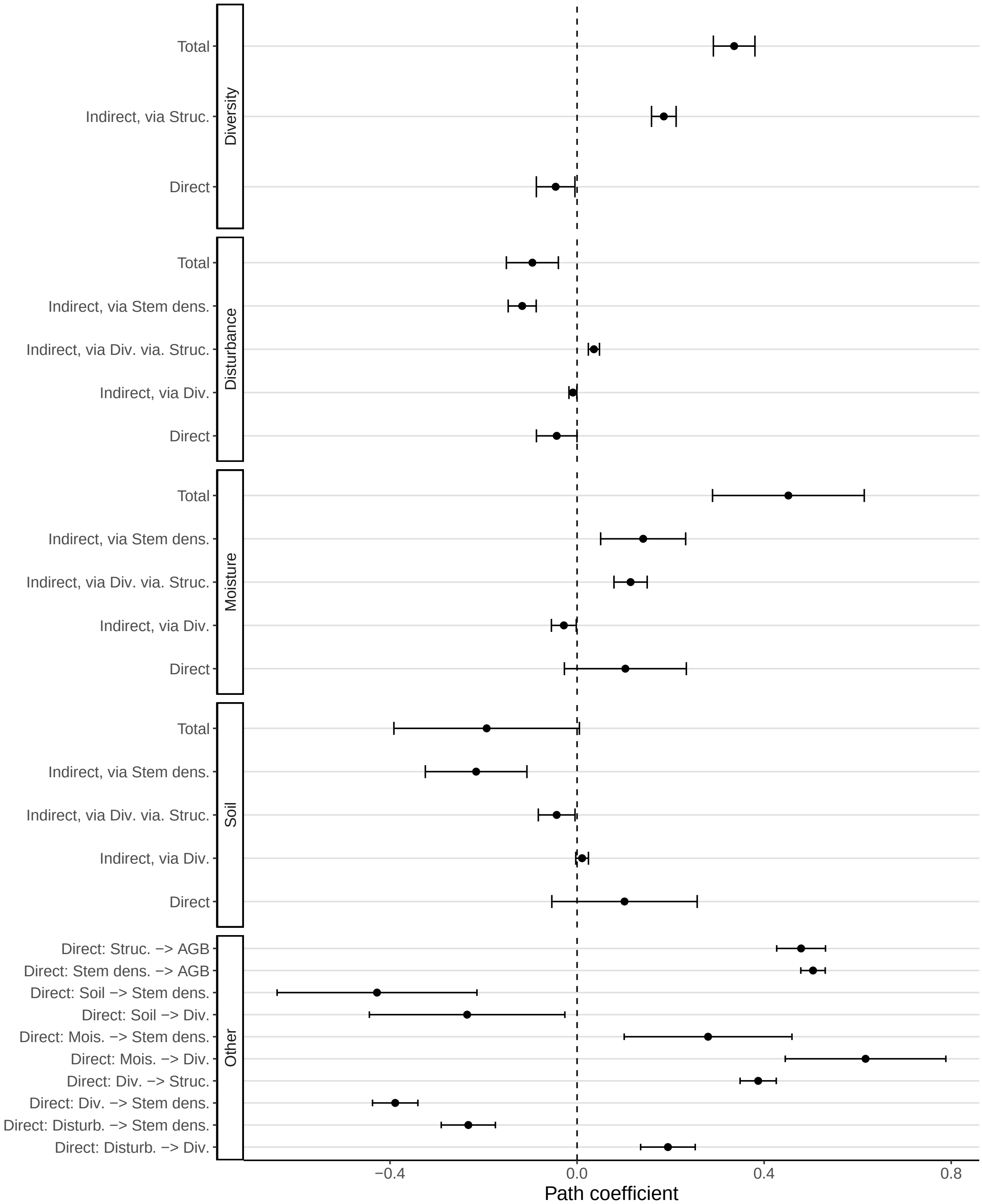

Figure 11: Unstandardised path coefficients for the full model including tree species diversity, environmental covariates and stem density. Path coefficients are ±1 standard error. Path coefficients where the interval (standard error) does not overlap zero are considered to be significant effects.