

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 at all 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, Duffy & Zavaleta, 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, Isbell & Cowles, 2014), to observational studies in natural ecosystems (van der 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.

37 Ecosystem functions are defined in broad terms as rate processes and aggregate properties of eco-
 38 systems that describe the nature of biotic activity within those ecosystems (Jax, 2005). Woody
 39 productivity and biomass storage are two of the most commonly studied ecosystem functions in
 40 forests and other wooded ecosystems (e.g. savannas) (Brockerhoff et al., 2017), due to their im-
 41 portance in the global carbon cycle (Pan et al., 2011) and their potential leverage as a tool to
 42 mitigate the effects of anthropogenic climate change while maintaining biodiversity (Pichancourt,
 43 Firn, Chadès & Martin, 2013). Theory predicts that biodiversity will have a positive effect on eco-
 44 system function via three principal mechanisms: 1) niche complementarity, whereby niche parti-
 45 tioning and ecosystem resource use efficiency is increased in diverse communities, minimising neg-
 46 ative density dependent effects such as conspecific competition and abundance of species-specific
 47 natural enemies (Barry et al., 2019); 2) selection effects, whereby diverse communities are more
 48 likely to include a high-yield species; and 3) facilitation effects, whereby diverse communities are
 49 more likely to contain species combinations which enhance each others' functional contribution
 50 (Wright, Wardle, Callaway & Gaxiola, 2017).

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

58 Disturbance-driven mesic savannas and open canopy woodlands cover >20% of the global land
 59 surface (Pennington, Lehmann & Rowland, 2018; Solbrig, Medina & Silva, 1996). They repres-
 60 ent the dominant vegetation type in Africa, spanning >4 million km² (Hopkins & White, 1987;
 61 Ratnam et al., 2011; Ryan et al., 2016) (Figure 1). Taken together, the above- and below-ground
 62 carbon stored in African mesic savannas may be comparable to that found in the wet forests of
 63 the Congo basin (Houghton, Hall & Goetz, 2009; Mayaux, Eva, Brink, Achard & Belward, 2008;
 64 Spawn, Sullivan, Lark & Gibbs, 2020). Globally, dry woodlands and savannas represent the largest,
 65 most sensitive and fastest increasing component of the terrestrial carbon sink (Ahlstrom et al.,
 66 2015). Yet their carbon dynamics remain poorly constrained (Sitch et al., 2015).

67 Despite their global importance, African savannas are severely under-represented in BEFR stud-
 68 ies (Clarke, York, Rasheed & Northfield, 2017; Liang et al., 2016). In savannas disturbance by fire
 69 (Lehmann et al., 2014) and herbivory (Levick, Asner, Kennedy-Bowdoin & Knapp, 2009; Sank-
 70 aran, Ratnam & Hanan, 2008) reduces woody stem density and biomass, diminishing competit-
 71 ive interactions between individuals, allowing competitors to co-exist where they would normally
 72 be excluded (Grime, 1979; Keddy, 1990). It is possible that a threshold woody stem density ex-
 73 ists below which the lack of competition precludes the detection of a biodiversity effect on ecosys-
 74 tem function via niche differentiation. Instead, stress tolerance and the functional contribution of
 75 particular species (selection effects) may be the predominant biotic forces influencing ecosystem
 76 function in these ecosystems (Lasky et al., 2014; Tobner et al., 2016). Additionally, stressful en-
 77 vironments appear to lessen the role of both niche complementarity and facilitation effects in driv-
 78 ing the BEFR, by replacing competition between individuals with stress tolerance as the limiting

factor on functional contribution (Paquette & Messier, 2010; Ratcliffe et al., 2017). 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, Ryan, Dexter, Ball & Williams, 2018; Mutowo & Murwira, 2012; Shirima, Pfeifer, Platts, Totland & Moe, 2015). 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 ($<2500 \text{ km}^2$), biodiversity shows a strong effect on ecosystem function, but at broader extents ($>100,000 \text{ km}^2$) biodiversity effects pale in significance compared to abiotic factors such as climate (Gonzalez et al., 2020). In West Africa, Mensah, Salako and Seifert (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, Scherer-Lorenzen and Batalha (2015) found that disturbance by fire reduced tree productivity via its effect on functional trait values. In contrast however, Carvalho, Batalha, Silva, Cianciaruso and Petchey (2014) also working in the Brazilian Cerrado, found that while disturbance by fire did reduce soil fertility, which is often closely related to productivity in savannas, functional trait diversity was unaffected by fire frequency. 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, de Bello, Doležal & Lepš, 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, weaken-

ing 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 functional form (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 (Hill & Hanan, 2011; Ratnam et al., 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, Lehmann, Bond, Hoffmann & Andersen, 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

158 stems only accounted for a median of 2.1% of the plot AGB.

159 All stems >10 cm DBH were measured within each plot resulting in a total of 66,758 stems with
160 measurements. A tree may be comprised of multiple stems and so tree-level richness estimates,
161 rather than stem-level estimates, were used to prevent bias from species which readily coppice.
162 For each tree, we recorded species, DBH and tree height to the top of the highest branch material.
163 Height was measured through a variety of means including laser rangefinders, manual clinometers
164 and measuring sticks. When DBH could not be measured at 1.3 m due to trunk abnormalities, it
165 was measured at the closest regular portion of the trunk to 1.3 m. The height of this measurement
166 was recorded and used to estimate the D_e at 1.3 m using a cubic polynomial regression, with para-
167 meters estimated using a test dataset from Ryan C., (unpublished), see Godlee et al. (2020).
168 AGB for each plot ($t\ ha^{-1}$) was calculated using Equation 1, taken from Chave et al. (2014):

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

169 where ρ is the species mean wood density ($g\ cm^{-3}$), D_e is the estimated DBH (cm) at 1.3 m, and
170 H is the tree height (m). Wood density estimates were taken from the global wood density data-
171 base for each species where possible (Chave et al., 2009; Zanne et al., 2009). Wood density for
172 species without species level estimates was estimated from the means of their respective genera.
173 For stems where tree height was unknown, the plots' climatic parameters, estimated from plot loc-
174 ation, were used to estimate tree height, according to Chave et al. (2014).

175 Climatic data were taken from the WorldClim database, using the BioClim variables (Fick & Hij-
176 mans, 2017). In addition to MAT and MAP, temperature stress was calculated as the mean di-
177 urnal temperature range (BIO2) and precipitation seasonality was calculated as the mean of the
178 coefficient of variation of monthly mean precipitation (BIO15). Soil fertility data were extracted
179 from the ISRIC gridded soil information data product at 250 m resolution, taking the grid cell
180 value for each plot centre (Hengl et al., 2017). We extracted Cation Exchange Capacity (CEC)
181 ($cmolc\ kg^{-1}$), soil organic carbon stocks ($kg\ m^{-2}$) percentage soil sand content (0.05-2 mm) by
182 weight and soil nitrogen content ($g\ kg^{-1}$). These data are a modelled product derived from vari-
183 ous remotely sensed and directly measured data sources. The degree of fire disturbance was cal-
184 culated using the MODIS monthly burned area product at 500 m resolution (MCD64A1, Giglio,
185 Justice, Boschetti and Roy 2015), counting the total number of times the plot pixel was classified
186 as burning, between 2001 and 2018. We initially aimed to include disturbance by herbivory in our
187 model, including total herbivore biomass from the Hempton, Archibald and Bond (2017) modelled
188 herbivory product, but this inclusion prevented models from converging due to its collinearity with
189 other observed variables, notably MAP and disturbance by fire.

190 2.3 Data analysis

191 2.3.1 Species diversity and structural diversity metrics

192 Estimated tree species richness was calculated for each plot using 'ChaoRichness()' from the 'iN-
193 EXT' package in R (Hsieh, Ma & Chao, 2016). This procedure uses Hill numbers of the order $q =$
194 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, Kroehne, Funke & Steyer, 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, 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 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 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.

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 due to collinearity with other variables, notably MAP and fire frequency. 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 among 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.

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 an SEM describing the effect of tree species diversity on AGB via the mediating effects of tree structural diversity and stem density (Figure 4), species diversity showed no direct effect on AGB ($\beta = 0.01 \pm 0.053$, $p = 0.88$), 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

313 Mopane ($\beta = 0.24 \pm 0.099$, $p < 0.05$), sparse miombo / *Baikiaea* ($\beta = 0.23 \pm 0.045$, $p < 0.01$) and
 314 Core miombo ($\beta = 0.23 \pm 0.041$, $p < 0.01$) (Figure 5). Relationships among structural diversity and
 315 AGB remained generally similar, with the same sign and overlap between the 95% confidence in-
 316 tervals of path coefficients. The R^2 of AGB was highest in ex-Acacia shrubland ($R^2 = 0.83$) and
 317 lowest in sparse miombo / *Baikiaea* ($R^2 = 0.46$). The total effect of species diversity on AGB re-
 318 mained strongly positive and there was a positive direct effect of species diversity on structural
 319 diversity, across all vegetation types. All models had adequate goodness-of-fit (Table 2), though
 320 confidence intervals around the unstandardised path coefficients were wide particularly for Mopane
 321 and ex-Acacia. χ^2 statistics were high for some vegetation types, but this appears to be highly
 322 correlated with sample size for each vegetation type (Hooper, Coughlan & Mullen, 2008).

3.3 Moderation of Diversity-AGB relationship by stem density

324 In the sub-sampling of the plot dataset by stem density, we found an increasing positive effect of
 325 tree species diversity on AGB as stem density increased (Figure 6e). There appears to be a min-
 326 imum stem density threshold at c. 180 stems > 10 cm DBH ha^{-1} below which there appears to be
 327 a reasonably constant baseline effect of tree diversity on biomass (Figure 6b). The effect of struc-
 328 tural diversity on AGB appears to remain constant with increasing stem density (Figure 6d). The
 329 indirect effect of tree species diversity on AGB via structural diversity increases as stem density
 330 increases (Figure 6c).

3.4 Environmental covariates and tree diversity

332 A model incorporating the latent variables of water availability, soil fertility and disturbance by
 333 fire showed that the total effect of tree species diversity on biomass was similar to that of water
 334 availability, soil fertility and disturbance (Figure 7, Figure S4). The direct effects of water avail-
 335 ability, soil fertility and disturbance on AGB were negligible (water: $\beta = 0.1 \pm 0.13$, $p = 0.43$, soil:
 336 $\beta = 0.1 \pm 0.155$, $p = 0.51$, disturbance: $\beta = -0.04 \pm 0.043$, $p = 0.32$), with nearly all of their ob-
 337 served effects on AGB coming from the indirect paths via stem density (water: $\beta = 0.14 \pm 0.091$,
 338 $p = 0.12$, soil: $\beta = -0.22 \pm 0.109$, $p < 0.05$, disturbance: $\beta = -0.12 \pm 0.03$, $p < 0.01$) and species
 339 diversity (water: $\beta = 0.62 \pm 0.172$, $p < 0.01$, soil: $\beta = -0.24 \pm 0.209$, $p = 0.26$, disturbance: $\beta =$
 340 0.19 ± 0.058 , $p < 0.01$). MAP and soil sand content had the greatest contributions to the latent
 341 variable of water availability. Model fit was acceptable: CFI = 0.925, TLI = 0.900, and RMSEA
 342 = 0.153, R^2 of AGB = 0.34.

343 Similar to the model that only considered tree species and structural diversity (Figure 4), the dir-
 344 ect effect of species diversity on structural diversity was positive, while structural diversity itself
 345 had a positive effect on AGB, leading to a strong positive indirect effect of species diversity on
 346 AGB via structural diversity ($\beta = 0.19 \pm 0.026$, $p < 0.01$) when environmental covariates were ac-
 347 counted for. Again, the direct effect of species diversity on AGB was negligible ($\beta = -0.05 \pm 0.041$,
 348 $p = 0.27$). The total effect of species diversity on AGB was positive ($\beta = 0.34 \pm 0.044$, $p < 0.01$).
 349 Compared to the simple model with no environmental covariates, the total explanatory power of
 350 tree species diversity and structural diversity in this model decreased, but the predictive power of
 351 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 (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-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. 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 (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.

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, Archibald & Levin, 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, Bond, Stock, van Rensburg & Waldram, 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.

As time since disturbance increases in any wooded ecosystem, it is expected that both species diversity and above-ground biomass will increase until an equilibrium is reached or another disturbance event occurs (Huston, 2014). Unless this effect is accounted for, there is the potential for mistaken causality as both diversity and biomass will 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, Beaulieu, Bever & Clay, 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 in-

creased 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, 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, Bauer, Persson, Matteucci & Masci, 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 (Bucini & Hanan, 2007; Muledi et al., 2017). 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.

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 *Julbernardia* 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 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 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, i.e. all wooded ecosystems. 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 actions in this region 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. 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.

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

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 (Above-Ground Biomass).

Cluster	n	χ^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

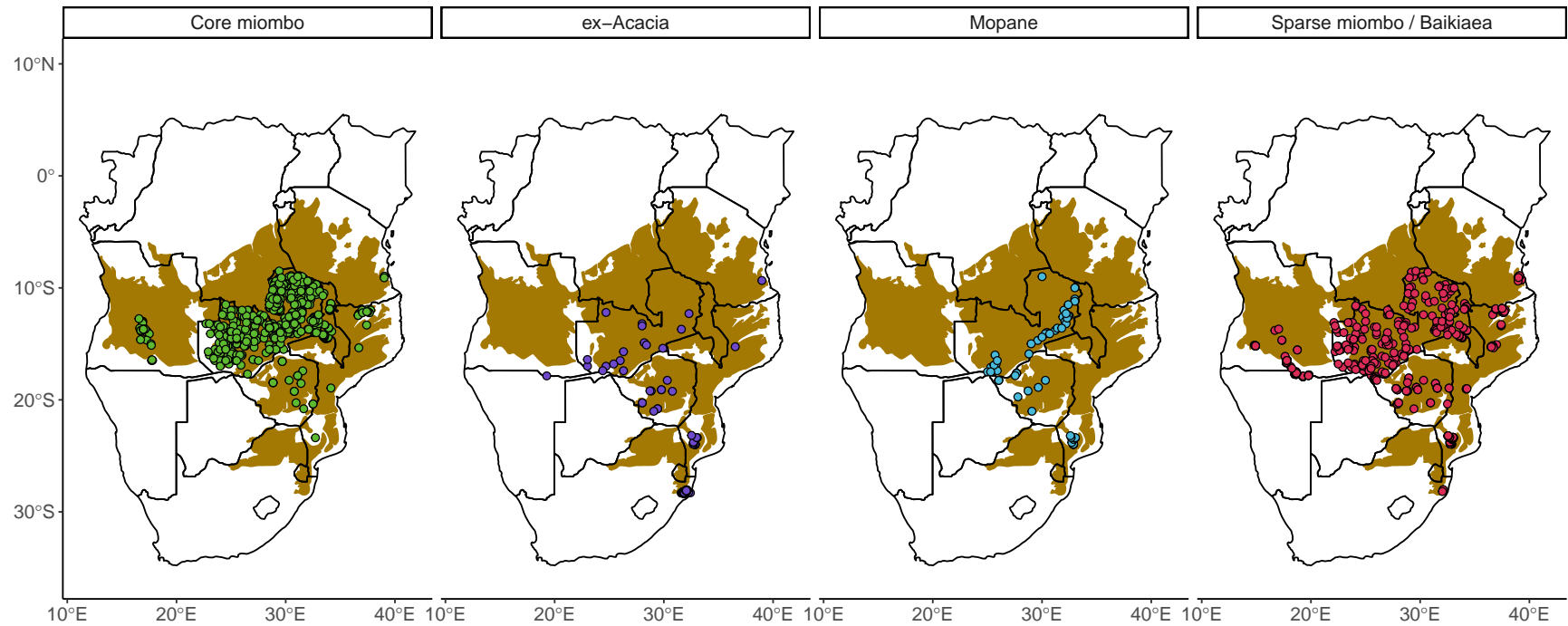


Figure 1: The locations of the 1235 plots used in this study, with respect to the distribution of mesic savanna vegetation according to Hopkins and White (1987). Each panel shows plots categorized by their vegetation type as defined by the vegetation types in Table 1.

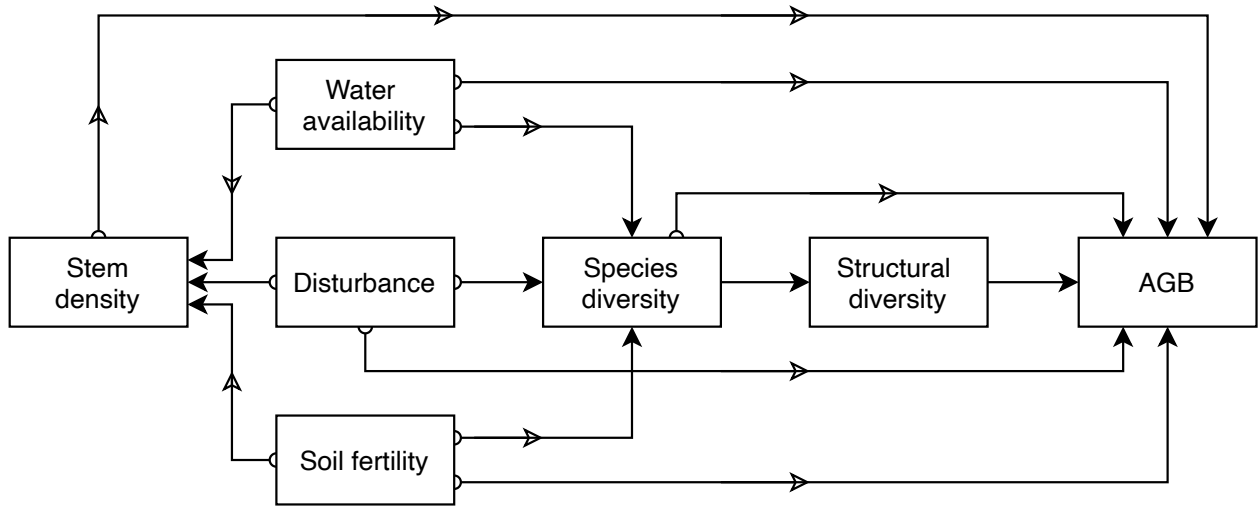


Figure 2: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural diversity, stem density, and AGB. Hypothesised paths of causation are depicted as arrows from predictor to response. Open arrow heads track the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

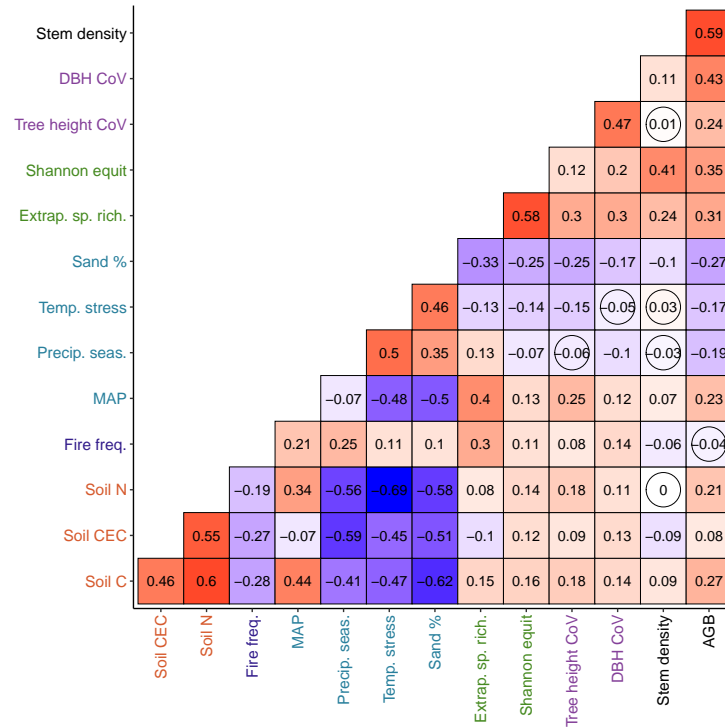


Figure 3: Correlation matrix of standardised observed variables used in the SEMs, with Pearson correlation coefficients (r) coloured according to sign (+ve red, -ve blue) and shaded by strength of correlation. Correlation coefficients marked by a circle indicate that the 95% confidence interval of r 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 Table S1 for a full assessment of correlation fit statistics.

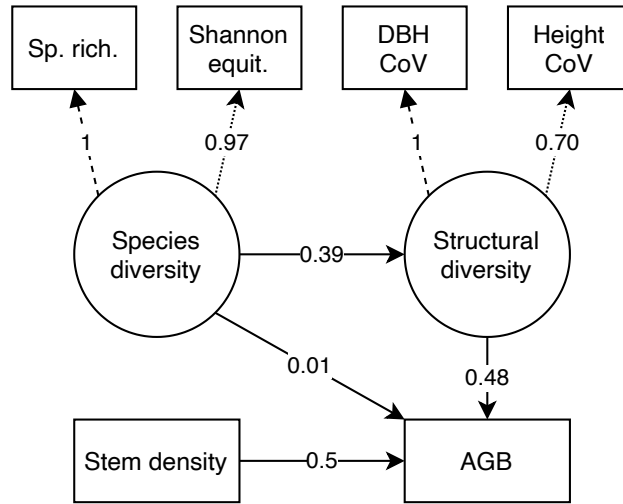


Figure 4: Path diagram with regression coefficients for the tree diversity SEM, including plots from all vegetation clusters. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are shown as solid arrows pointing from predictor to response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

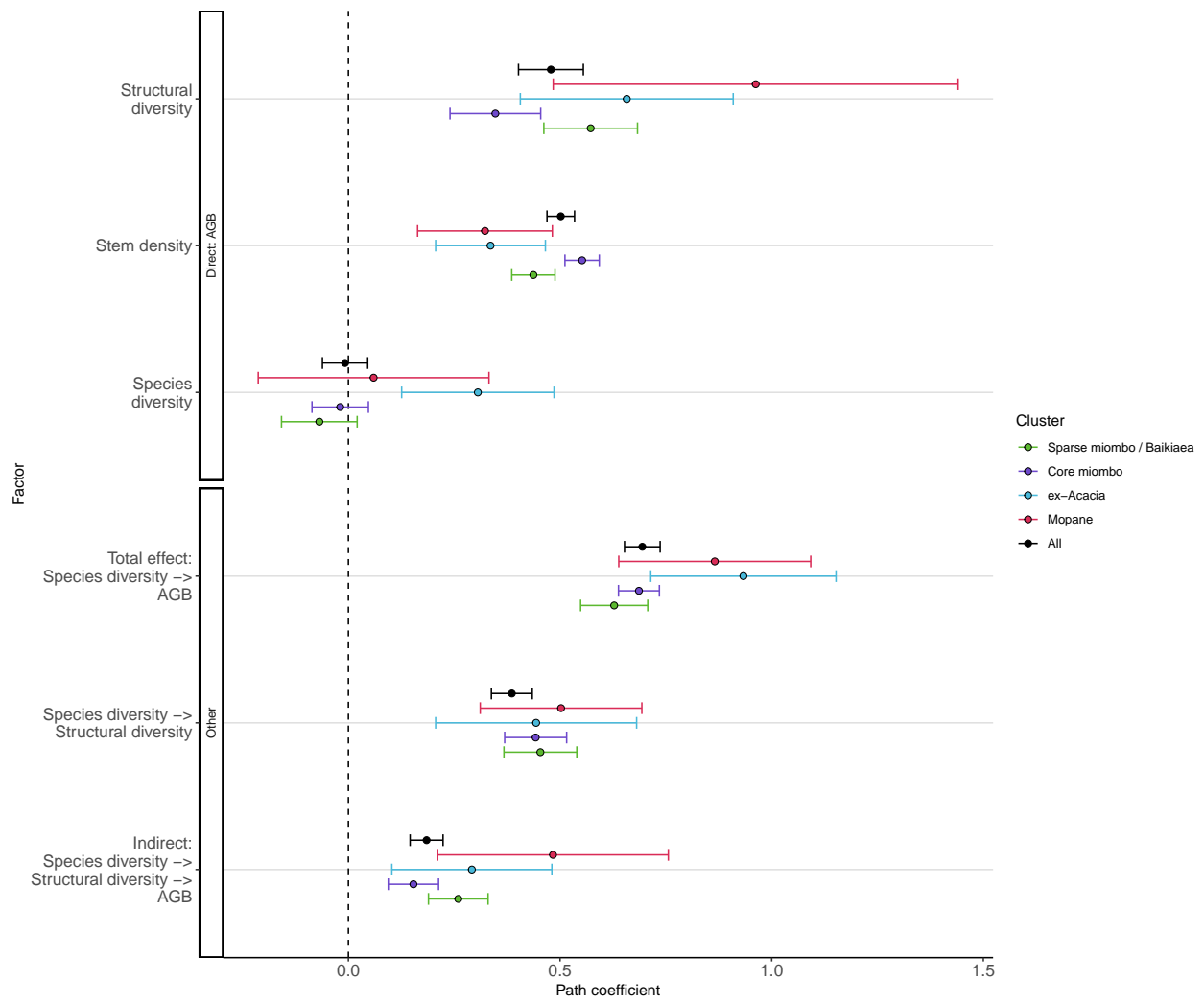


Figure 5: Unstandardised path coefficients for the effects of tree diversity on AGB, mediated by the effect of stand structural diversity. Path coefficients are ± 1 standard error. Path coefficients where the interval (standard error) does not overlap zero are considered to be significant effects.

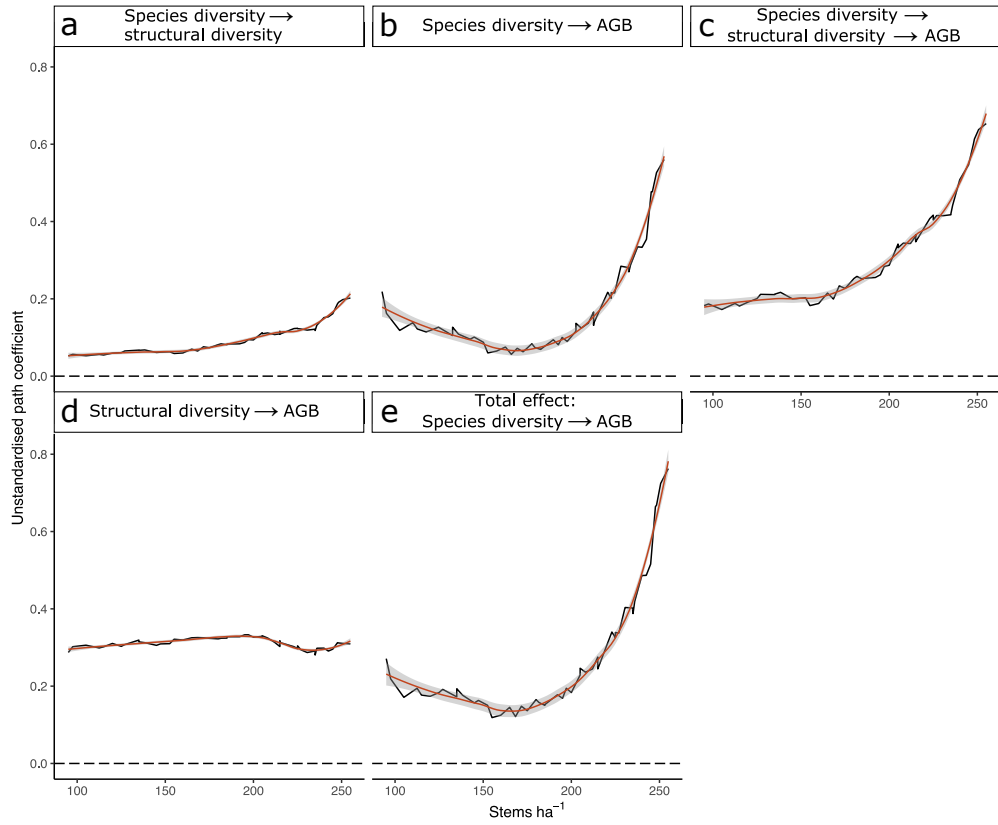


Figure 6: Line plots showing the variation in SEM path coefficients across datasets with different mean stem density. Smoothed lines are loess curves with ± 1 standard error shaded bars. AGB = Above-Ground woody Biomass, arrows in plot titles indicate causal paths in SEM models. Where multiple arrows are present, as in c), this indicates an indirect pathway via an intermediate variable.

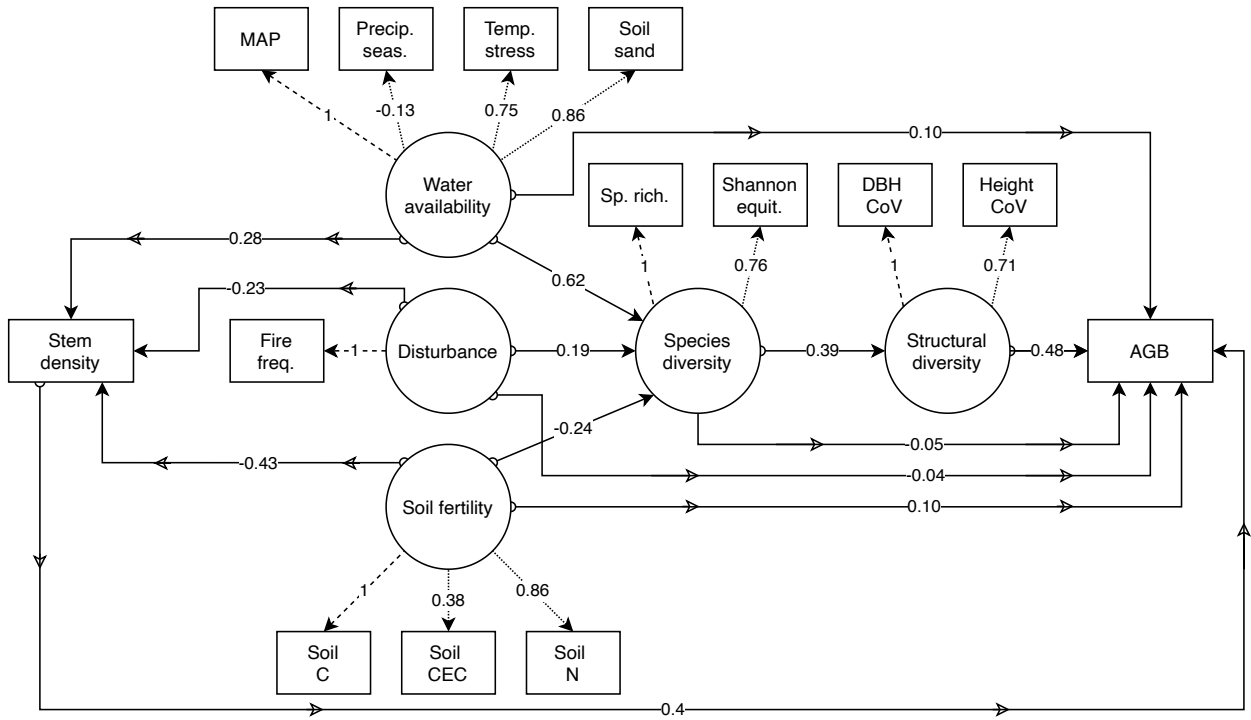


Figure 7: Path diagram with regression coefficients for the SEM incorporating environmental covariates and tree species and structural diversity across all five vegetation types. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are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

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9 Author contribution

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 Data Availability

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available at the time of submission due to privacy restrictions regarding plot locations. An anonymised version will be made available in a data repository following review.

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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.

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