# Title: Structural diversity and tree density drives variation in the biodiversity-ecosystem function relationship of woodlands and savannas

## Summary

- Positive biodiversity-ecosystem function relationships (BEFRs) have been widely documented, but it is unclear if BEFRs should be expected in disturbance-driven systems. Disturbance may limit competition and niche differentiation, which are frequently posited to underlie BEFRs. We provide the first exploration of the relationship between tree species diversity and biomass, one measure of ecosystem function, across southern African woodlands and savannas, an ecological system rife with disturbance from fire, herbivores and humans.

- We used >1000 vegetation plots distributed across 10 southern African countries, and structural equation modelling, to determine the relationship between tree species diversity and aboveground woody biomass, accounting for interacting effects of resource availability, disturbance by fire, tree stem density and vegetation type.

- We found positive effects of tree species diversity on aboveground biomass, operating via increased structural diversity. The observed BEFR was highly dependent on organismal density, with a minimum threshold of c. 180 mature stems ha$^{-1}$. We found that water availability mainly affects biomass indirectly, via increasing species diversity.

- The study underlines the close association between tree diversity, ecosystem structure, environment and function in highly disturbed savannas and woodlands. We suggest that tree diversity is an under-appreciated determinant of wooded ecosystem structure and function.

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

## 1 Introduction

Understanding the relationship between biodiversity and ecosystem function has become a central endeavour in ecological science, as we seek to predict the consequences of global biodiversity change (Naeem et al., 2012). Over the past two decades, study of the Biodiversity-Ecosystem Function Relationship (BEFR) has grown from small-scale experimental studies mostly in temperate grasslands (Cardinale et al., 2009; Tilman & Downing, 1994; Tilman et al., 2014), to observational studies in natural ecosystems (Plas, 2019). While positive BEFRs which align with theory have been frequently reported, a complex picture has emerged whereby the strength and direction of the BEFR varies depending on the ecosystem studied (Liang et al., 2016), the ecosystem function(s) of interest (Hector & Bagchi, 2007), and the inclusion of environmental covariates in statistical models (Vilà et al., 2005). The goal now should be to study the BEFR in different environmental and ecological contexts, in order to develop an ecosystem-agnostic understanding of the complex interactions between biodiversity, abiotic environment, and ecosystem function.

Ecosystem functions are defined in broad terms as rate processes and aggregate properties of ecosystems that describe the nature of biotic activity within those ecosystems (Jax, 2005). Woody productivity and biomass storage are two of the most commonly studied ecosystem functions in forests and other wooded ecosystems (e.g. savannas) (Brockerhoff et al., 2017), due to their importance in the global carbon cycle (Pan et al., 2011) and their potential leverage as a tool to mitigate the effects of anthropogenic climate change while maintaining biodiversity (Pichancourt et al., 2013). Theory predicts that biodiversity will have a positive effect on ecosystem function via three principal mechanisms: 1) niche complementarity, whereby niche partitioning and ecosystem resource use efficiency is increased in diverse communities, minimising negative density dependent effects such as conspecific competition and abundance of species-specific natural enemies (Barry et al., 2019); 2) selection effects, whereby diverse communities are more likely to include a high-yield species; and 3) facilitation effects, whereby diverse communities are more likely to contain species combinations which enhance each others' functional contribution (Wright et al., 2017).

There has been extended debate on whether positive BEFRs should be expected in all wooded ecosystems (Liang et al., 2016). In temperate and wet tropical forests, where the majority of BEFR studies in natural forest ecosystems have been conducted (Plas, 2019), the mechanism of niche complementarity, which contributes the majority of the observed biodiversity effect (Poorter et al., 2015; Sande et al., 2017; Wright et al., 2017), hinges on the condition that conspecific competition between trees is the limiting factor to ecosystem functioning, but this may not hold true in all systems.

Disturbance-driven mesic savannas and open canopy woodlands cover >20% of the global land surface (Pennington et al., 2018; Solbrig et al., 1996). They represent the dominant vegetation type in Africa, spanning >4 million km$^2$ (Hopkins & White, 1987; Ratnam et al., 2011; Ryan et al., 2016) (Figure 1). Taken together, the above- and below-ground carbon stored in African mesic savannas may be comparable to that found in the wet forests of the Congo basin (Houghton et al., 2009; Mayaux et al., 2008; Spawn et al., 2020). Globally, dry woodlands and savannas represent the largest, most sensitive and fastest increasing component of the terrestrial carbon sink (Ahlstrom et al., 2015). Yet their carbon dynamics remain poorly constrained (Sitch et al., 2015).

Despite their global importance, African savannas are severely under-represented in BEFR studies (Clarke et al., 2017; Liang et al., 2016). In savannas disturbance by fire (Lehmann et al., 2014) and herbivory (Sankaran et al., 2008; Levick et al., 2009) reduces woody stem density and biomass, diminishing competitive interactions between individuals, allowing competitors to co-exist where they would normally be excluded (Grime, 1979; Keddy, 1990). It is possible that a threshold woody stem density exists below which the lack of competition precludes the detection of a biodiversity effect on ecosystem function via niche differentiation. Instead, stress tolerance and the functional contribution of particular species (selection effects) may be the predominant biotic forces influencing ecosystem function in these ecosystems (Lasky et al., 2014; Tobner et al., 2016). Additionally, stressful environments appear to lessen the role of both niche complementarity and facilitation effects in driving the BEFR, by replacing competition between individuals with stress tolerance as the limiting factor on functional contribution (Ratcliffe et al., 2017; Paquette & Messier, 2010). This potential mismatch in the contribution of different mechanisms to the BEFR among resource-, disturbance-, and competition-limited ecosystems requires further investigation if we are to derive a generalisable BEFR.

A number of studies in miombo woodlands, the dominant savanna type in southern Africa (Campbell, 1996), have found that above-ground woody carbon/biomass stocks correlate positively with tree species richness (McNicol et al., 2018; Shirima et al., 2015; Mutowo & Murwira, 2012). These studies however, lacked the spatial extent required to account for the interacting effects of variation in abiotic environment, disturbance regime, and biogeography which are expected to affect the BEFR. Studies of the BEFR often find that within a small spatial extent ($<$2500 km$^2$), biodiversity shows a strong effect on ecosystem function, but at broader extents ($>$100,000s km$^2$) biodiversity effects pale in significance compared to abiotic factors such as climate (Gonzalez et al., 2020). In West Africa, Mensah et al. (2020) found that woodlands and forests showed a positive effect of tree species richness on above-ground carbon, while sparse savannas did not, implying that tree stem density and the presence of dominant large trees may affect the strength of the observed BEFR. In the Brazilian Cerrado savanna, Loiola et al. (2015) found that disturbance by fire reduced tree productivity via its effect on functional trait values. Furthermore, Carvalho et al. (2014) found that disturbance by fire in the Brazilian Cerrado reduced soil fertility, causing an indirect effect of fire frequency on functional trait diversity via soil fertility. Other studies focussing on the herbaceous diversity in disturbance-prone grasslands in North America and Europe have shown that disturbance by fire, mowing and herbivory reduces herbaceous productivity (Grace et al., 2007), allowing weak competitors to co-exist where otherwise they would be excluded (Mason et al., 2011), thus weakening the observable BEFR. Thus, there is a case that in highly disturbed systems, a relationship between diversity and ecosystem function may not exist at all. While these studies together offer some glimpse into how the BEFR may operate in disturbance-prone systems, none provide a full and comprehensive assessment of the interacting effects of diversity, abiotic environment, disturbance and ecosystem function, particularly for wooded ecosystems. Additionally, due to differences in community assembly, evolutionary history and contemporary drivers between the neotropics and the African tropics, inferences from one continent cannot necessarily be applied to the other (Dexter et al., 2015).

In this study, we make the first known estimation of the Biodiversity-Ecosystem Function Relationship (BEFR) in disturbance-driven wooded ecosystems (savannas and woodlands), using southern Africa as our study region. We aim to understand the synergistic effects of environmental and biotic drivers of variation in the BEFR, with a view to creating a general model of the BEFR in disturbance-prone wooded ecosystems, which is currently lacking in the BEFR literature. We posit 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 organismal density (number of stems ha$^{-1}$), with competitive interactions becoming more pronounced as stem proximity increases. Relatedly, we expect that an increase in disturbance by fire will decrease organismal 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 due to inter-specific variation in size strategy (i.e. physiognomic diversity), providing an indirect path by which tree diversity increases woody biomass.

# 2 Materials and Methods

## 2.1 Study location

The study used 1235 woodland monitoring plots from a larger pool of 5395 plots in the larger SEOSAW database (SEOSAW, 2020), 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 c. 460 mm y$^{-1}$ in southern Mozambique and southern Zimbabwe to c. 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 the SEOSAW database based on the quality and completeness of data collection, and plot configuration. 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, or savannas (Ratnam et al., 2011; Hill & Hanan, 2011). Plots with evidence of farming, human resource extraction, experimental treatments such as prescribed burning or herbivore exclusion, or containing termite mounds 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 biomass 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 here a separate biome with very different species composition (Parr et al., 2014). 3760 plots within the SEOSAW database were arranged in clusters of four 20x50 m plots, with 20 m between plots. Plots within each spatial 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.

## 2.2 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 living 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 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, tree height to the top of the highest branch material, and the DBH of each stem >10 cm DBH. Height was measured through a variety of means including laser rangefinders, manual clinometers and measuring sticks. When stem DBH could not be reliably 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 used to estimate diameter at 1.3 m using a cubic polynomial regression to account for stem taper, 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 as the sum of the AGB of each stem >5 cm DBH ($AGB_i$), divided by the plot area, using Equation 1 taken from Chave et al. (2014):

$$AGB_i = 0.0673 \times (\rho D^2 H)^{0.976} \times 1000 \tag{1}$$

where $\rho$ is the species mean wood density (g cm$^{-3}$), $D$ is the stem diameter (cm) measured or estimated 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 (Fick & Hijmans, 2017), which uses ANUSPLIN to generate bioclimatic variables (Booth et al., 2014). 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 et al. 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 et al. (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.

## 2.3 Data analysis

### 2.3.1 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 uses Hill numbers of the order $q = 0$ to extrapolate a species rarefaction curve to its predicted asymptote and uses this value as its estimated species richness value (Jost, 2006). Extrapolated species richness accounts for variation in plot size present in the dataset (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. In terms of the theory of niche complementarity, both species richness and abundance evenness contribute to the positive total diversity effect on ecosystem function. Holding either species richness or abundance evenness constant while increasing the other will have the similar effect of reducing the likelihood that a neighbour is a conspecific, thus reducing the occurrence of negative density dependent competition effects and therefore increasing ecosystem function. We quantified tree structural diversity for each plot by calculating the Coefficient of Variation of DBH (DBH CoV) and tree height (Height CoV).

### 2.3.2 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.

### 2.3.3 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 consideration in 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).

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 (Figure S1, Figure S2). 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 et al., 2017).

First, we used a simple mediation model which excluded the environmental covariates, to assess the role of tree species diversity and tree structural diversity in determining AGB. This model allowed direct effects of species diversity, structural diversity, and stem density on AGB, and also the indirect effect of species diversity on AGB via structural diversity. 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 & 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 biodiversity effects on ecosystem function increase in strength as stem density increases, we repeatedly sub-sampled the available plot dataset to create 50 data subsets with similar stem density. For each data subset we separately fitted a model including tree species and structural diversity latent variables to predict AGB. As we controlled for stem density via the dataset sub-sampling process, the effect of stem density on AGB was not included in the model. We examined how the unstandardised path coefficients for each path in the SEM varied according to the median stem density of the data subsets.

Second, we fitted the full model with environmental covariates, 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 among paths in the model to understand the relative contribution of each path to explain variance in AGB. Due to sample size issues, and because some vegetation types were narrow in their climate space, particularly in the water availability latent variable, we could not fit the model including environmental covariates separately for each vegetation type, as we encountered issues with model convergence. Preliminary models that included herbivore biomass (Hempson et al., 2017) did not converge. This is possibly due to the spatially coarse nature of the available data, or to collinearity with other variables, notably MAP and fire frequency. We therefore did not include herbivory in our final model.

# 3 Results

Pairwise correlations between all observed variables used in the Structural Equation Models (SEMs) showed that all tree species diversity (extrapolated tree species richness, Shannon equitability index) and structural diversity (coefficients of variation of DBH and height) variables had moderate positive correlations with AGB (Figure 3, Figure S3). 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: $r = 0.01$, $p = 0.86$).

## 3.1 Structural and species diversity models

In the reduced SEM, which included stem density and the mediating effect of species diversity on AGB via structural diversity (Figure 4), species diversity showed no direct effect on AGB ($\beta = 0.01 \pm 0.053$, $p = 0.88$), but did have an indirect positive effect via structural diversity ($\beta = 0.18 \pm 0.039$, $p < 0.01$) (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 ($\beta = 0.5 \pm 0.033$, $p < 0.01$).

## 3.2 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 ($\beta = 0.16 \pm 0.121$, $p = 0.18$) but negligible in Mopane ($\beta = 0.24 \pm 0.099$, $p < 0.05$), sparse miombo / *Baikiaea* ($\beta = 0.23 \pm 0.045$, $p < 0.01$) and Core miombo ($\beta = 0.23 \pm 0.041$, $p < 0.01$) (Figure 5). Relationships among 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 and there was a positive direct effect of species diversity on structural diversity, across all vegetation types. 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. $\chi^2$ 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).

## 3.3 Moderation of Diversity-AGB relationship by stem density

In the 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 6e). There appears to be a minimum stem density threshold at c. 180 stems >10 cm DBH $ha^{-1}$ below which there appears to be a reasonably constant baseline effect of tree diversity on biomass (Figure 6b). The effect of structural diversity on AGB appears to remain constant with increasing stem density (Figure 6d). The indirect effect of tree species diversity on AGB via structural diversity increases as stem density increases (Figure 6c).

## 3.4 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 S4). The direct effects of water availability, 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 effects 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 (water: $\beta = 0.62 \pm 0.172$, $p < 0.01$, 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 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 ($\beta = 0.19 \pm 0.026$, $p < 0.01$) when environmental covariates were accounted for. Again, the direct effect of species diversity on AGB was negligible ($\beta = -0.05 \pm 0.041$, p = 0.27). The total effect of species diversity on AGB was positive ($\beta$ = 0.34±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.

# 4 Discussion

We assessed the importance of a) tree species diversity, b) tree structural diversity, c) resource availability, d) disturbance by fire, e) organismal density and their interactions on above-ground woody biomass (AGB) across southern African savannas and woodlands, using a network of 1235 woodland plots in conjunction with 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). Within the latent variable of tree species diversity we found similarly strong factor loadings for both species richness and abundance evenness. This demonstrates that species richness and abundance evenness measure different and largely uncorrelated axes of diversity. We found that the effect of tree species diversity on AGB increased with stem density ($H_2$), with an apparent threshold of 180 stems >10 cm DBH ha$^{-1}$, below which the effect of species diversity on AGB remained at a low baseline level. The strongest direct 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 of the BEFR.

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

We found a consistent positive effect of tree species diversity on AGB. Within southern African woodlands we therefore find support for the hypothesis that higher tree species richness and evenness leads to higher above-ground woody biomass. 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-driven and poorly studied ecological system.

Much of the total variation in AGB was driven by variation in organismal 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 independent of 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. Additionally, the volume of tree above-ground structures is generally correlated with the volume of below-ground structures (Paul et al., 2019). In water and nutrient limited ecosystems especially, variation in rooting depth may constitute a second related axis of niche partitioning driving the observed positive effect of above-ground structural diversity on AGB (Kulmatiski & Beard, 2013). 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 et al., 2014). Indeed, our finding that the strength of the effect of tree diversity on AGB increases with stem density supports this mechanism (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 c. 180 trees ha$^{-1}$. In frequently disturbed woodlands such as those studied here, 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.

Alternatively, due to the non-linear relationship between biomass and tree size (Bastin et al., 2018), the positive relationship between structural diversity and biomass may also be partly driven by an increased number of large sized trees in plots with higher structural diversity, with large trees contributing disproportionately to biomass. The positive effect of species diversity on AGB via structural diversity may therefore be due to selection effects, with higher diversity plots supporting larger trees due to species specific variation in functional form (Díaz et al., 2015).

## 4.2 Organismal density and disturbance

Disturbance by fire had a negative total effect on AGB, with most of this negative effect coming from the indirect pathway via stem density. This is expected as increased fire frequency is a key mechanism by which savannas maintain an open canopy, rather than shifting to a closed canopy forest (Staver et al., 2011). 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 with a sparse understorey (Chidumayo, 2013; Mutowo & Murwira, 2012). In our study however, we found a positive effect of fire frequency on species diversity, perhaps suggesting that disturbance prevents domination of woodlands by a single dominant species (Chidumayo, 2013; Durigan et al., 2020; Staver et al., 2009). It is suggested that in savannas where the tree-species pool is largely adapted to fire, increased fire may actually increase tree species diversity by allowing weak competitors to co-exist.

Disturbances such as fire have the potential to reduce both species diversity and above-ground biomass in the short term, due to increased mortality (Huston, 2014). Unless this effect is accounted for, there is the potential for mistaken causality as both diversity and biomass may correlate. In our model, time since disturbance is accounted for within each plot via the stem density term. Disturbance reduces stem density of large stems (>10 cm DBH), which is expected to increase until the effects of competition preclude further increase (Johnson et al., 2012). Furthermore, our rarefied measure of species diversity accounts for variation in sampling effort and is therefore independent of stem density. Tree species richness should also increase with time since disturbance as with increased stem density the likelihood of including a new species also increases. Outside of the stem density effect, there are multiple causes for variation in tree species diversity in this study. Vegetation types and localities differ in their available species pool, for example. Variation in abiotic environmental factors will also affect species accumulation.

## 4.3 Effects of water availability and soil fertility

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; Ali et al., 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.

A negative total effect of soil fertility on AGB is in contrast to other studies in the region and general ecological theory, which predicts a positive effect of soil nutrients on biomass (Scarascia-Mugnozza et al., 2000). 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 in southern African woodlands (Muledi et al., 2017; Bucini & Hanan, 2007). It is therefore not surprising that this model path is poorly constrained. Lehmann et al. (2014) found similarly weak and poorly constrained relationships for soil in a Structural Equation Model including precipitation, temperature, soil, and fire to predict tree basal area in southern African woodlands. Plot-specific soil data are time-consuming to collect and difficult to compare across studies when different protocols are used. Our study points to 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. Alternatively, Gourlet-Fleury et al. (2011) found that environmental filtering of fast-growing species with low wood density on resource poor soils resulted in a decoupling of the soil fertility - AGB relationship. It is possible that at regional scales, variation in species composition could offset resource availability constraints on AGB. However, unlike Gourlet-Fleury et al. (2011) disturbance by fire in our study region may further complicate this environmental filtering effect.

## 4.4 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 can produce large canopy dominating trees in the so-called “Cathedral mopane”. 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 et al., 2010), a positive effect of tree species diversity on AGB was observed. In previous studies across multiple biomes it has been found that the effect of adding species on ecosystem function is stronger in low diversity assemblages (Cardinale et al., 2006; Srivastava & Vellend, 2005). This has been attributed to an increase in functional redundancy as species diversity increases. Mopane woodlands also have a negligible effect of species diversity on structural diversity. This may be due to the particular functional forms of species which co-exist with *C. mopane*, many of which are small shrub-like trees rather than large canopy trees (Timberlake et al., 2010). Larger canopy trees tend to have greater variation in physical structure (Seidel et al., 2019) which would drive an effect of species diversity on structural diversity as we observed in miombo woodlands.

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. Additionally, many more species species in ex-Acacia woodlands are found in the Mimosoideae and Papilionoideae sub-families, of which most are nitrogen-fixing (Tedersoo et al., 2018). Nitrogen availability is often a limiting factor in productivity, making nitrogen-fixing species strong competitors. It is possible that in ex-Acacia dominated woodlands, the presence of a large number of nitrogen-fixing tree species reduces functional redundancy, meaning that the effect of adding species on ecosystem function saturates at a higher species richness.

# 5 Conclusions

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). Our findings contribute to our understanding of a universal biodiversity-ecosystem function relationship, one which is moderated in a predictable manner by environmental covariates and their interaction with biodiversity and ecosystem structure. 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 processes operate across the region to determine ecosystem function. We advocate for explicit inclusion of environmental covariates in regional scale models of biodiversity and ecosystem function. We assert that this is necessary to develop our understanding of the biodiversity-ecosystem function relationship in real-world ecosystems, to progress from experimental mesocosms. We found that much of the effect of species diversity on biomass exists as an indirect effect by increasing the structural diversity of trees, exemplifying a key mechanism by which tree species diversity determines ecosystem function in savannas, woodlands and forests, where trees comprise a significant, canopy-forming component. 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 previous studies despite its intuitive logic as a determinant of niche complementarity effects in wooded ecosystems. Our study shows that biodiversity change through extensive human-induced land use change in this region will have the greatest negative impact on ecosystem function in areas of high stems density, and in certain vegetation types, specifically Mopane and ex-Acacia woodlands. This raises concerns about the robustness of these ecosystems to further resource extraction and biodiversity loss. Finally, our results provide further evidence of the complex interaction of factors governing biomass and therefore carbon dynamics in disturbance-driven wooded ecosystems, which currently represent the greatest uncertainty in the global terrestrial carbon sink.

# 6 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 (Above-Ground woody Biomass) within each cluster. N = number of plots in 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 | Species Richness | Stem density (stems ha$^{-1}$) | AGB (t ha$^{-1}$) |
|---|---|---|---|---|---|---|
| Core miombo | *Brachystegia spiciformis*<br>*Julbernardia paniculata*<br>*Brachystegia boehmii* | *Parinari curatellifolia*<br>*Uapaca kirkiana*<br>*Brachystegia spiciformis* | 523 | 20(16.9) | 204(142.5) | 44.2(36.11) |
| ex-Acacia | *Spirostachys africana*<br>*Senegalia burkei*<br>*Senegalia nigrescens* | *Euclea racemosa*<br>*Vachellia nilotica*<br>*Spirostachys africana* | 188 | 12(10.3) | 181(166.5) | 54.5(61.33) |
| Mopane | *Colophospermum mopane*<br>*Androstachys johnsonii*<br>*Kirkia acuminata* | *Colophospermum mopane*<br>*Psuedolachnostylis maprouneifolia*<br>*Lannea discolor* | 58 | 10(10.2) | 186(125.6) | 42.7(32.83) |
| Sparse miombo / Baikiaea | *Baikiaea plurijuga*<br>*Burkea africana*<br>*Pterocarpus angolensis* | *Burkea africana*<br>*Baikiaea plurijuga*<br>*Pterocarpus angolensis* | 466 | 12(13.7) | 178(129.5) | 36.9(26.98) |

Table 2: Model fit statistics for Structural Equation Models investigating the effects of tree diversity and stem density on AGB (Figure 4). N = number of plots in cluster, $\chi^2$ = 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 (Above-Ground Biomass).

| Cluster | N | $\chi^2$ | DoF | CFI | TLI | RMSEA | $R^2$ AGB |
|---|---|---|---|---|---|---|---|
| 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 |
| Sparse miombo / Baikiaea | 466 | 43.870 | 6 | 0.914 | 0.784 | 0.130 | 0.580 |
| All | 1235 | 91.380 | 6 | 0.937 | 0.843 | 0.120 | 0.490 |

## 7 Figures

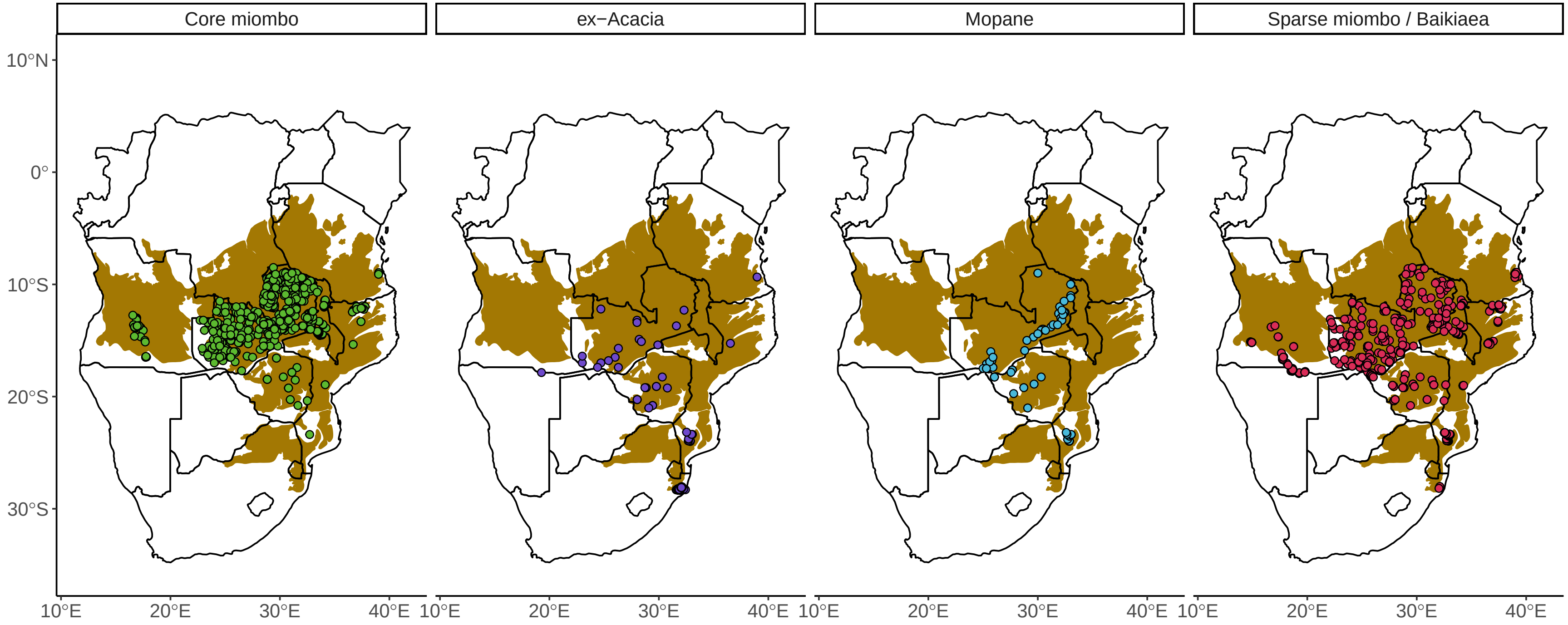


Figure 1: The locations of the 1235 plots used in this study, with respect to the distribution of mesic savanna vegetation according to Hopkins & White (1987). Each panel shows plots categorized by their vegetation type as defined by the vegetation types in Table 1.

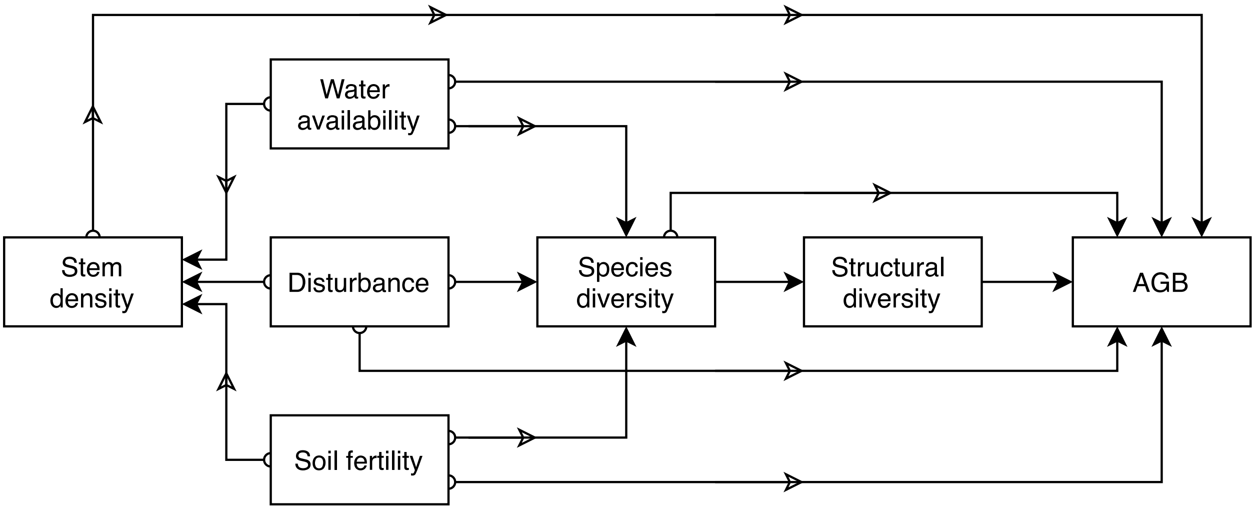
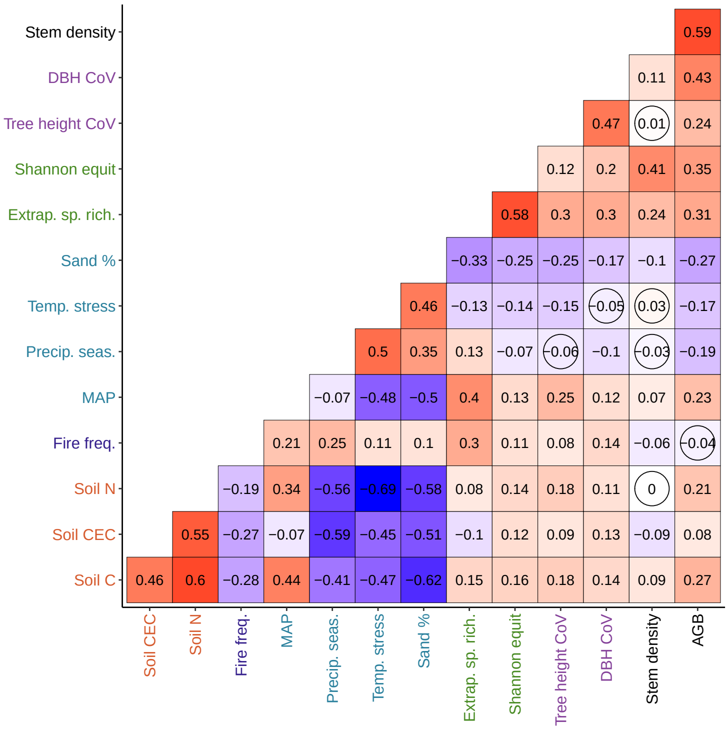


Figure 2: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural diversity, stem density, and AGB (Above-Ground Woody Biomass). Hypothesised paths of causation are depicted as arrows from predictor to response. Open arrow heads track the direction of each arrow along its path.



| | Soil CEC | Soil N | Fire freq. | MAP | Precip. seas. | Temp. stress | Sand % | Extrap. sp. rich. | Shannon equit | Tree height CoV | DBH CoV | Stem density | AGB |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stem density | | | | | | | | | | | | | 0.59 |
| DBH CoV | | | | | | | | | | | | 0.11 | 0.43 |
| Tree height CoV | | | | | | | | | | | 0.47 | 0.01 | 0.24 |
| Shannon equit | | | | | | | | | | 0.12 | 0.2 | 0.41 | 0.35 |
| Extrap. sp. rich. | | | | | | | | | 0.58 | 0.3 | 0.3 | 0.24 | 0.31 |
| Sand % | | | | | | | | −0.33 | −0.25 | −0.25 | −0.17 | −0.1 | −0.27 |
| Temp. stress | | | | | | | 0.46 | −0.13 | −0.14 | −0.15 | −0.05 | 0.03 | −0.17 |
| Precip. seas. | | | | | | 0.5 | 0.35 | 0.13 | −0.07 | −0.06 | −0.1 | −0.03 | −0.19 |
| MAP | | | | | −0.07 | −0.48 | −0.5 | 0.4 | 0.13 | 0.25 | 0.12 | 0.07 | 0.23 |
| Fire freq. | | | | 0.21 | 0.25 | 0.11 | 0.1 | 0.3 | 0.11 | 0.08 | 0.14 | −0.06 | −0.04 |
| Soil N | | | −0.19 | 0.34 | −0.56 | −0.69 | −0.58 | 0.08 | 0.14 | 0.18 | 0.11 | 0 | 0.21 |
| Soil CEC | | 0.55 | −0.27 | −0.07 | −0.59 | −0.45 | −0.51 | −0.1 | 0.12 | 0.09 | 0.13 | −0.09 | 0.08 |
| Soil C | 0.46 | 0.6 | −0.28 | 0.44 | −0.41 | −0.47 | −0.62 | 0.15 | 0.16 | 0.18 | 0.14 | 0.09 | 0.27 |

Figure 3: Correlation matrix of standardised observed variables used in the SEMs (Structural Equation Models), 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 Table S1 for a full assessment of correlation fit statistics.

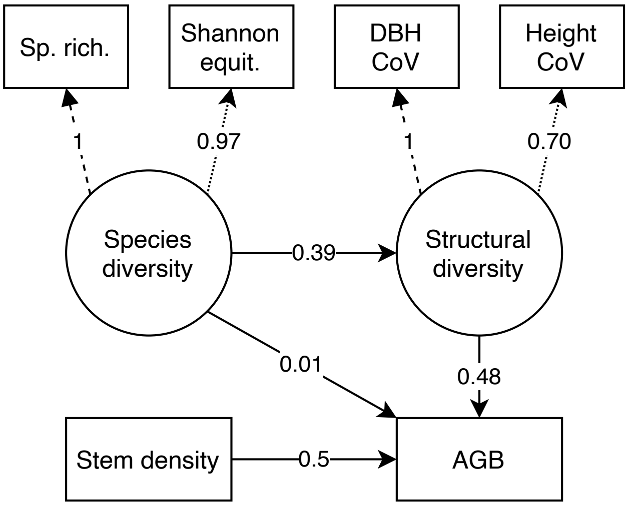


Figure 4: Path diagram with regression coefficients for the tree diversity SEM (Structural Equation Model), including plots from all vegetation clusters. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are shown as solid arrows pointing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

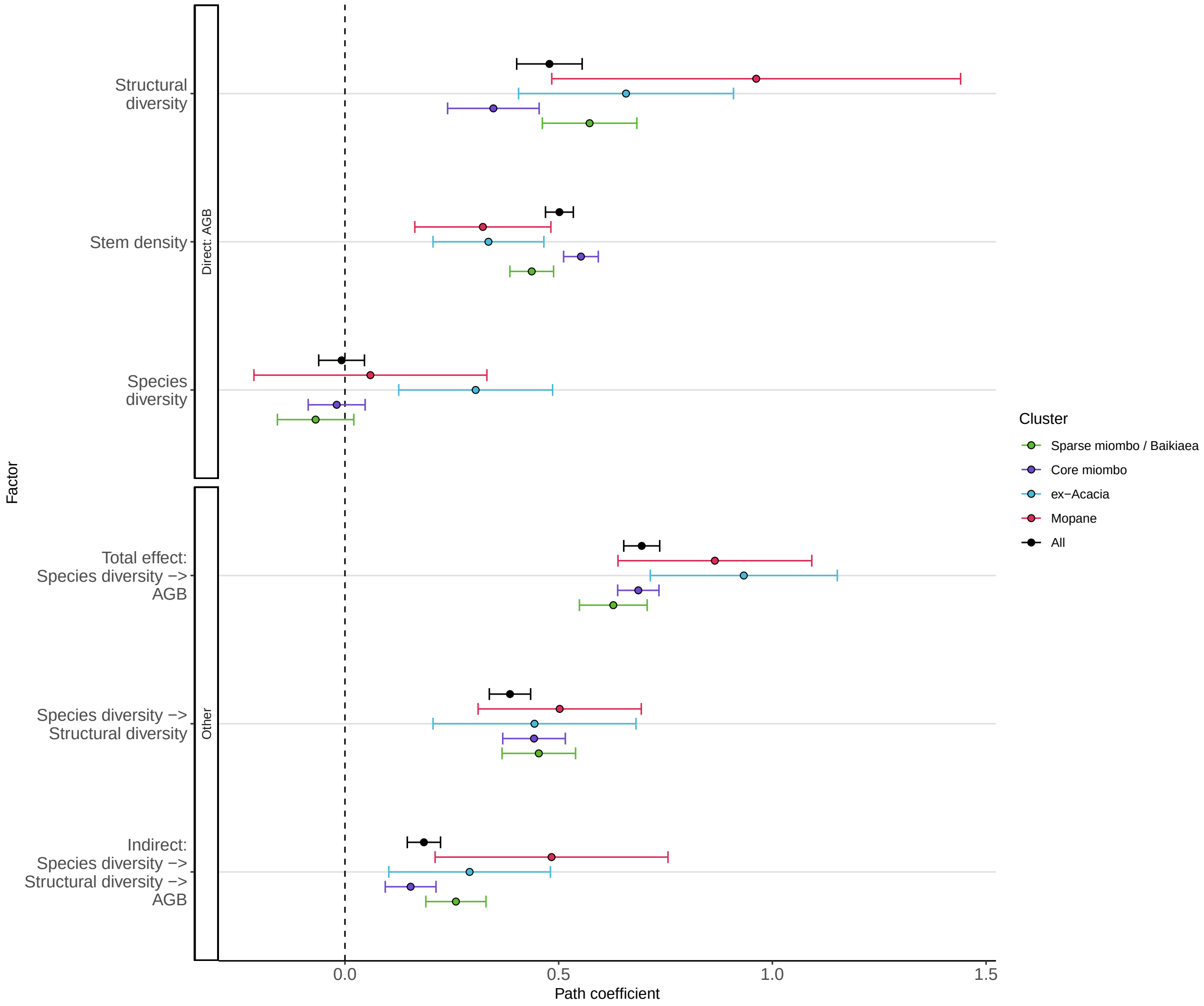


Figure 5: Unstandardised path coefficients for the effects of tree diversity on AGB (Above-Ground Woody Biomass), mediated by the effect of stand structural diversity. Path coefficients are ±1 standard error. Path coefficients where the interval (standard error) does not overlap zero are considered to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

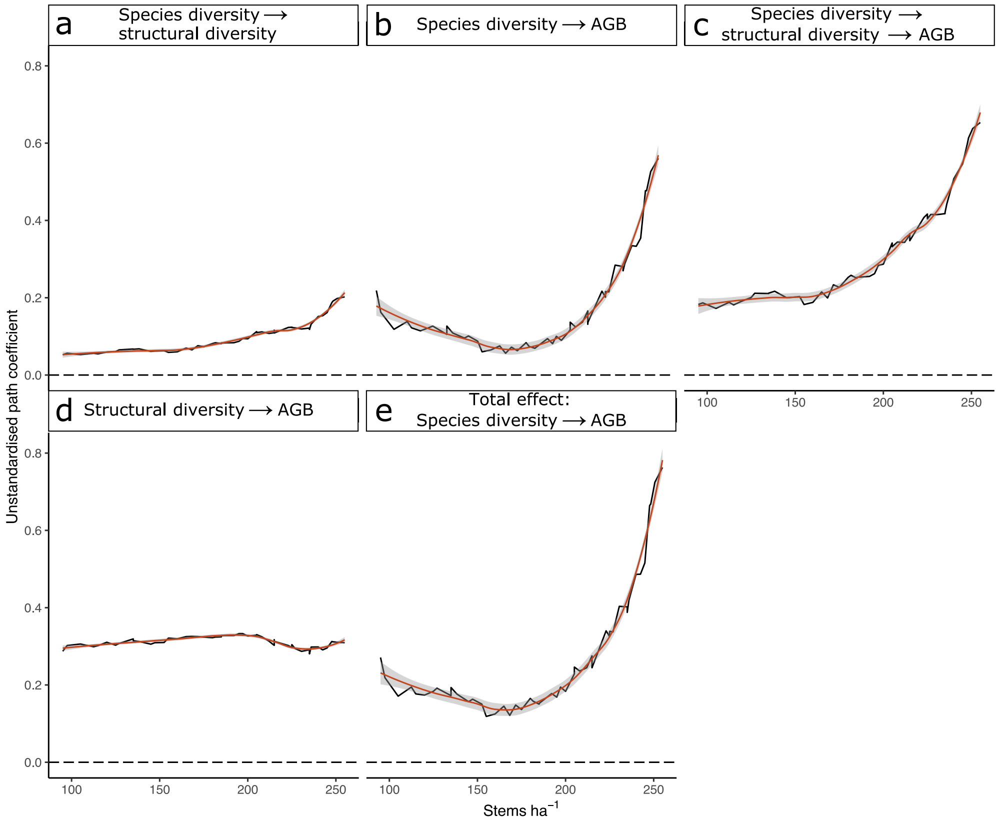


Figure 6: Line plots showing the variation in SEM (Structural Equation Model) path coefficients among latent variables, across datasets with different mean stem density. Smoothed lines are loess curves with ±1 standard error shaded bars. AGB = Above-Ground woody Biomass. Arrows in plot titles indicate causal paths in SEM models. Where multiple arrows are present, as in c), this indicates an indirect pathway via an intermediate variable. a) shows the direct effect of species diversity on structural diversity. b) and d) show the direct effects of species diversity and structural diversity on AGB, respectively. c) shows the indirect effect of species diversity on AGB via structural diversity. e) shows the total effect of species diversity on AGB, incorporating both the direct effect and the indrect effect via structural diversity.

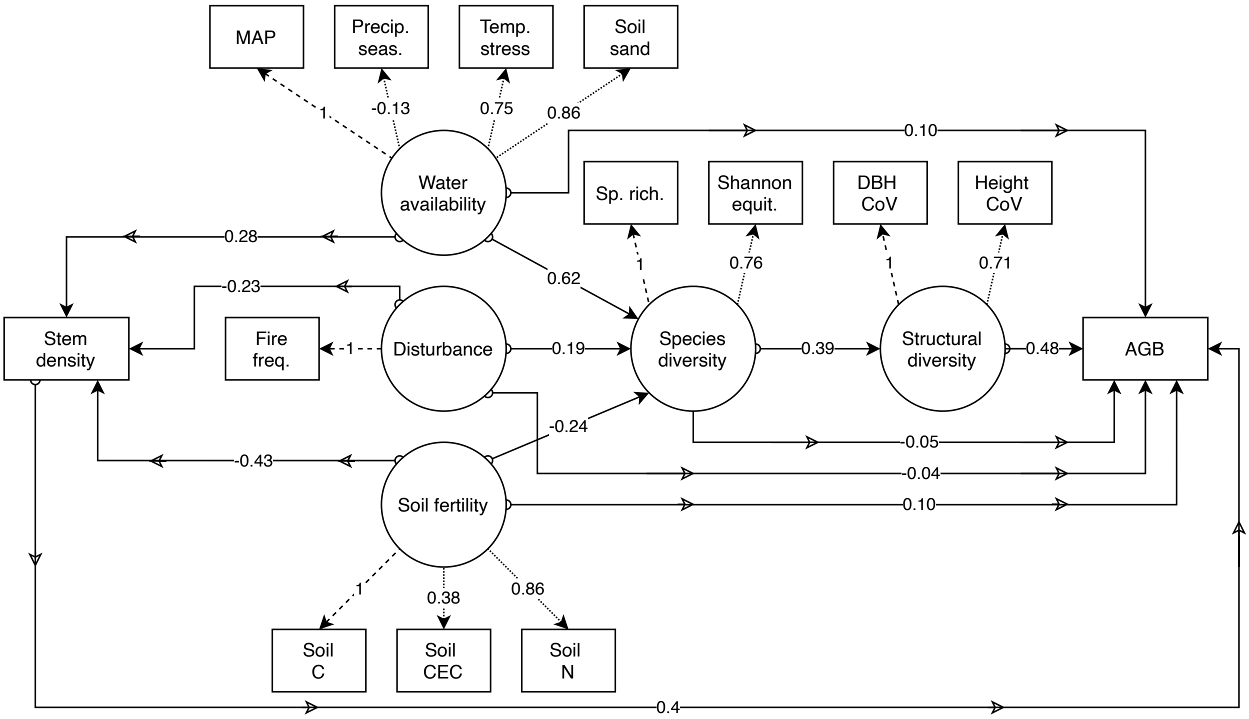


Figure 7: Path diagram with regression coefficients for the SEM (Structural Equation Model) incorporating environmental covariates and tree species and structural diversity across all five vegetation types. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised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

# 8 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 in collecting plot data. JMBC was supported by the Natural Environment Research Council (Agreement PR140015 between NERC and the National Centre for Earth Observation).

# 9 Author contribution

JLG and KGD conceived the study. JLG conducted data analysis, data management for further versions of the SEOSAW dataset, and wrote the manuscript. CMR conceived the SEOSAW database and conducted data management for earlier versions of the SEOSAW dataset. JLG, CMR, DB, ETAM, HGT, JMBC, KGD, MF, MW, MtB, RMH and SS contributed to manuscript revisions. JLG, AM, AS, AVC, CMR, DJD, FMG, IM, JJT, JPGMC, JW, MF, MtB, MW, NSR, RR, SJB, SM and SS contributed to experimental design, field data collection, data preparation and data management of parts of the dataset used in this study.

# 10 Data Availability

An anonymised version of the data that support the findings of this study are available at this DOI: `https://doi.org/10.7488/ds/3095`.

# References

Ahlstrom, A., M. R. Raupach, G. Schurgers, B. Smith, A. Arneth, M. Jung, M. Reichstein, J. G. Canadell, P. Friedlingstein, A. K. Jain et al. (2015). 'The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink'. In: *Science* 348.6237, pp. 895–899. DOI: `10.1126/science.aaa1668`.

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

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

Barry, K. E., L. Mommer, J. van Ruijven, C. Wirth, A. J. Wright, Y. Bai, J. Connolly, G. B. De Deyn, H. de Kroon, F. Isbell et al. (2019). 'The future of complementarity: Disentangling causes from consequences'. In: *Trends in Ecology & Evolution* 34.2, pp. 167–180. DOI: `10.1016/j.tree.2018.10.013`.

Bastin, J., E. Rutishauser, J. R. Kellner, S. Saatchi, R. Pélissier, B. Hérault, F. Slik, J. Bogaert, C. De Cannièire, A. R. Marshall et al. (2018). 'Pan-tropical prediction of forest structure from the largest trees'. In: *Global Ecology and Biogeography* 27.11, pp. 1366–1383. DOI: `https://doi.org/10.1111/geb.12803`.

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

Booth, Trevor H., Henry A. Nix, John R. Busby & Michael F. Hutchinson (2014). 'BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies'. In: 20.1, pp. 1–9. DOI: `10.1111/ddi.12144`. URL: `https://doi.org/10.1111%2Fddi.12144`.

Brockerhoff, E. G., L. Barbaro, B. Castagneyrol, D. I. Forrester, B. Gardiner, J. R. González-Olabarria, P. O'B. Lyver, N. Meurisse, A. Oxbrough, H. Taki et al. (2017). 'Forest biodiversity, ecosystem functioning and the provision of ecosystem services'. In: *Biodiversity and Conservation* 26.13, pp. 3005–3035. DOI: `10.1007/s10531-017-1453-2`.

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

Campbell, B. M., ed. (1996). *The miombo in transition: Woodlands and welfare in Africa.* Bogor, Indonesia: Centre for International Forestry Research.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran & C. Jouseau (2006). 'Effects of biodiversity on the functioning of trophic groups and ecosystems'. In: *Nature* 443.7114, pp. 989–992. DOI: `10.1038/nature05202`.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, C. Jouseau, M. W. Cadotte, I. T. Carroll, J. J. Weis et al. (2009). 'Effects of biodiversity on the functioning of ecosystems: a summary of 164 experimental manipulations of species richness'. In: *Ecology* 90, pp. 854–854. DOI: `10.1890/08-1584.1`.

Carvalho, G. H., M. A. Batalha, I. A. Silva, M. V. Cianciaruso & O. L. Petchey (2014). 'Are fire, soil fertility and toxicity, water availability, plant functional diversity, and litter decomposition related in a Neotropical savanna?' In: *Oecologia* 175.3, pp. 923–935. DOI: `10.1007/s00442-014-2937-3`.

Cham, H., E. Reshetnyak, B. Rosenfeld & W. Breitbart (2017). 'Full information maximum likelihood estimation for latent variable interactions with incomplete indicators'. In: *Multivariate Behavioural Research* 52, pp. 12–30. DOI: `10.1080/00273171.2016.1245600`.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson & A. E. Zanne (2009). 'Towards a worldwide wood economics spectrum'. In: *Ecology Letters* 12, pp. 351–366. DOI: `10.1111/j.1461-0248.2009.01285.x`.

Chave, J., M. Réjou-Méchain, A. Búrquez, E. Chidumayo, M. S. Colgan, W. B. C. Delitti, A. Duque, T. Eid, P. M. Fearnside, R. C. Goodman et al. (2014). 'Improved allometric models to estimate the aboveground biomass of tropical trees'. In: *Global Change Biology* 20, pp. 3177–3190. DOI: `10.1111/gcb.12629`.

Chidumayo, E. N. (2013). 'Forest degradation and recovery in a miombo woodland landscape in Zambia: 22 years of observations on permanent sample plots'. In: *Forest Ecology and Management* 291, pp. 154–161. DOI: `10.1016/j.foreco.2012.11.031`.

Clarke, D. A., P. H. York, M. A. Rasheed & T. D. Northfield (2017). 'Does biodiversity - ecosystem function literature neglect tropical ecosystems'. In: *Trends in Ecology & Evolution* 32, pp. 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'. In: *Journal of Biogeography* 36, pp. 728–744. DOI: `10.1111/j.1365-2699.2008.02038.x`.

Dexter, K. G., B. Smart, C. Baldauf, T. R. Baker, M. P. B. Bessike Balinga, R. J. W. Brienen, S. Fauset, T. R. Feldpausch, L. Ferreira-da Silva, J. I. Muledi et al. (2015). 'Floristics and biogeography of vegetation in seasonally dry tropical regions'. In: *International Forestry Review* 17.S2, pp. 10–32. DOI: `http://dx.doi.org/10.1505/146554815815834859`.

Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. C. Prentice et al. (2015). 'The global spectrum of plant form and function'. In: *Nature* 529.7585, pp. 167–171. DOI: `10.1038/nature16489`.

Dufrêne, M. & P. Legendre (1997). 'Species assemblages and indicator species: The need for a flexible asymmetrical approach'. In: *Ecological Monographs* 67.3, pp. 345–366. DOI: `10.1890/0012-9615(1997)067[0345:saaist]2.0.co;2`.

Durigan, G., N. A. L. Pilon, R. C. R. Abreu, W. A. Hoffmann, M. Martins, B. F. Fiorillo, A. Z. Antunes, A. P. Carmignotto, J. B. Maravalhas, J. Vieira et al. (2020). 'No net loss of species diversity after prescribed fires in the Brazilian savanna'. In: *Frontiers in Forests and Global Change* 3. DOI: `10.3389/ffgc.2020.00013`.

Fayolle, A., M. D. Swaine, J. Aleman, A. F. Azihou, D. Bauman, M. te Beest, E. N. Chidumayo, J. P. G. M. Cromsigt, H. Dessard, M. Finkch et al. (2018). 'A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas'. In: *Journal of Biogeography* 46, pp. 1–12. DOI: `10.1111/jbi.13475`.

Fick, S. E. & R. J. Hijmans (2017). 'WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas'. In: *International Journal of Climatology* 37, pp. 4302–4315. DOI: `10.1002/joc.5086`.

Giglio, L., C. Justice, L. Boschetti & D. Roy (2015). *MCD64A1 MODIS/Terra+Aqua Burned Area Monthly L3 Global 500m SIN Grid V006 [Data set]*. NASA EOSDIS Land Processes DAAC. [Accessed 2020-04-20].

Godlee, J. L., F. M. Gonçalves, J. J. Tchamba, A. V. Chisingui, J. I. Muledi, M. N. Shutcha, C. M. Ryan, T. K. Brade & K. G. Dexter (2020). 'Diversity and structure of an arid woodland in southwest Angola, with comparison to the wider miombo ecoregion'. In: *Diversity* 12, pp. 1–20. DOI: `10.3390/d12040140`.

Gonzalez, A., R. M. Germain, D. S. Srivastava, E. Filotas, L. D. Dee, D. Gravel, D. L. Thompson, F. Isbell, S. Wang, S. Kéfi et al. (2020). 'Scaling-up biodiversity-ecosystem functioning research'. In: *Ecology Letters* 23.4, pp. 757–776. DOI: `10.1111/ele.13456`.

Gourlet-Fleury, S., V. Rossi, M. Réjou-Méchain, V. Freycon, A. Fayolle, L. Saint-André, G. Cornu, J. Gérard, J. Sarrailh, J. Flores et al. (2011). 'Environmental filtering of dense-wooded species controls above-ground biomass stored in African moist forests'. In: *Journal of Ecology* 99.4, pp. 981–990. DOI: `10.1111/j.1365-2745.2011.01829.x`.

Grace, J. B., T. M. Anderson, M. D. Smith, E. Seabloom, S. J. Andelman, G. Meche, E. Weiher, L. K. Allain, H. Jutila, M. Sankaran et al. (2007). 'Does species diversity limit productivity in natural grassland communities?' In: *Ecology Letters* 10.8, pp. 680–689. DOI: `10.1111/j.1461-0248.2007.01058.x`.

Grime, J. P. (1979). *Plant strategies and vegetation processes*. Chichester, UK: John Wiley and Sons. ISBN: 0471496014.

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

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

Hengl, T., J. Mendes de Jesus, G. B. M. Heuvelink, M. R. Gonzalez, M. Kilibarda, A. Blagotić, W. Shangguan, M. N. Wright, X. Geng, B. Bauer-Marschallinger et al. (2017). 'SoilGrids250m: Global gridded soil information based on machine learning'. In: *PLoS ONE* 12, pp. 1–40. DOI: `10.1371/journal.pone.0169748`.

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

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

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

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

Hsieh, T. C., K. H. Ma & A. Chao (2016). 'iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers)'. In: *Methods in Ecology and Evolution* 7, pp. 1451–1456. DOI: `10.1111/2041-210X.12613`.

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

Huston, M. A. (2014). ‘Disturbance, productivity, and species diversity: Empiricism vs. logic in ecological theory’. In: *Ecology* 95.9, pp. 2382–2396. DOI: `10.1890/13-1397.1`.

Jax, K. (2005). ‘Function and “functioning” in ecology: what does it mean?’ In: *Oikos* 111, pp. 641–648. DOI: `10.1111/j.1600-0706.2005.13851.x`.

Johnson, D. J., W. T. Beaulieu, J. D. Bever & K. Clay (2012). ‘Conspecific Negative Density Dependence and Forest Diversity’. In: *Science* 336.6083, pp. 904–907. DOI: `10.1126/science.1220269`.

Jost, L. (2006). ‘Entropy and diversity’. In: *Oikos* 113.2, pp. 363–375. DOI: `10.1111/j.2006.0030-1299.14714.x`.

Keddy, P. A. (1990). ‘Competitive hierarchies and centrifugal organization in plant communities’. In: *Perspectives on plant competition.* Ed. by J. B. Grace & D. Tilman. San Diego CA, USA: Academic Press, pp. 266–287. ISBN: 0122944526.

Kraaij, T. & D. Ward (2006). ‘Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa’. In: *Plant Ecology* 186, pp. 235–246. DOI: `10.1007/s11258-006-9125-4`.

Kulmatiski, A. & K. H. Beard (2013). ‘Root niche partitioning among grasses, saplings, and trees measured using a tracer technique’. In: *Oecologia* 171.1, pp. 25–37. DOI: `10.1007/s00442-012-2390-0`.

Lasky, J. R., M. Uriarte, V. K. Boukili, D. L. Erickson, W. J. Kress & R. L. Chazdon (2014). ‘The relationship between tree biodiversity and biomass dynamic changes with tropical forest succession’. In: *Ecology Letters* 17, pp. 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., T. M. Anderson, M. Sankaran, S. I. Higgins, S. Archibald, W. A. Hoffmann, N. P. Hanan, R. J. Williams, Fenshamm R. J., J. Felfili et al. (2014). ‘Savanna vegetation-fire-climate relationships differ among continents’. In: *Science* 343, pp. 548–552. DOI: `10.1126/science.1247355`.

Levick, S. R., G. P. Asner, T. Kennedy-Bowdoin & D. E. Knapp (2009). ‘The relative influence of fire and herbivory on savanna three-dimensional vegetation structure’. In: *Biological Conservation* 142, pp. 1693–1700. DOI: `10.1016/j.biocon.2009.03.004`.

Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E.-D. Schulze, A. D. McGuire, F. Bozzato, H. Pretzsch et al. (2016). ‘Positive biodiversity-productivity relationship predominant in global forests’. In: *Science* 354, aaf8957–aaf8957. DOI: `10.1126/science.aaf8957`.

Loiola, P. P., M. Scherer-Lorenzen & M. A. Batalha (2015). ‘The role of environmental filters and functional traits in predicting the root biomass and productivity in savannas and tropical seasonal forests'. In: *Forest Ecology and Management* 342, pp. 49–55. DOI: `10.1016/j.foreco.2015.01.014`.

Mason, N. W. H., F. de Bello, J. Doležal & J. Lepš (2011). 'Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities'. In: *Journal of Ecology* 99.3, pp. 788–796. DOI: `10.1111/j.1365-2745.2011.01801.x`.

Mayaux, P., H. Eva, A. Brink, F. Achard & A. Belward (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*. Berlin, Germany: Springer-Verlag, pp. 85–108. DOI: `10.1007/978-1-4020-6358-9_5`.

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

Mensah, S., V. K. Salako & T. Seifert (2020). 'Structural complexity and large-sized trees explain shifting species richness and carbon relationship across vegetation types'. In: *Functional Ecology* 34.8, pp. 1731–1745. DOI: `10.1111/1365-2435.13585`.

Muledi, J. I., D. Bauman, T. Drouet, J. Vleminckx, A. Jacobs, J. Lejoly, P. Meerts & M. N. Shutcha (2017). 'Fine-scale habitats influence tree species assemblage in a miombo forest'. In: *Journal of Plant Ecology* 10, pp. 958–969. DOI: `10.1093/jpe/rtw104`.

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

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

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

Naeem, S., J. E. Duffy & E. Zavaleta (2012). 'The functions of biological diversity in an age of extinction'. In: *Science* 336.6087, pp. 1401–1406. DOI: `10.1126/science.1215855`.

Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. L. Phillips, A. Shvidenko, S. L. Lewis, J. G. Canadell et al. (2011). 'A large and persistent carbon sink in the world's forests'. In: *Science* 333.6045, pp. 988–993. DOI: `10.1126/science.1201609`.

Paquette, A. & C. Messier (2010). 'The effect of biodiversity on tree productivity: from temperate to boreal forests'. In: *Global Ecology and Biogeography* 20.1, pp. 170–180. DOI: `10.1111/j.1466-8238.2010.00592.x`.

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

Paul, K. I., J. Larmour, Spechtm A., A. Zerihun, P. Ritson, S. H. Roxburgh, S. Sochacki, T. Lewis, C. V. M. Barton, J. R. England et al. (2019). 'Testing the generality of below-ground biomass allometry across plant functional types'. In: *Forest Ecology and Management* 432, pp. 102–114. DOI: `10.1016/j.foreco.2018.08.043`.

Pennington, R. T., C. E. R. Lehmann & L. M. Rowland (2018). 'Tropical savannas and dry forests'. In: *Current Biology* 28.9, R541–R545. DOI: `10.1016/j.cub.2018.03.014`.

Pichancourt, J., J. Firn, I. Chadès & T. G. Martin (2013). 'Growing biodiverse carbon-rich forests'. In: *Global Change Biology* 20.2, pp. 382–393. DOI: `10.1111/gcb.12345`.

Plas, F. van der (2019). 'Biodiversity and ecosystem functioning in naturally assembled communities'. In: *Biological Reviews* 94, pp. 1220–1245. DOI: `10.1111/brv.12499`.

Poorter, L., M. T. van der Sande, E. J. M. M. Arets, N. Ascarrunz, B. J. Enquist, B. Finegan, J. C. Licona, M. Martínez-Ramos, L. Mazzei, J. A. Meave et al. (2017). 'Biodiversity and climate determine the functioning of neotropical forests'. In: *Global Ecology and Biogeography* 26, pp. 1423–1434. DOI: `10.1111/geb.12668`.

Poorter, L., M. T. van der Sande, J. Thompson, E. J. M. M. Arets, A. Alarcòn, J. Àlvarez-Sànchez, N. Ascarrunz, P. Balvanera, G. Barajas-Guzmàn, A. Boit et al. (2015). 'Diversity enhances carbon storage in tropical forests'. In: *Global Ecology and Biogeography* 24, pp. 1314–1328. DOI: `10.1111/geb.12364`.

Pretzsch, H. (2014). 'Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures'. In: *Forest Ecology and Management* 327, pp. 251–264. DOI: `10.1016/j.foreco.2014.04.027`.

R Core Team (2019). *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing. Vienna, Austria. URL: `https://www.R-project.org/`.

Ratcliffe, S., C. Wirth, T. Jucker, F. van der Plas, M. Scherer-Lorenzen, K. Verheyen, E. Allan, R. Benavides, H. Bruelheide, B. Ohse et al. (2017). 'Biodiversity and ecosystem functioning relations in European forests depend on environmental context'. In: *Ecology Letters* 20, pp. 1414–1426. DOI: `10.1111/ele.12849`.

Ratnam, J., W. J. Bond, R. J. Fensham, W. A. Hoffmann, S. Archibald, C. E. R. Lehmann, M. T. Anderson, S. I. Higgins & M. Sankaran (2011). 'When is a 'forest' a savanna, and why does it matter?' In: *Global Ecology and Biogeography* 20, pp. 653–660. DOI: `10.1111/j.1466-8238.2010.00634.x`.

Roberts, D. W. (2019). *labdsv: Ordination and Multivariate Analysis for Ecology.* R package version 2.0-1. URL: `https://CRAN.R-project.org/package=labdsv`.

Rosseel, Y. (2012). 'lavaan: An R Package for Structural Equation Modeling'. In: *Journal of Statistical Software* 48, pp. 1–36. URL: `http://www.jstatsoft.org/v48/i02/`.

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

Sande, M. T. van der, L. Poorter, L. Kooistra, P. Balvanera, K. Thonicke, J. Thompson, E. J. M. M. Arets, N. G. Alaniz, L. Jones, F. Mora et al. (2017). ‘Biodiversity in species, traits, and structure determines carbon stocks and uptake in tropical forests’. In: *Biotropica* 49, pp. 593–603. DOI: `10.1111/btp.12453`.

Sankaran, M., J. Ratnam & N. P. Hanan (2008). ‘Woody cover in African savannas: The role of resources, fire and herbivory’. In: *Global Ecology and Biogeography* 17, pp. 236–245. DOI: `10.1111/j.1466-8238.2007.00360.x`.

Scarascia-Mugnozza, G., G. A. Bauer, H. Persson, G. Matteucci & A. Masci (2000). ‘Tree biomass, growth and nutrient pools’. In: *Ecological Studies*. Springer Berlin Heidelberg, pp. 49–62. DOI: `10.1007/978-3-642-57219-7_3`.

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

SEOSAW (2020). ‘A network to understand the changing socio-ecology of the southern African woodlands (SEOSAW): Challenges, benefits, and methods’. In: *Plants, People, Planet*. DOI: `10.1002/ppp3.10168`.

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

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

Sitch, S., P. Friedlingstein, N. Gruber, S. D. Jones, G. Murray-Tortarolo, A. Ahlström, S. C. Doney, H. Graven, C. Heinze, C. Huntingford et al. (2015). ‘Recent trends and drivers of regional sources and sinks of carbon dioxide’. In: *Biogeosciences* 12.3, pp. 653–679. DOI: `10.5194/bg-12-653-2015`.

Smith, B. & J. B. Wilson (1996). ‘A consumer’s guide to evenness indices’. In: *Oikos* 76, pp. 70–82. DOI: `10.2307/3545749`.

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

Spawn, S. A., C. C. Sullivan, T. J. Lark & H. K. Gibbs (2020). ‘Harmonized global maps of above and belowground biomass carbon density in the year 2010’. In: *Scientific Data* 7.1. DOI: `10.1038/s41597-020-0444-4`.

Srivastava, D. S. & D. S. Vellend (2005). ‘Biodiversity-ecosystem function research: Is it relevant to conservation?’ In: *Annual Review of Ecology, Evolution, and Systematics* 36.1, pp. 267–294. DOI: `10.1146/annurev.ecolsys.36.102003.152636`.

Staver, A. C., S. Archibald & S. A. Levin (2011). ‘The Global Extent and Determinants of Savanna and Forest as Alternative Biome States’. In: *Science* 334.6053, pp. 230–232. DOI: `10.1126/science.1210465`.

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

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

Tedersoo, L., L. Laanisto, S. Rahimlou, A. Toussaint, T. Hallikma & M. Pärtel (2018). 'Global database of plants with root-symbiotic nitrogen fixation: NodDB'. In: *Journal of Vegetation Science* 29.3, pp. 560–568. DOI: `10.1111/jvs.12627`.

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

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

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

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

Vilà, M., P. Inchausti, J. Vayreda, O. Barrantes, C. Gracia, J. J. Ibàñez & T. Mata (2005). 'Confounding factors in the observational productivity-diversity relationship in forests'. In: *Ecological Studies* 176, pp. 65–86.

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

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

## Supporting Information

Additional supporting information may be found in the online version of this article.

**Figure S1** Histograms of raw untransformed observed variables used in final analyses.

**Figure S2** Histograms of observed variables transformed to achieve a normal frequency distribution.

**Figure S3** Bivariate scatter plots for each observed variable used in SEMs, based on hypothesised paths of causality.

**Figure S4** Unstandardised path coefficients for full SEM model.

**Table S1** Table of correlation fit statistics for each pairwise Pearson correlation test of observed variables used in Structural Equation Models.