

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

3 Authors: Godlee, J. L.¹, Dexter, K. G.¹, Ryan, C. M.¹

4 ¹: School of GeoSciences, University of Edinburgh, Edinburgh, United Kingdom

5 ²: Some other address

6 Corresponding author:

7 John L. Godlee

8 johngodlee@gmail.com

9 School of GeoSciences, University of Edinburgh, Edinburgh, United Kingdom

10 Acknowledgements

11 This work is funded by a NERC E3 Doctoral Training Partnership PhD studentship at the Uni-
12 versity of Edinburgh (J. L. Godlee, Grant No. NE/L002558/1). The data provided for this study
13 was contributed by a number of independently funded projects and was assembled and prepared
14 by SEOSAW (A Socio-Ecological Observatory for Southern African Woodlands), an activity of
15 the Miombo Network and NERC-funded project (Grant No. NE/P008755/1). We thank all data
16 providers and the field assistance they received when collecting plot data.

17 Biosketch

18 SEOSAW (A Socio-Ecological Observatory for Southern African Woodlands, [https://seosaw.](https://seosaw.github.io)
19 [github.io](https://seosaw.github.io)) aims to understand the response of southern African woodlands to global change.
20 The goal of SEOSAW is to produce novel analyses of the determinants of ecosystem structure and
21 function for the southern Africa region, based on syntheses of plot data. Additionally the group
22 hopes to develop infrastructure for a long-term regional plan for plot remeasurement in the south-
23 ern African region. While working on a multitude of diverse projects in the dry tropics at large,
24 all authors have a broad interest in community ecology and ecosystem assemblage in southern
25 African woodlands.

Blinded Main Text File

Title: An assessment of the biodiversity - ecosystem function relationship in southern African woodlands

Running title: Ecosystem function in southern African woodlands

Abstract

Aim: Positive correlations between tree biodiversity and ecosystem function have been widely documented, but the nature of the relationship in highly disturbed and ecophysiologically stressful systems is less clear. Here, we explore the relationship between tree biodiversity and aboveground biomass across southern African savannas and woodlands, with respect to gradients in stem density, resource availability and disturbance through fire, to build a general understanding of the biodiversity - ecosystem function relationship in this understudied ecological context.

Location: Southern African savannas and woodlands

Time period: 2010-2019

Major taxa studied: Trees

Methods: We used a network of 1767 savanna and woodland plots located across the southern African sub-continent in which each tree >10 cm diameter was measured and identified to species level. We used structural equation modelling and path analysis to determine the relationship between tree species diversity and aboveground woody biomass, accounting for the interactive effects of resource availability and along a gradient of stem density.

Results: A positive effect of tree species diversity on aboveground biomass was demonstrated, observed largely as an indirect effect of increasing woodland structural diversity. We also found that the effect of tree species diversity on biomass increases with stem density. Finally, we found that resource availability affects biomass in southern African woodlands largely indirectly via its effect on species diversity.

Main conclusions: The study underlines the close association between tree diversity, ecosystem structure and function of highly disturbed southern African savannas and woodlands. Our results demonstrate the importance of including environmental conditions and vegetation type in models to accurately describe a general relationship between biodiversity and ecosystem function at a regional level. Biodiversity loss predominantly by human actions in southern Africa may have detrimental outcomes for ecosystem function, particularly in species poor *Baikiaea* woodlands, which showed the strongest biodiversity - ecosystem function relationship.

Introduction

Numerous studies have shown relationships between biodiversity and ecosystem function (e.g. Liang et al. 2016; ?; Cardinale et al. 2009). The strength and direction of these observed Biodiversity-Ecosystem Function Relationships (BEFRs) varies depending on the ecosystem being studied, the ecosystem function(s) of interest (Hector and Bagchi, 2007), and the inclusion of environmental covariates in statistical models (Vilà et al., 2005), but there appears to be a generalisable positive correlation between biodiversity and ecosystem function (Liang et al., 2016). Over the past decade, many observational studies of the BEFR have been conducted, mostly in wet tropical and temperate forests, and grasslands (Chen et al., 2011). These studies support early findings from small scale experimental studies predominantly in grassland patches, which began in earnest during the 1990s as concern grew over the global loss of biodiversity (Tilman and Downing, 1994; Tilman et al., 2014).

Ecosystem functions can be defined in broad terms as rate processes and properties of ecosystems which describe the degree of biotic activity within an ecosystem (Jax, 2005). This includes basic processes of primary production such as gross primary productivity and atmospheric nitrogen fixation, but can be extended to indirect measures of function such as resistance of productivity to disturbance, and further to ecosystem properties which themselves influence process, such as trophic complexity and total vegetative biomass. The frequently reported and intuitive relationship between biodiversity and ecosystem function invokes three main mechanisms which drive the relationship (Tilman et al., 2014): 1) niche complementarity, whereby communities with greater diversity fill a greater breadth of realised niche space and avoid competition due to differences in their traits, 2) selection effects, whereby communities with greater diversity are more likely to include a species which contributes highly to the measured ecosystem function, and 3) facilitation effects, whereby communities with greater diversity are more likely to include combinations of species which together increase the others' functional contribution.

Compared to ~~other forested~~forest ecosystems, dry tropical woodlands and savannas are highly structured by disturbance, mainly through fire, and in Africa notably by herbivory also (Sankaran et al., 2008; ?). High levels of disturbance may weaken the role of competition in determining local species distribution and allow weak competitors to co-exist where they would normally be excluded (Grime, 1979; Keddy, 1990). This means that interspecific competition and therefore the effect of niche complementarity, which contributes the majority of the observed biodiversity effect on ecosystem function in temperate and wet tropical forests (Wright et al., 2017; Poorter et al., 2015; van der Sande et al., 2017), may not be as apparent in dry woodland/savanna ecosystems. Instead, stress tolerance and the functional contribution of more abundant species (selection effects) may be the predominant forces which influence ecosystem functions (Lasky et al., 2014; Tobner et al., 2016). Similarly, more diverse species assemblages may lead to facilitation effects between certain species combinations ~~in environments which are more hostile to growth under limiting environmental conditions such as low water availability () or high maximum temperature ()~~. Across European forests Ratcliffe et al. (2017) found stronger positive relationships between tree species richness and various ecosystem functions in more arid environments. They suggest that in dry ecosystems, facilitative effects and selection effects may be more important than niche complementarity in driving the relationship between species diversity and ecosystem function. This potential mismatch in the contribution of different mechanisms to the BEFR between dry tropical woodlands and other forested ecosystems demands further investigation in order to characterise a generalisable biodiversity-ecosystem function relationship.

The representation of dry tropical ecosystems in the BEFR literature is poor compared to other ecosystems. Clarke et al. (2017) conducted a meta-analysis of 182 published BEFR studies, finding that only 13% were conducted in the tropics generally, with 42% of those being conducted in the wet tropical forests of Costa Rica, which hold many endemic species and unique ecosystem assemblages (Barthlott et al., 2005). A severe lack of study in dry tropical ecosystems, especially given the potential mismatch in BEFR mechanism described above, suggests that a focus on these ecosystems could greatly strengthen our understanding of a general BEFR and its environmental determinants. Savannas and woodlands are the dominant vegetation type across the southern African region, spanning >4 million km^2 (?Ratnam et al., 2011; Ryan et al., 2016) (Figure 1). The carbon stored in this vegetation is comparable to that found in the wet forests of the Congo basin and is of global importance to the carbon cycle (Houghton et al., 2009; Mayaux et al., 2008). Climatic conditions and biogeography vary across southern African vegetation, resulting in a diverse range of savanna and woodland tree species assemblages, which retain the common features of an open tree canopy and an understorey generally dominated by C4 grass species. Southern African savannas and woodlands (SAWs) are highly diverse, thought to harbour ~8500 plant species of which there are >300 tree species (Frost, 1996), and have been identified by previous studies as a priority for conservation efforts (Byers, 2001; Mittermeier et al., 2003). Many conservation projects in the region currently aim to conserve biodiversity and woody biomass stocks simultaneously under the directive of the United Nations REDD+ programme or

the similar Forest Carbon Partnership Facility (FCPF) (Hinsley et al., 2015). Despite these efforts however, human actions are driving rapid changes in biodiversity, with largely un-quantified consequences for ecosystem structure and function.

A small number of studies in SAWs have shown that above ground woody carbon/biomass stocks correlate positively with tree species richness (McNicol et al., 2018; Shirima et al., 2015; Mutowo and Murwira, 2012). However, studies conducted over small environmental gradients often find that at fine scales, diversity shows a strong effect on ecosystem function, but at broad scales diversity effects pale in significance compared to abiotic factors such as climate (Pasari et al., 2013). Fine scale studies may therefore be over-estimating the effect of diversity. Due to the highly variable environmental conditions within which SAWs occur (Frost, 1996), and given the potential importance of environment and biogeography in defining the strength and form of a relationship between biodiversity and above ground woody biomass (), it is important to sample across geographic and environmental gradients to be able to infer a truly regional scale relationship between diversity and biomass.

In forests, climatic variation is known to affect both woody biomass (Michaletz et al., 2014, 2018) and species diversity independently (Spasojevic et al., 2014). It is important therefore to account for climatic factors and understand how they interact with biomass and diversity to effectively model and correctly attribute the effects of biodiversity on woody biomass in analyses at broad spatial scales. Sankaran et al. (2005) used data from 854 African woodland field sites to show that mean annual precipitation (MAP) sets the upper limit for woody cover in savannas, which is positively correlated with biomass (Chisholm et al., 2013; Prado-Junior et al., 2016). Similarly, Condit et al. (2013) found that dry season intensity was the main determinant of tree species distribution and abundance evenness in a wet Panamanian tropical forest.

Solbrig et al. (1996) writes that SAWs possess structurally diverse tree canopies, with trees occupying distinct layers of the canopy at different growth stages and among species. This structural diversity may be one mechanism through which diversity influences woody biomass. (Kunz et al., 2019) found that crown complementarity and crown plasticity both increased with species richness in a seasonally dry subtropical forest. They also found that trees growing in species rich neighbourhoods exhibited enhanced biomass production. Occupation of multiple canopy layers allows a more full canopy with a greater total foliage density, enhancing productivity and allowing greater standing woody biomass in a smaller area via a form of niche complementarity. This mechanism however, which has been supported by experiments and observational studies in temperate and wet tropical ecosystems (Hardiman et al., 2011; Stark et al., 2012), may not be relevant in savannas, which are structured by disturbance rather than competition. Instead, disturbance history may override the effects of species diversity on structural diversity nullifying the effects of species diversity on structural diversity.

High levels of disturbance in SAWs may moderate the observable BEFR through its effect on ecosystem composition. Fire disturbance in forests has been linked to abundance dependent mortality among smaller tree stems (Roques et al., 2001; Staver et al., 2009; Bond and Keeley, 2005). Some species in the regional species pool may be excluded from woodland plots with high levels of disturbance if they are unable to escape the fire bottleneck and grow to become a large tree. Selection effects may therefore be more important in maximising ecosystem function in disturbance prone woodlands. If the regional species pool contains a large number of species, it is more likely that one of them will possess the necessary growth strategy to grow to a large tree with high AGB under an intense disturbance regime.

In this study, we made the first known regional estimation of the Biodiversity-Ecosystem Function Relationship across southern African savannas and woodlands (SAWs), using inventory plots which span environmental and biogeographical gradients (Figure 1). We used aboveground woody biomass of trees and compared the relative effects of tree species biodiversity with that of environmental factors known to affect ecosystem productivity and biomass accumulation, namely water availability, energy input and soil fertility. We also investigated the potential moderating effects

of environmental covariates on the relationship between tree species diversity and biomass. We incorporated vegetation type based on major tree species compositional units as a factor in our analyses to understand how species composition as well as species biodiversity affected ecosystem function and assess the generality of our results. We used Structural Equation Modelling (SEM) and path analysis as a preferred method to simultaneously account for environmental and biotic factors, which may interact their effect on ecosystem structure and therefore biomass. Initially, we made three hypotheses: (1) water availability and soil fertility will indirectly positively affect woody biomass via an increase in tree species diversity, (2) the effect size of species diversity on woody biomass will increase with stem density, due to an increased importance of niche complementarity as competition increases, and (3) tree species diversity will increase tree structural diversity, which will provide an indirect path by which tree diversity increases woody biomass.

Materials and methods

Study location

The study used 1767 woodland monitoring plots from the larger SEOSAW network (SEOSAW, 2019) located across 10 countries within southern Africa in the so-called miombo woodland eco-region (Figure 1, ?). The study region spans a precipitation gradient from ~ 460 mm y^{-1} in southern Mozambique and southern Zimbabwe to ~ 1700 mm y^{-1} in northern Zambia, Malawi and northern Mozambique. The study sites span the core climate space of the region as a whole. The 2D convex hull of Mean Annual Precipitation (MAP) and Mean Annual Temperature (MAT) of the study sites covers 94.4% of the pixel-wise climate space of the miombo woodland eco-region as defined by ?, using WorldClim estimates of temperature and precipitation between the year 1970 and 2000 with a pixel size of 30 arc seconds (0.86 km² at the equator) (Fick and Hijmans, 2017).

Plots were chosen from a larger pool of 5395 plots based on the quality and completeness of data collection, and plot setup. Plot vegetation was identified under the broad term of “savanna”, which includes “woodland”, “savanna woodland”, and “tree savanna”, variously defined in other areas of the scientific literature and here referred to collectively as southern African woodlands (SAWs) (Ratnam et al., 2011; Hill and Hanan, 2011). Plots with evidence of farming, human resource extraction or experimental treatments such as prescribed burning or herbivore exclusion were excluded from the initial pool. Only plots >0.1 hectares were used in analysis, as area based biomass estimation from small plots is highly influenced by rare large trees (Stegen et al., 2011), leading to inaccurate estimates. Only plots with a stem density >10 stems ha^{-1} (>10 cm stem diameter) were used, to ensure all plots were within woodland rather than “grassy savanna”, which are considered a separate biome with very different species composition (Parr et al., 2014).

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

After the initial plot data cleaning described above, we conducted an outlier removal procedure of plots with rare tree species composition. We used the `outlier()` function from the `dave` R package (Wildi, 2017), which uses a nearest neighbour criterion for each plot in species abundance ordination space and a threshold value for the minimum nearest neighbour distance to identify outliers. We set the threshold value to remove the top 5% of plots with the largest nearest neighbour distances in multidimensional species composition space (Otto, 2013), thus removing 87 plots (Appendix A).

216 Data collection

217 We considered only trees and shrubs in our calculations of above-ground woody biomass (AGB),
218 including woody species such as palms and cycads which are functionally tree-like, but excluding
219 lianas, which fill a different ecological niche (Selaya and Anten, 2008). Only stems >10 cm DBH
220 (Diameter at Breast Height, 1.3 m) were included in analyses. Many plots in the dataset did not
221 include data on stems <10 cm DBH. For those plots with stem measurements <10 cm DBH, those
222 small stems only accounted for a median average of 2.2% of the plot level AGB.

223 All stems >10 cm DBH were measured within each plot resulting in a total of 93,242 stems with
224 measurements. A tree may be comprised of multiple stems, but for this analysis each stem is treated
225 as an individual. For each stem we measured species, DBH and tree height to the top of the high-
226 est branch material. Height was measured through a variety of means including laser rangefind-
227 ers, manual clinometers and measuring sticks. When DBH could not be measured at 1.3 m due
228 to trunk abnormalities, it was measured at the closest regular portion of the trunk to 1.3 m. The
229 height of this measurement was recorded and used to estimate the DBH_e at 1.3 m using a cubic
230 polynomial regression, with parameters estimated using a test dataset from (Ryan C., unpub-
231 lished) (Appendix B).

232 AGB for each plot was calculated using Equation 1, taken from Chave et al. (2014). Wood den-
233 sity estimates were taken from the global wood density database for each species where possible
234 (Chave et al., 2009; Zanne et al., 2009). Wood density for species without species level estimates
235 was estimated from the mean of their respective genus.

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

236 Where ρ is the species level mean wood density, D is the DBH_e at 1.3 m, and H is the tree height.
237 Climatic data were collected from the ECMWF ERA5 dataset, generated using Copernicus Cli-
238 mate Change Service Information (Copernicus Climate Change Service, 2017). Values of Mean
239 Annual Temperature (MAT) and Mean Annual Precipitation (MAP) were calculated from daily
240 data between 2000 and 2018, then averaged across years to provide a single mean annual estimate
241 per plot. Temperature seasonality (TS) and precipitation seasonality (PS) were both calculated
242 as the mean of the coefficient of variation of daily MAT and MAP, respectively, for each of the
243 18 years of available data. Soil fertility data was extracted from the ISRIC gridded soil informa-
244 tion data product at 250 m resolution, taking the grid cell value for each plot centre (Hengl et al.,
245 2017). We extracted Cation Exchange Capacity (CEC), percentage soil organic carbon by volume
246 (Org. C %), and percentage soil sand content by volume (Sand %). These data are a modelled
247 product derived from various remotely sensed and directly measured data sources.

248 Data analysis

249 Estimated tree species richness was calculated for each plot using `ChaoRichness()` from the `iNEXT`
250 package in R (Hsieh et al., 2016). This procedure extrapolates a species rarefaction curve to its
251 predicted asymptote and uses this value as its estimated species richness value. Extrapolated species
252 richness accounts for variation in plot size (0.1-10 ha) and therefore sampling effort among plots.
253 Larger plots will tend to encompass more individuals, and therefore more species (Dengler, 2009).

254 To measure tree species abundance evenness, the Shannon Equitability index ($E_{H'}$) (Smith and
255 Wilson, 1996) (??) was calculated as the ratio of estimated Shannon diversity to the natural log of
256 estimated species richness. Abundance evenness allows for greater niche complementarity at small
257 scales due to an increased spatial heterogeneity of functional traits. We calculated tree struc-
258 tural diversity for each plot by calculating the coefficient of variation of DBH (DBH CV) and tree
259 height (Height CV).

260 Vegetation clusters

261 Plots were assigned to vegetation type groups based on tree species composition. Groups were
262 identified in [Fayolle et al. \(2018\)](#) in an Africa wide analysis of floristic units using plot data in sa-
263 vannas and woodlands with tree species diversity and relative abundance data. Groups were iden-
264 tified using unconstrained correspondence analysis and ordination, followed by clustering based on
265 dominant ordination axes. Plot data used in this study occurred in four vegetation type groups.
266 See [Table 1](#) for a description of each vegetation cluster and [Figure 1](#) for the spatial distribution of
267 plots from each of these clusters .

Table 1: Description of the biogeographical clusters (C1-C5) to which each plot in the study was assigned. Indicator species were generated using Dufrene-Legendre indicator species analysis (Dufrêne and Legendre, 1997) implemented with `indval()` from the `labdsv` R package (Roberts, 2019) and represent species which define the given cluster. Dominant species were identified by choosing the species with the largest AGB contribution within each cluster. Numeric values of species richness, stems ha⁻¹ and AGB are medians and interquartile ranges (75th percentile - 25th percentile).

| Cluster | Dominant species | Indicator species | N plots | Species rich. | Stems ha ⁻¹ | AGB (t ha ⁻¹) |
|-----------------|---------------------------------|---|---------|---------------|------------------------|---------------------------|
| Marginal miombo | <i>Julbernadia</i> spp. | <i>Diplorhynchus condylocarpon</i> | 688 | 11(11.2) | 152(135.2) | 32.9(30.57) |
| | <i>Brachystegia spiciformis</i> | <i>Burkea africana</i> | | | | |
| | <i>Baikieaea plurijuga</i> | <i>Pseudolachnostylis maprouneifolia</i> | | | | |
| Core miombo | <i>Julbernadia</i> spp. | <i>Julbernardia paniculata</i> | 754 | 18(17.5) | 193(174.1) | 44.8(41.43) |
| | <i>Brachystegia</i> spp. | <i>Isoberlinia angolensis</i> | | | | |
| | <i>Isoberlinia angolensis</i> | <i>Brachystegia longifolia</i> | | | | |
| Baikieaea | <i>Spirostachys africana</i> | <i>Baikieaea plurijuga</i> | 226 | 10(10) | 162(152) | 45.3(47.36) |
| | <i>Senegalia</i> spp. | <i>Senegalia ataxacantha</i> | | | | |
| | <i>Euclea racemosa</i> | <i>Combretum collinum</i> | | | | |
| Mopane | <i>Colophospermum mopane</i> | <i>Colophospermum mopane</i> <i>Combretum</i> spp. | 99 | 7(8.2) | 190(155.7) | 41.5(36.93) |

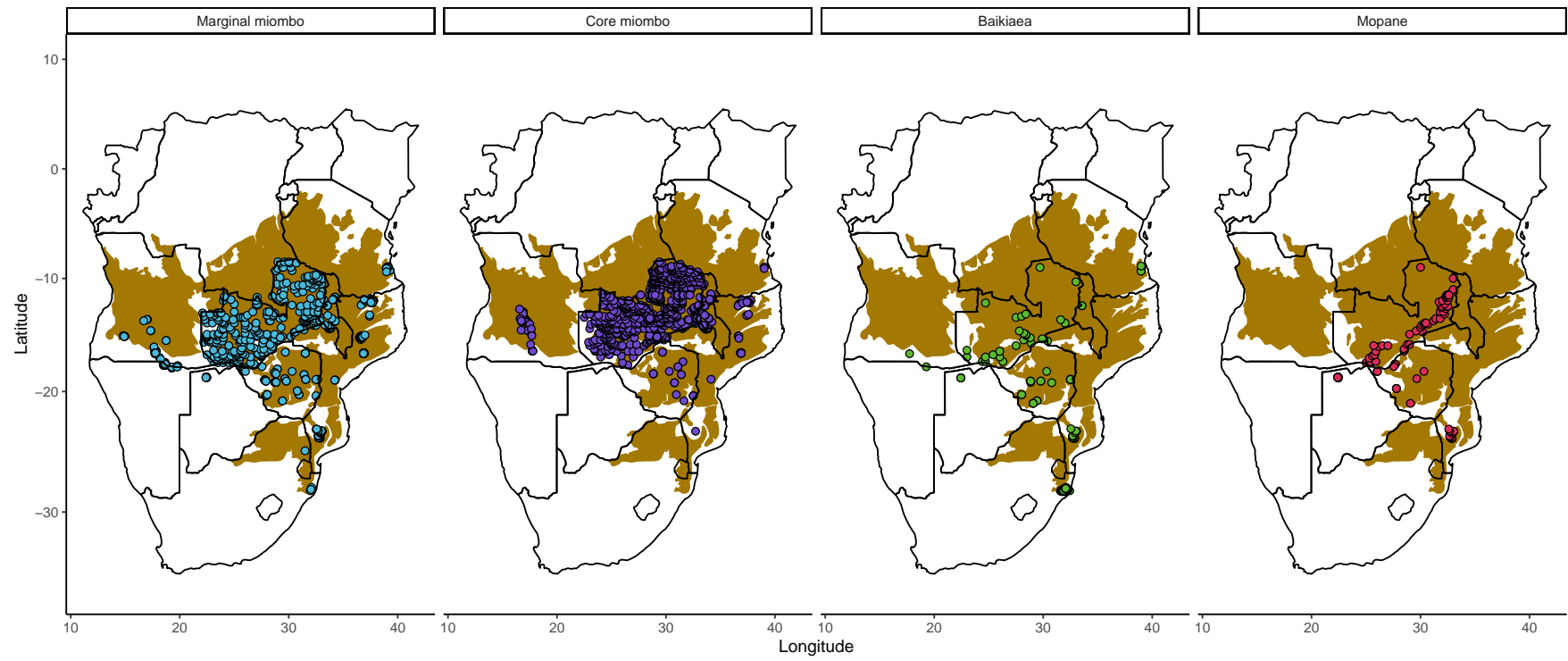


Figure 1: The locations of the 1767 plots used in this study, as points by geographic location with respect to the distribution of miombo woodland vegetation according to ?. Each panel shows plots categorized by their vegetation type as defined by the vegetation types in [Table 1](#).

269 Structural Equation Models (SEM) investigated the determinants of AGB. All SEMs were con-
 270 structed and analysed in the `lavaan` package (Rosseel, 2012) in R version 3.6.0 (R Core Team,
 271 2019). SEM was used because of its suitability for modelling complex causal interactions in eco-
 272 logical systems (Lee, 2007). A key aspect to our decision to use SEMs is that they can explicitly
 273 model and partition variance to indirect effects, which is challenging in standard multiple regres-
 274 sion. Using SEMs also allowed us to describe theoretical latent constructs which have been sug-
 275 gested to act upon diversity and biomass/productivity in previous studies despite these factors
 276 not having single observable measures in our dataset. Structural equation modelling is also neces-
 277 sary to properly account for potential feedback mechanisms between aspects of climate and tree
 278 species diversity, which could otherwise increase the chances of Type I error and wrongly attribute
 279 inference due to covariance of explanatory variables when using conventional regression analyses
 280 (Nachtigall et al., 2003).

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

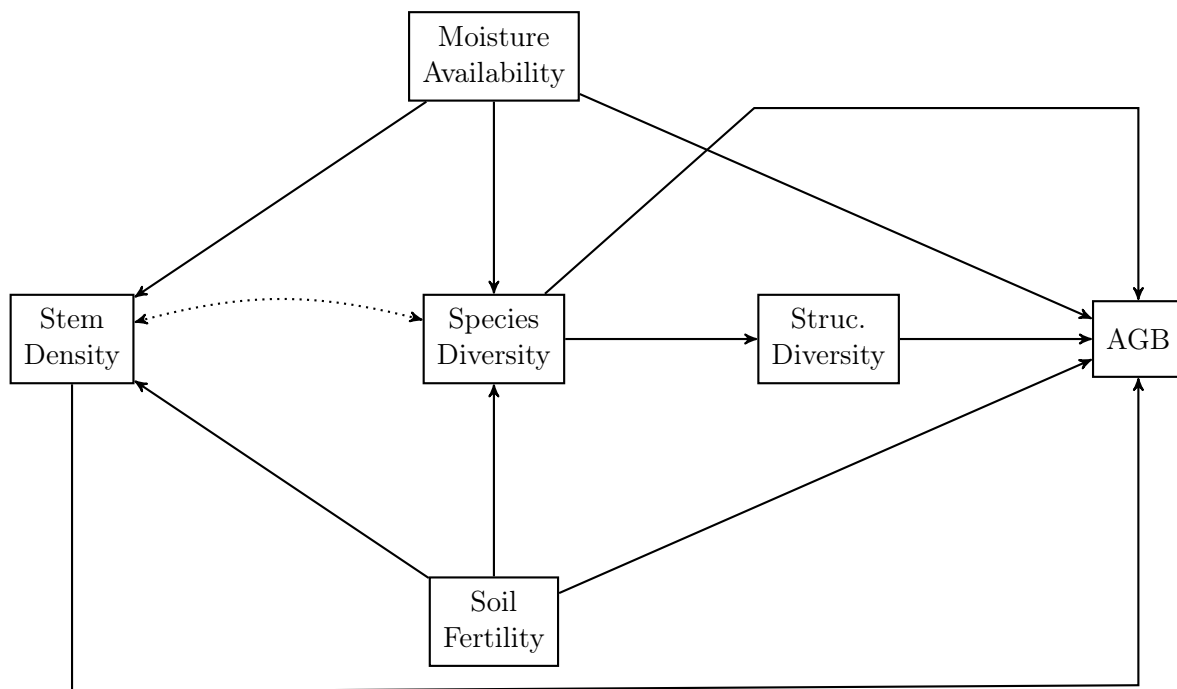


Figure 2: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural diversity, tree stem density, and AGB. Hypothesised paths of causation are depicted as arrows from predictor to response. Correlations are depicted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

284 Observed variables were transformed to achieve normality where necessary and standardised to Z-
 285 scores prior to analysis (Appendix C). Standardisation put each latent variable on the same scale,
 286 with a mean of zero and a standard deviation of one. Standardisation allows path regression coef-
 287 ficients to be easily compared between paths in the same model to assess their relative effect size,
 288 and eliminates confusion in model interpretation arising from the observed variables being on dif-
 289 ferent scales (Beaujean, 2014). Standardisation also controls for variables with different orders of
 290 magnitude which could otherwise prevent adequate model estimation from the covariance matrix
 291 in `lavaan`. To ensure that observed variables within a latent variable had consistent directions of
 292 influence, some observed variables were reversed by multiplying by -1. For example, soil fertility
 293 is expected to decrease as soil sand content increases, so soil percentage sand content was reversed

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

The factor loadings of the observed variable assumed to contribute most to each latent variable were set to 1 as per convention, with other observed variables being allowed to vary (Beaujean, 2014). We tested the robustness of our assumptions with a chi-squared test of all possible combinations of observed variable factor loadings set to 1, while ensuring no factor loadings were in excess of 1. We found no significant difference between model specifications ($p > 0.05$). Full Information Max-Likelihood (FIML) was used in each model to estimate the values of missing data in each latent variable (Cham et al., 2017).

We assessed the role of structural diversity and species diversity in determining AGB via a simple mediation model which allowed species diversity to influence AGB both directly and indirectly via structural diversity. To account for variation in stem density which may covary with species diversity we also included it as an predictor in our model. To explore variation in the model among woodland vegetation types, we fit the model both at the regional scale and for each vegetation cluster separately. We compared unstandardised path coefficients among these vegetation cluster scale models to understand the effect that vegetation type has on the relationship between tree species diversity, structural diversity, stem density and AGB. Path coefficients show the effect of a path with other paths of inference held constant. Models were estimated using the “MLM” estimator, because it is robust to multivariate non-normality (Shapiro, 1983). Model fit was evaluated using the robust Comparative Fit Index (CFI), the robust Tucker Lewis Index (TLI), the Root Mean Squared Error (RMSEA) and the R^2 coefficient of determination for AGB. We critically assess model fit in each case, taking into consideration the recommendations of Hu and Bentler (1999) which define threshold values of acceptability for these model fit indices: CFI > 0.85 , TLI > 0.85 , RMSEA < 0.15 , alongside our judgement of the model estimates.

To explore the hypothesis that complementarity effects increase in strength as stem density increases, we repeatedly sub-sampled the available plot dataset to create 50 datasets of similar size with varying median stem density. We used each of these datasets separately to fit the model including only tree species and structural diversity latent variables to predict AGB. We excluded the effect of stem density on AGB and the correlation between stem density and species diversity from this model as we were deliberately controlling stem density in our subsampling. We then examined how the unstandardised path coefficients for each path in the SEM varied according to the median stem density of subsampled dataset.

We incorporated environmental covariates into our model to understand the relative effects of moisture availability and soil fertility on AGB both directly and indirectly via species diversity and stem density. We compared standardised path coefficients between paths in the model to understand the relative contribution of each path to explain variance in AGB. Vegetation type specific models could not be reliably fitted for this more complex model specification with environmental covariates, due to sample size issues and because some vegetation clusters were narrow in their climate space leading to a lack of variance particularly in moisture availability.

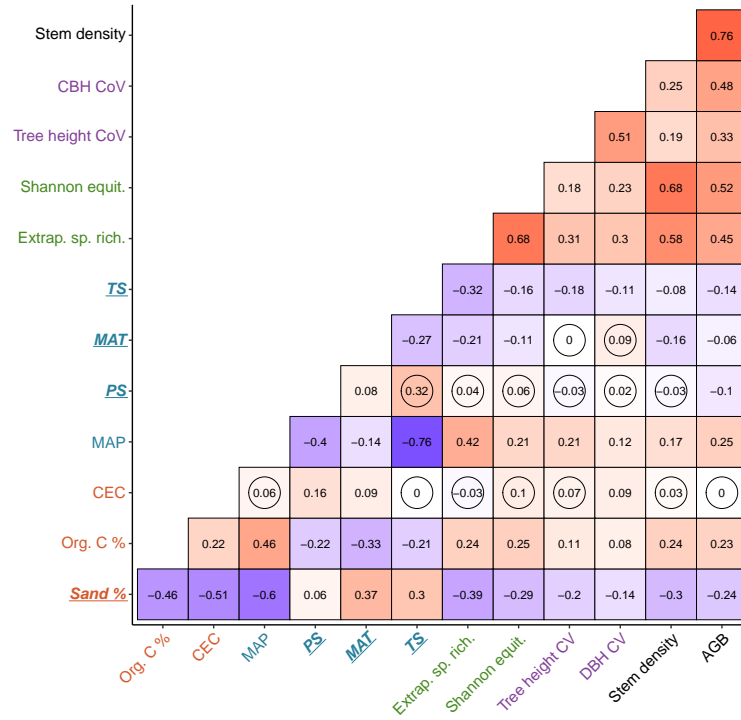


Figure 3: Correlogram of standardised observed variables used in the SEMs, with Pearson correlation coefficients (r) coloured according to sign (+ve red, -ve blue) and shaded by strength of correlation. Variables in bold and underlined on the axis labels were later reversed for SEMs to maintain positive correlations for all observed variables within each latent variable. Correlation coefficients marked by a circle indicate that the 95% confidence interval of this correlation overlapped zero. Colours of variable names group them into latent variables used in the SEMs: red = soil fertility, blue = moisture availability, green = tree species diversity, purple = tree structural diversity. See [Appendix D](#) for a full assessment of correlation fit statistics.

Pairwise correlations between all observed variables used in the Structural Equation Models (SEMs) showed that all tree species diversity and structural diversity variables had moderate positive correlations with AGB. Stem density had the strongest correlation with AGB of all variables ($r = 0.77$, $p < 0.01$). Environmental variables had weaker correlations with AGB than diversity variables, with all environmental variables having significant correlations with AGB, except CEC and MAT.

The direction of these correlations was used as a test of our assumptions of the direction of influence of latent variables later used in the SEMs. As expected, there was a positive correlation between MAP and AGB ($r = 0.22$, $p < 0.01$), and a weak negative correlation between the seasonality of precipitation and AGB ($r = -0.11$, $p < 0.01$). MAT and temperature seasonality (TS) negatively correlated weakly with AGB (MAT: $r = -0.09$, $p < 0.01$; TS: $r = -0.14$, $p < 0.01$). As expected, there was a negative correlation between soil sand content and AGB ($r = -0.27$, $p < 0.01$), and a positive correlation between soil organic carbon and AGB ($r = 0.25$, $p < 0.01$).

MAP had positive correlations with tree species richness ($r = 0.39$, $p < 0.01$), abundance evenness ($r = 0.1$, $p < 0.01$), tree height diversity ($r = 0.21$, $p < 0.01$) and tree stem density ($r = 0.09$, $p < 0.01$). MAT had weak correlations with tree species and structural diversity variables. Tree species diversity variables had clear positive correlations with stem density (Species richness: $r = 0.57$, $p < 0.01$; Shannon equitability: $r = 0.48$, $p < 0.01$).

Structural and species diversity models

In an SEM describing the effect of tree species diversity on AGB via the mediating effects of stand structural diversity and stem density (Figure 4), species diversity had a small positive direct effect on AGB ($\beta = 0.11 \pm 0.039$, $p < 0.01$), and indirectly via structural diversity ($\beta = 0.15 \pm 0.023$, $p < 0.01$) (Figure 4). Tree species diversity had a positive correlation with stem density. Model fit was good with high factor loadings for all observed variables, all path coefficients were significant ($p < 0.01$) (Table 2). The R^2 of AGB was 0.69. The strongest direct effect on AGB was from stem density ($\beta = 0.74 \pm 0.033$, $p < 0.01$).

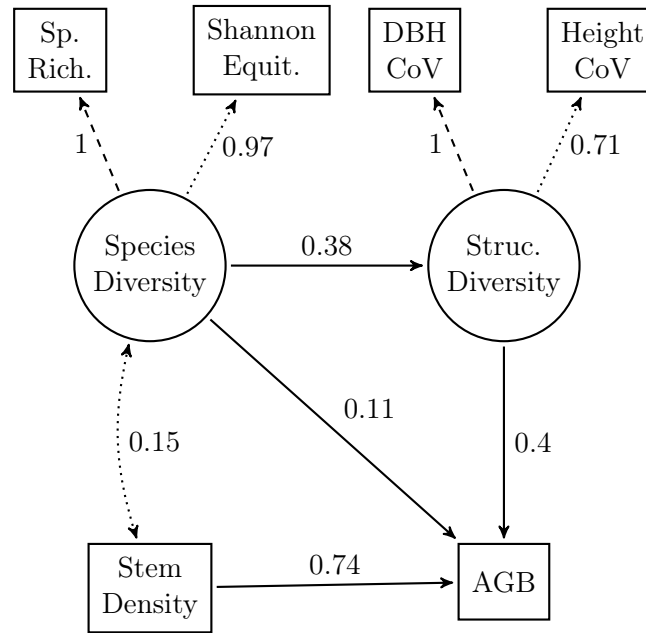


Figure 4: Path diagram with regression coefficients for the tree diversity SEM, including plots from all vegetation clusters. Latent variables are circles while observed variables are rectangles. Standardised path coefficients are solid arrows pointing from predictor to response with the effect size of the path coefficient expressed in terms of standard deviations on the latent variable response scale. The observed variables which inform the latent variables are connected by dotted arrows, observed variables with loading set to 1 are connected by dashed arrows. Correlations between variables are depicted as dotted curved arrows. Measurement errors of exogenous variables are omitted for clarity.

Variation among vegetation types

When the tree species and structural diversity model (Figure 4) was refitted separately using data from each of the 4 vegetation types the strengths of unstandardised path coefficients varied. The direct effect of tree species diversity on AGB was positive in Baikiaea and Mopane, but negative in Marginal and Core miombo (Figure 5). Relationships between structural diversity and AGB remained generally similar with the same sign and significant overlap between the 95% confidence intervals of path coefficients. The total effect of species diversity on AGB remained strongly positive for all vegetation types. All vegetation types except Mopane exhibited a positive effect of species diversity on structural diversity. All models had adequate goodness-of-fit (Table 2), though confidence intervals around the unstandardised path coefficients were wide particularly for Mopane and Baikiaea. χ^2 statistics were high for some vegetation types, but this appears to be highly correlated with sample size for each vegetation type (Hooper et al., 2008).

The strongest total effect of tree species diversity on AGB was in Baikiaea woodland ($\beta = 0.19 \pm 0.154$, $p = 0.22$), which was species rich but highly variable in species diversity compared to other vegetation types (Table 1). The R^2 of AGB was highest in Marginal miombo ($R^2 = 0.71$) and lowest

376 in the Core miombo ($R^2 =$
377 strucbrsqstrucbrsq).

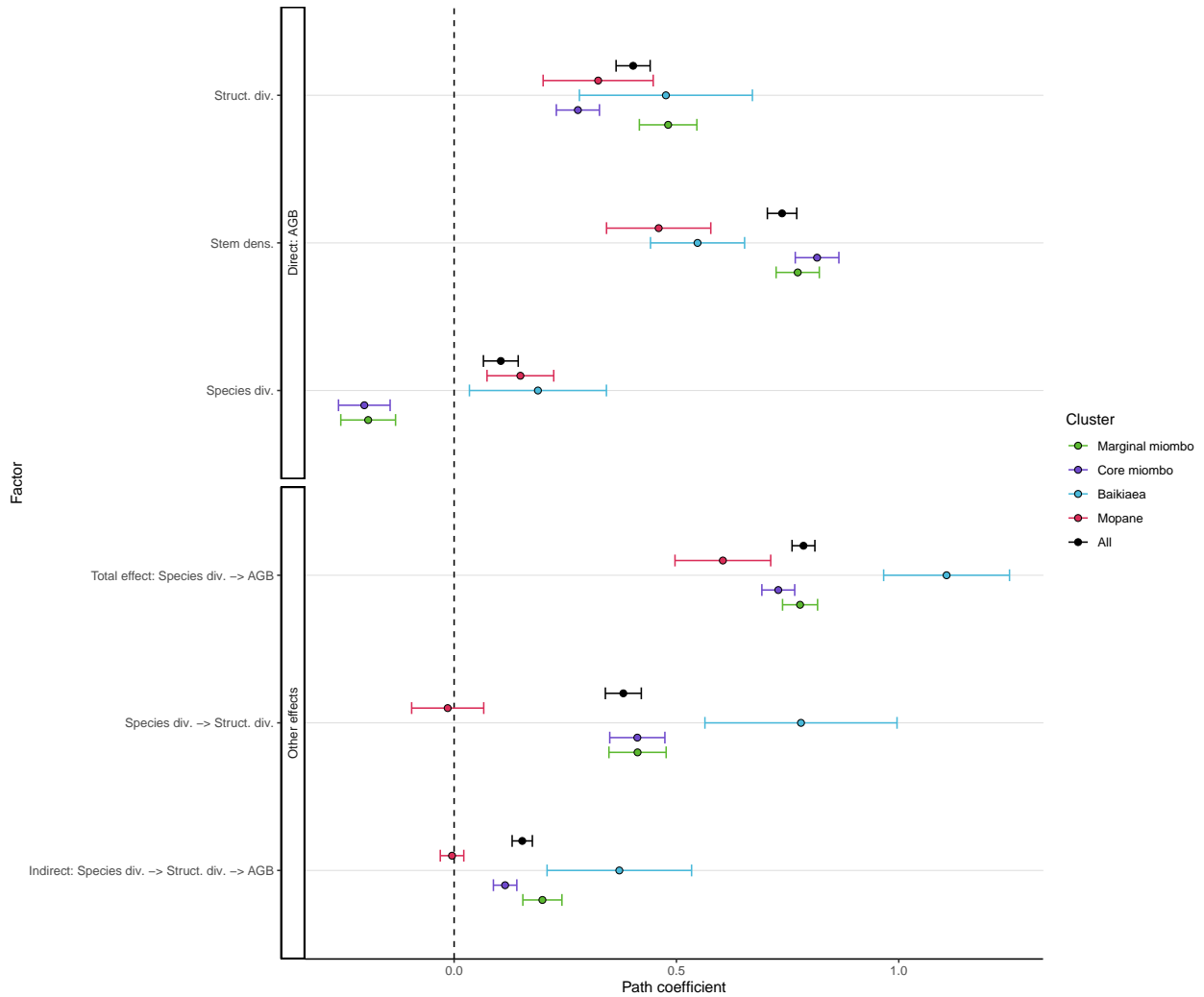


Figure 5: Unstandardised path coefficients for the effects of tree diversity on AGB, mediated by the effect of stand structural diversity. Path coefficients are ± 1 standard error. Path coefficients where the standard error does not overlap zero are considered to be significant effects.

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

| Cluster | n | χ^2 | DoF | CFI | TLI | LogLik | RMSEA | R^2 AGB |
|-----------------|------|----------|-----|-------|-------|-----------|-------|-----------|
| Marginal miombo | 525 | 44.750 | 6 | 0.966 | 0.916 | -3714.000 | 0.110 | 0.710 |
| Core miombo | 668 | 57.210 | 6 | 0.962 | 0.904 | -4224.000 | 0.100 | 0.680 |
| Baikiaea | 47 | 5.860 | 6 | 0.998 | 0.994 | -324.600 | 0.030 | 0.720 |
| Mopane | 84 | 9.420 | 6 | 0.971 | 0.927 | -591.600 | 0.080 | 0.450 |
| All | 1324 | 78.430 | 6 | 0.975 | 0.936 | -9119.000 | 0.090 | 0.690 |

378 Moderation of Diversity-AGB relationship by stem density

379 We repeatedly sub-sampled the plot dataset to build 50 datasets of varying mean stem density
380 in order to test how the relationship between species diversity, structural diversity and biomass

381 varied with stem density. Each dataset consisted of approximately 892 plots with overlap of plot
 382 identity between subsampled datasets. **Figure 6** shows a positive effect of tree species diversity on
 383 AGB as stem density increases. There appears to be a minimum stem density threshold at ~ 180
 384 stems ha^{-1} below which there appears to be a reasonably constant low baseline effect of tree di-
 385 versity on biomass. The effect of structural diversity on AGB appears to remain constant with
 386 increasing stem density. The indirect effect of species diversity on AGB via structural diversity
 387 climbs slightly as stem density increases.

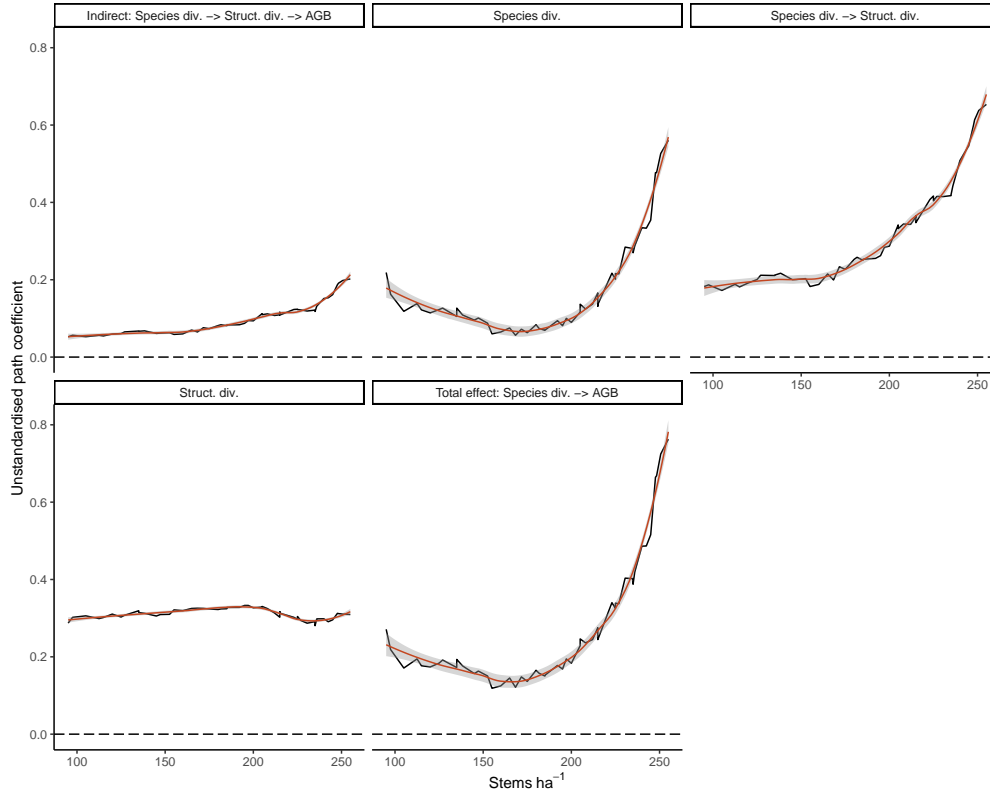


Figure 6: Line plots showing the variation in path coefficients in the SEM, using datasets with different mean stem density. Smoothed lines are loess curves with standard error shaded bars.

388 Environmental covariates and diversity

389 A model incorporating the latent variables of moisture availability and soil fertility showed that
 390 the total effect of species diversity on biomass was greater than that of both moisture availability
 391 and soil fertility (**Figure 7**). Surprisingly, the direct effects of moisture availability and soil fertil-
 392 ity on biomass were negligible, with nearly all of their observed effect on AGB coming from the
 393 indirect path via species diversity (moisture: $\beta = -0.01 \pm 0.005$, $p < 0.01$, soil: $\beta = -0.04 \pm 0.012$, p
 394 < 0.01). MAP and temperature seasonality (TS) had the greatest contributions to the latent vari-
 395 able of moisture availability. Moisture availability and soil fertility also had negligible direct effects
 396 on stem density. Model fit was acceptable: CFI = 0.924, TLI = 0.905, and RMSEA = 0.163, R^2
 397 of AGB = 0.7.

398 Similar to the model which only considered tree species and structural diversity (**Figure 4**), the
 399 direct effect of species diversity on structural diversity was positive, while structural diversity itself
 400 had a positive effect on AGB, leading to a strong positive indirect effect of species diversity on
 401 AGB via structural diversity ($\beta = 0.16 \pm 0.023$, $p < 0.01$). The total effect of species diversity on
 402 AGB was positive ($\beta = 0.64 \pm 0.041$, $p < 0.01$).

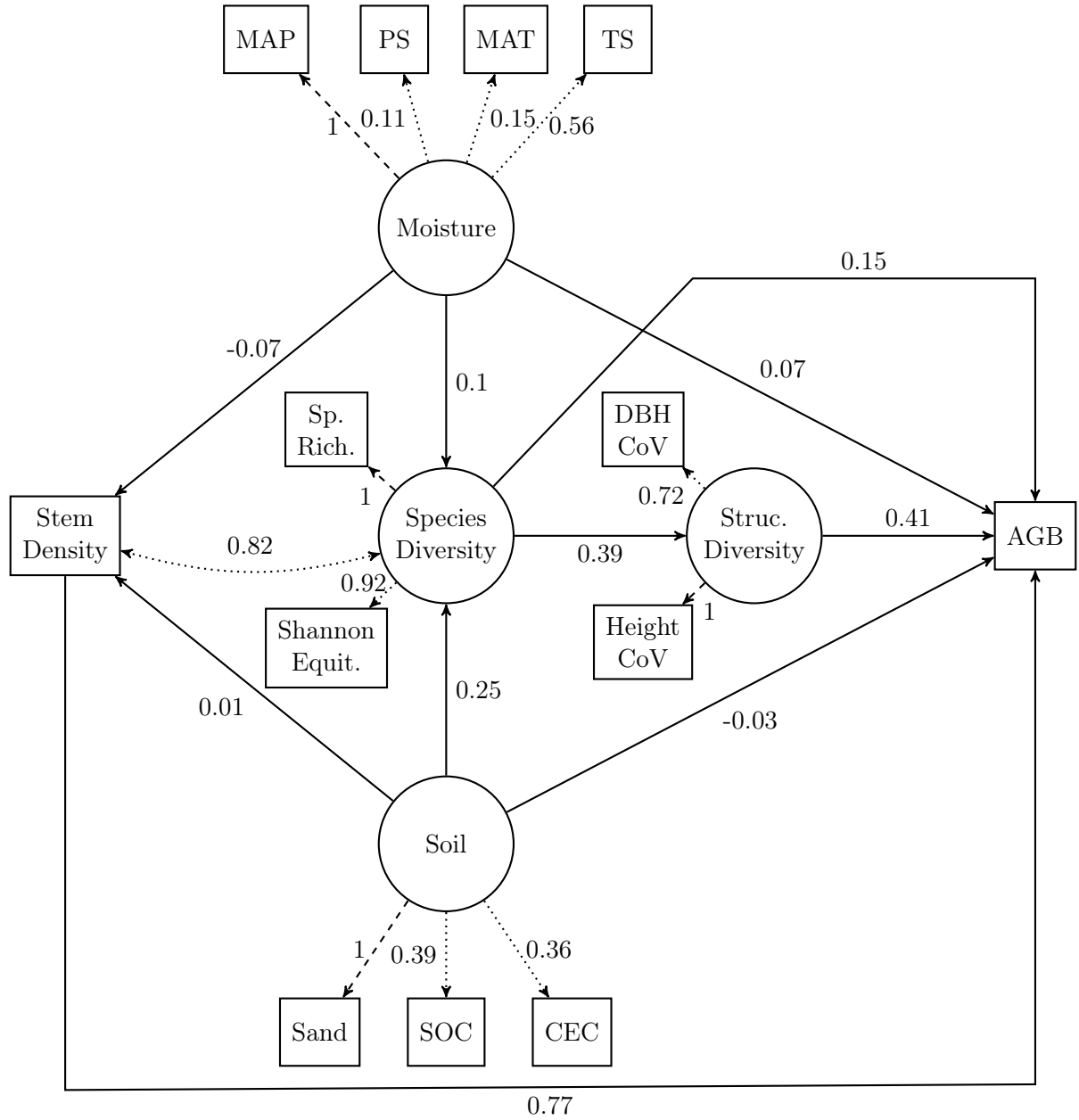


Figure 7: Path diagram with regression coefficients for the SEM incorporating environmental covariates and tree species and structural diversity across all five vegetation types. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are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

Discussion

In this study, we assessed the importance of [a] tree species richness, [b] tree structural diversity, [c] resource availability, i.e. moisture availability and soil fertility, [d] stem density and their interactions on above ground woody biomass (AGB) across SAWs, using a network of 1767 woodland survey plots. Using latent variables and Structural Equation Modelling (SEM), we found support for a general positive relationship between tree species diversity and AGB, with an indirect influence of tree species diversity on AGB via structural diversity (H_1). We found that the effect size

of tree species diversity on AGB increased with stem density (H_2). Tree diversity, structural diversity and stem density accounted for 69% of the variation in AGB across the region, while models for specific vegetation types showed even greater explanatory power in some cases (Table 2). The strongest effect on AGB was that of stem density. Interestingly, when the effects of tree species diversity, structural diversity and stem density were controlled for, we found little evidence of a direct effect of resource availability, in the form of moisture or soil fertility, on AGB (H_3).

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

We found a consistent positive effect of tree species diversity on AGB across all models in this study. Within SAWs we therefore find support that higher tree species richness and evenness causes higher woody AGB. This finding is in agreement with many other studies across different ecosystems and biomes, supporting that there is a generalisable positive association between diversity and ecosystem function (Liang et al., 2016; Cardinale et al., 2009). Our study provides a novel dissection of the mechanisms underlying this relationship, particularly in the context of SAWs, a disturbance-structured and poorly studied ecological system.

Much of the total variation in AGB was driven by variation in stem density. Stem density also correlated with species diversity in our SEMs. It is possible that within SAWs a higher species diversity allows for a greater density of tree stems, leading to an increase in total AGB. The opposite is also plausible however, with increased stem density causing higher species richness through an increased probability of encountering new species. We suggest that an increase in tree species diversity through species richness and evenness produces an assemblage of species which can occupy a greater proportion of the total woodland canopy volume with leaf area, utilising more of the available light resulting in greater total AGB at the plot level (). This is supported by the moderately strong indirect positive effect of tree species diversity on AGB via structural diversity.

We found evidence that tree species diversity led to an increase in AGB indirectly via tree structural diversity and we therefore find support for our hypothesis (H_2). A higher tree species diversity allows for a greater structural diversity of trees, i.e. greater variation in DBH and height. This may act as a mechanism of niche complementarity, with a highly diverse canopy being able to take advantage of a greater proportion of the available light. Although we did not measure it here, we would also expect that tree species diversity allows for a greater range of tree functional forms (), i.e. wider variation in canopy shape and overall growth form; bushy understorey vs. emergent canopy, for example. Variation in structural diversity may be a joint result of disturbance history and tree species diversity, with highly disturbed plots generally having a less structurally diverse canopy (LaRue et al., 2019). In forests, where the tree canopy is effectively closed, as the stand matures a more diverse canopy emerges via competition and tree mortality events which open canopy gaps (Muscolo et al., 2014). Indeed, our finding that the strength of the effect of tree diversity on AGB increases with stem density supports this. In frequently disturbed woodlands such as those studied here however, a woodland canopy similar to that of a forest is frequently not reached. Instead, a simple open canopy is maintained that can be made more complex and productive via an increase in species diversity. While we did not have access to adequate data on disturbance history in our plots, previous studies have found that SAWs with higher species diversity tend to be less disturbed and tend to form a more closed canopy (Chidumayo, 2013; Mutowo and Murwira, 2012).

We found a non linear positive effect of stem density on the relationship between tree species diversity and AGB (Figure 6). At low stem densities competition between trees may not occur, meaning that the niche complementarity provided by an increase in tree species richness might not make any difference to plot level AGB, accounting for the low and constant effect of tree species diversity on AGB below ~ 180 stems ha^{-1} .

Effects of moisture availability and soil fertility

Surprisingly, moisture availability and soil fertility had only small effects on AGB compared to that of tree species diversity. We expected that higher moisture availability and soil fertility would lead to higher AGB under the assumption that higher resource availability would allow for a greater stem density per unit area, greater productivity per unit area and additionally greater tree species diversity due to niche partitioning (Kraaij and Ward, 2006; Shirima et al., 2015).

Previous studies in tropical forests have shown that moisture availability increases AGB both directly and indirectly via increasing tree species diversity and via increasing stand structural diversity (Ali et al., 2019a,b; Poorter et al., 2017). In this study, while we observed weak indirect effects via species diversity, we saw no evidence for a direct effect of moisture availability on AGB. Compared to moist tropical forests, moisture availability is more of a limiting factor to tree growth in SAWs, which are frequently droughted. It is possible that the range of observed moisture availability in this study ($\sim 460\text{--}1700\text{ mm y}^{-1}$) may not have been able to capture variation in AGB. Due to the high levels of adaptation of tree species to drought conditions in southern Africa, at the large scale we conducted our experiment turnover in species composition along the moisture gradient may have obscured a direct relationship being observed between moisture availability and AGB.

In SAWs moisture availability is closely linked with the intensity of disturbance from seasonal fires. The growth of C4 grasses in wetter woodlands leads to more intense seasonal fires which limit tree growth (Charles-Dominique et al., 2018), and may also limit species diversity (Linder, 2014). It is possible therefore that the effect of moisture availability, which is expected to increase AGB, is confounded in its effect on AGB with the unmeasured variable of fire regime intensity, which is expected to decrease AGB. The direct effect of moisture availability on stem density may also be confounded in this way. This may also have caused us to not observe a stronger effect between moisture availability and AGB.

We expected a positive effect of soil fertility on AGB, but found no evidence of this in our models. We measured soil fertility using the observed variables of soil organic carbon content, sand particle content and Cation Exchange Capacity (CEC). In wet tropical forests a clear relationship has been observed between these variables and AGB (??).

Vegetation type specific responses

Core miombo and marginal miombo woodland vegetation exhibited a small negative direct effect of tree species diversity on AGB, while the total effect, incorporating the indirect effect via structural diversity, remained positive in these vegetation types. Compared to Baikiaea and Mopane woodlands, miombo woodlands have higher median tree species richness. Baikiaea and Mopane woodlands are also dominated by fewer tree species, notably *Baikiaea plurijuga* in Baikiaea woodlands and *Colophospermum mopane* in Mopane woodlands which often produce large canopy dominating trees. We postulate that this negative effect of tree species richness on AGB in miombo woodlands may be due to an increase in interspecific competition through canopy crowding, but that this effect is not present in Baikiaea and Mopane woodlands, where the woodland canopy is dominated often by a single species. Higher functional redundancy among tree species in miombo woodlands may lead to smaller trees with lower AGB in the most diverse plots, more resembling thicket vegetation. Again, these highly diverse plots in miombo woodlands may be the result of disturbance which can promote a mosaic of woodland of different successional stages and stem densities. Alternatively, this small negative direct effect may be an artefact of particularly noisy data, especially given that the overall effect of diversity on AGB is positive.

Despite Mopane woodland having very low species diversity generally, with often monospecific stands (Timberlake et al., 2010), a positive effect of tree species diversity on AGB was observed. In previous studies across ecosystem types it has been found often that the effect on ecosystem function of adding species is stronger in low diversity assemblages (Hector and Bagchi, 2007). This

has been attributed to an increase in functional redundancy as species diversity increases. *I.e.* with more species, it is more likely that the addition of a new species will occupy the same ecological niche space as an existing species, meaning niche complementarity will not occur and competition will lead to niche partitioning, while making little difference to overall ecosystem functioning. Mopane woodlands also have a negligible effect of species diversity on structural diversity. This may be due to the species which tend to co-exist with *C. mopane*, many of which are small shrub-like trees which do not grow into large canopy trees (Timberlake et al., 2010). Larger canopy trees tend to have greater variation in physical structure (Seidel et al., 2019).

Baikiaea woodland had the strongest total effect of species diversity on AGB. Baikiaea also has relatively low median species richness compared to miombo, but the addition of new species appears to make a larger difference to the AGB of these plots than in mopane woodlands. We suggest that this is due mostly to the particular identity of species found in Baikiaea woodlands and their contribution to ecosystem functioning. Unlike mopane woodlands, Baikiaea woodlands do sometimes contain species other than *B. plurijuga* which grow to be high biomass canopy trees.

Conclusion

In this study we found that across southern African woodlands (SAWs), there is a generalisable positive association between tree species diversity and woody biomass as a measure of ecosystem function. Additionally, we found that much of this effect of species diversity on biomass exists as an indirect effect by increasing the structural diversity of woodland tree canopies. We found that the multiple vegetation types which comprise SAWs exhibit variation in the strength of the relationship between species diversity and woody biomass, inferring that models of regional and global biodiversity-ecosystem function relationships could benefit from including vegetation type terms and the structural properties of those vegetation types, such as structural diversity and stem density. In contrast to previous studies, we found that across the region, the direct effects of moisture availability and soil fertility on woody biomass were negligible, with most of their effect being indirectly through species and structural diversity. A gap in available data means that we could not incorporate disturbance history into our models adequately, but this factor likely plays a large part in the association between species diversity and woody biomass in SAWs.

SAWs are relied heavily upon for their ecosystem service provision, which is itself affected by ecosystem function. Resource extraction by humans in southern Africa is directly influencing biodiversity via selective tree-felling for timber, among other forest products. Our study shows that biodiversity change through human actions will have the greatest negative impact on ecosystem function in areas of high stem density and Baikiaea woodlands, which are predominantly targeted for tree felling. This raises concerns about the robustness of these ecosystems to further resource extraction and biodiversity loss.

References

- Ali, A., Lin, S., He, J., Kong, F., Yu, J. and Jiang, H. (2019a), ‘Big-sized trees overrule remaining trees’ attributes and species richness as determinants of aboveground biomass in tropical forests’, *Global Change Biology* **25**, 2810–2824.
- Ali, A., Lin, S., He, J., Kong, F., Yu, J. and Jiang, H. (2019b), ‘Climate and soils determine aboveground biomass indirectly via species diversity and stand structural complexity in tropical forests’, *Forest Ecology and Management* **432**, 823–831.
- Barthlott, W., Mutke, J., Rafiqpoor, D., Kier, G. and Kreft, H. (2005), ‘Global centers of vascular plant diversity’, *Nova Acta Leopoldina* **92**(342), 61–83.
- Beaujean, A. A. (2014), *Latent variable modeling using R*, Routledge, New York NY, USA.

551 Bond, W. J. and Keeley, J. E. (2005), ‘Fire as a global ‘herbivore’: the ecology and evolution of
552 flammable ecosystems’, *Trends in Ecology and Evolution* **20**(7), 387–394.

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

554 Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M.,
555 Jouseau, C., Cadotte, M. W., Carroll, I. T., Weis, J. J., Hector, A. and Loreau, M. (2009), ‘Ef-
556 fects of biodiversity on the functioning of ecosystems: a summary of 164 experimental manipu-
557 lations of species richness’, *Ecology* **90**(3), 854–854.

558 Cham, H., Reshetnyak, E., Rosenfeld, B. and Breitbart, W. (2017), ‘Full information maximum
559 likelihood estimation for latent variable interactions with incomplete indicators’, *Multivariate*
560 *Behavioural Research* **52**(1), 12–30.

561 Charles-Dominique, T., Midgley, G. F., Tomlinson, K. W. and Bond, W. J. (2018), ‘Steal the
562 light: shade vs fire adapted vegetation in forest-savanna mosaics’, *New Phytologist* **218**, 1419–
563 1429.

564 Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G. and Zanne, A. E. (2009), ‘To-
565 wards a worldwide wood economics spectrum’, *Ecology Letters* **12**, 351–366.

566 Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C.,
567 Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrizar, A., Mu-
568 gasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira,
569 E. M., Ortiz-Malavassi, E., Péliissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G. and Vieille-
570 dent, G. (2014), ‘Improved allometric models to estimate the aboveground biomass of tropical
571 trees’, *Global Change Biology* **20**(10), 3177–3190.

572 Chen, I., Hill, J. K., Ohlemüller, R., Roy, D. B. and Thomas, C. D. (2011), ‘Rapid range of
573 species associated with high levels of climate warming’, *Science* **333**, 1024–1026.

574 Chidumayo, E. N. (2013), ‘Forest degradation and recovery in a miombo woodland landscape in
575 Zambia: 22 years of observations on permanent sample plots’, *Forest Ecology and Management*
576 **291**, 154–161.

577 Chisholm, R. A., Muller-Landau, H. C., Rahman, K. A., Bebb, D. P., Bin, Y., Bohlman, S. A.,
578 Bourg, N. A., Brinks, J., Bunyavejchewin, S., Butt, N., Cao, H., Cao, M., Cárdenas, D., Chang,
579 L., Chiang, J., Chuyong, G., Condit, R., Dattaraja, H. S., Davies, S., Duque, A., Fletcher, C.,
580 Gunatilleke, N., Gunatilleke, S., Hao, Z., Harrison, R. D., Howe, R., Hsieh, C., Hubbell, S. P.,
581 Itoh, A., Kenfack, D., Kiratiprayoon, S., Larson, A. J., Lian, J., Lin, D., Liu, H., Lutz, J. A.,
582 Ma, K., Malhi, Y., McMahon, S., McShea, W., Meegaskumbura, M., Razman, S. M., Morecroft,
583 M. D., Nytch, C. J., Oliveira, A., Parker, G. G., Pulla, S., Punchi-Manage, R., Romero-Saltos,
584 H., Sang, W., Schurman, J., Su, S., Sukumar, R., Sun, I., Suresh, H. S., Tan, S., Thomas, D.,
585 Thomas, S., Thompson, J., Valencia, R., Wolf, A., Yap, S., Ye, W., Yuan, Z. and Zimmermann,
586 J. K. (2013), ‘Scale-dependent relationships between tree species richness and ecosystem func-
587 tion in forests’, *Journal of Ecology* **101**, 1214–1224.

588 Clarke, D. A., York, P. H., Rasheed, M. A. and Northfield, T. D. (2017), ‘Does biodiversity -
589 ecosystem function literature neglect tropical ecosystems’, *Trends in Ecology & Evolution*
590 **32**(5), 320–323.

591 Condit, R., Engelbrecht, B. M. J., Pino, D., Pérez, R. and Turner, B. L. (2013), ‘Species distribu-
592 tions in response to individual soil nutrients and seasonal drought across a community of tropi-
593 cal trees’, *Proceedings of the National Academy of Sciences* **110**(13), 5064–5068.

594 Copernicus Climate Change Service (2017), *ERA5: Fifth generation of ECMWF atmospheric re-*
595 *analyses of the global climate*, Copernicus Climate Change Service Climate Data Store (CDS).
596 Accessed: 2019-09-03.

- Dengler, J. (2009), ‘Which function describes the species-area relationship best? a review and empirical evaluation’, *Journal of Biogeography* **36**, 728–744.
- Dufrêne, M. and Legendre, P. (1997), ‘Species assemblage and indicator species: the need for a flexible asymmetrical approach’, *Ecological Monographs* **67**(3), 345–366.
- Fayolle, A., Swaine, M. D., Aleman, J., Azihou, A. F., Bauman, D., te Beest, M., Chidumayo, E. N., Cromsigt, J. P. G. M., Dessard, H., Finkch, M., Gonçalves, F. M. P., Gillet, J., Gorel, A., Hick, A., Holdo, R., Kirunda, B., Mahy, G., McNicol, I., Ryan, C. M., Revermann, R., Plumptre, A., Pritchard, R., Nieto-Quintano, P., Schmitt, C. B., Seghieri, J., Swemmer, A., Talila, H. and Woollen, E. (2018), ‘A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas’, *Journal of Biogeography* **46**(2), 1–12.
- Fick, S. E. and Hijmans, R. J. (2017), ‘Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas’, *International Journal of Climatology* **37**(12), 4302–4315.
- Frost, P. (1996), The ecology of miombo woodlands, in B. Campbell, ed., ‘The miombo in transition: woodlands and welfare in Africa’, Center for International Forestry Research, Bogor, Indonesia, pp. 11–55.
- Grime, J. P. (1979), *Plant strategies and vegetation processes*, John Wiley and Sons, Chichester, UK.
- Hardiman, B. S., Bohrer, G., Gough, C. M., Vogel, C. S. and Curtis, P. S. (2011), ‘The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest’, *Ecology* **92**(9), 1818–1827.
- Hector, A. and Bagchi, R. (2007), ‘Biodiversity and ecosystem multifunctionality’, *Nature* **448**, 188–190.
- Hengl, T., Mendes de Jesus, J., Heuvelink, G. B. M., Gonzalez, M. R., Kilibarda, M., Blagotić, A., Shangquan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. A., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B., Ribeiro, E., Wheeler, I., Mantel, S. and Kempen, B. (2017), ‘Soilgrids250m: global gridded soil information based on machine learning’, *PLoS ONE* **12**(2), 1–40.
- Hill, M. J. and Hanan, N. P., eds (2011), *Ecosystem function in savannas*, CRC Press, Boca Raton FL, USA.
- Hinsley, A., Entwistle, A. and Pio, D. V. (2015), ‘Does the long-term success of REDD+ also depend on biodiversity’, *Oryx* **49**(2), 216–221.
- Hooper, D., Coughlan, J. and Mullen, M. R. (2008), ‘Structural equation modelling: guidelines for determining model fit’, *Electronic Journal of Business Research Methods* **6**(1), 53–60.
- Houghton, R. A., Hall, F. and Goetz, S. J. (2009), ‘Importance of biomass in the global carbon cycle’, *Journal of Geophysical Research* **114**, 1–13.
- Hsieh, T. C., Ma, K. H. and Chao, A. (2016), ‘iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers)’, *Methods in Ecology and Evolution* **7**, 1451–1456.
- Hu, L. and Bentler, P. M. (1999), ‘Cutoff criteria for fit indexes in covariance structure analysis: conventional criteria versus new alternatives’, *Structural Equation Modeling* **6**(1), 1–55.
- Jax, K. (2005), ‘Function and “functioning” in ecology: what does it mean?’, *Oikos* **111**(3), 641–648.
- Keddy, P. A. (1990), Competitive hierarchies and centrifugal organization in plant communities, in J. B. Grace and D. Tilman, eds, ‘Perspectives on plant competition’, Academic Press, San Diego CA, USA, pp. 266–287.

- Kraaij, T. and Ward, D. (2006), 'Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa', *Plant Ecology* **186**, 235–246.
- Kunz, M., Fichtner, A., Hardtle, W., Raumonen, P., Bruelheide, H. and von Oheimb, G. (2019), 'Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees', *Ecology Letters* pp. 1–11.
- LaRue, E. A., Hardiman, B. S., Elliott, J. M. and Fei, S. (2019), 'Structural diversity as a predictor of ecosystem function', *Environmental Research Letters* **14**, 114011.
- Lasky, J. R., Uriarte, M., Boukili, V. K., Erickson, D. L., Kress, W. J. and Chazdon, R. L. (2014), 'The relationship between tree biodiversity and biomass dynamic changes with tropical forest succession', *Ecology Letters* **17**, 1158–1167.
- Lee, S. Y. (2007), *Structural Equation Modeling: A Bayesian Approach*, Wiley, New York, USA.
- Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A. D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Herault, B., Scherer-Lorenzen, M., Barrett, C. B., Glick, H. B., Hengeveld, G. M., Nabuurs, G.-J., Pfautsch, S., Viana, H., Vitrans, A. C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J. V., Chen, H. Y. H., Lei, X., Schelhaas, M.-J., Lu, H., Gianelle, D., Parfenova, E. I., Salas, C., Lee, E., Lee, B., Kim, H. S., Bruelheide, H., Coomes, D. A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonke, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E. B., Neldner, V. J., Ngugi, M. R., Baraloto, C., Frizzera, L., Ba azy, R., Oleksyn, J., Zawi a Nied wiecki, T., Bouriaud, O., Bussotti, F., Finer, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A. M., Peri, P. L., Gonmadje, C., Marthy, W., OBrien, T., Martin, E. H., Marshall, A. R., Rovero, F., Bitariho, R., Niklaus, P. A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N. L., Ferreira, L. V., Odeke, D. E., Vasquez, R. M., Lewis, S. L. and Reich, P. B. (2016), 'Positive biodiversity-productivity relationship predominant in global forests', *Science* **354**(6309), aaf8957–aaf8957.
- Linder, H. P. (2014), 'The evolution of African plant diversity', *Frontiers in Ecology and Evolution* **2**(38), 1–14.
- Mayaux, P., Eva, H., Brink, A., Achard, F. and Belward, A. (2008), Remote sensing of land-cover and land-use dynamics, in 'Earth Observation of Global Change: The Role of Satellite Remote Sensing in Monitoring the Global Environment', Springer-Verlag, Berlin, Germany, pp. 85–108.
- McNicol, I. M., Ryan, C. M., Dexter, K. G., Ball, S. M. J. and Williams, M. (2018), 'Aboveground carbon storage and its links to stand structure, tree diversity and floristic composition in south-eastern Tanzania', *Ecosystems* **21**, 740–754.
- Michaletz, S. T., Cheng, D., Kerkhoff, A. J. and Enquist, B. J. (2014), 'Convergence of terrestrial plant production across global climate gradients', *Nature* **512**, 39–43.
- Michaletz, S. T., Kerkhoff, A. J. and Enquist, B. J. (2018), 'Drivers of terrestrial plant production across broad geographical gradients', *Global Ecology and Biogeography* **27**, 166–174.
- Mittermeier, R. A., Mittermeier, C. G., Brooks, T. M., Pilgrim, J. D., Konstant, W. R., da Fonseca, G. A. B. and Kormos, C. (2003), 'Wilderness and biodiversity conservation', *Proceedings of the National Academy of Sciences* **100**(18), 10309–10313.
- Muscolo, A., Bagnato, S., Sidari, M. and Mercurio, R. (2014), 'A review of the roles of forest canopy gaps', *Journal of Forestry Research* **25**(4), 725–736.
- Mutowo, G. and Murwira, A. (2012), 'Relationship between remotely sensed variables and tree species diversity in savanna woodlands of southern Africa', *International Journal of Remote Sensing* **33**(20), 6378–6402.

- 686 Nachtigall, C., Kroehne, U., Funke, F. and Steyer, R. (2003), ‘(Why) should we use SEM? pros
687 and cons of structural equation modeling’, *Methods of Psychological Research* **8**(2), 1–22.
- 688 Otto, W. (2013), *Data analysis in vegetation ecology*, Wiley-Blackwell, Chichester, UK.
- 689 Parr, C. L., Lehmann, C. E. R., Bond, W. J., Hoffmann, W. A. and Andersen, A. N. (2014),
690 ‘Tropical grassy biomes: misunderstood, neglected, and under threat’, *Trends in Ecology and*
691 *Evolution* **29**(4), 205–213.
- 692 Pasari, J. R., Levi, T., Zavaleta, E. S. and Tilman, D. (2013), ‘Several scales of biodiversity affect
693 ecosystem multifunctionality’, *Proceedings of the National Academy of Sciences* **110**(25), 10219–
694 10222.
- 695 Poorter, L., van de Sande, M. T., Thompson, J., Arets, E. J. M. M., Alarcón, A., Álvarez-Sánchez,
696 J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G., Boit, A., Bongers, F., Carvalho, F. A.,
697 Casanoves, F., Cornejo-Tenorio, G., Costa, F. R. C., de Castilho, C. V., Duivenvoorden, J. F.,
698 Dutrieux, L. P., Enquist, B. J., Fernández-Méndez, F., Finegan, B., Gormley, L. H. L., Healey,
699 J. R., Hoosbeek, M. R., Ibarra-Manríquez, G., Junqueira, A. B., Levis, C., Licona, J. C., Lis-
700 boa, L. S., Magnusson, W. E., Martínez-Ramos, M., Martínez-Yrizar, A., Martorano, L. G.,
701 Maskell, L. C., Mazzei, L., Meave, J. A., Mora, F., Muñoz, R., Nytch, C., Pansonato, M. P.,
702 Parr, T. W., Paz, H., Pérez-García, E. A., Rentería, L. Y., Rodríguez-Velázquez, J., Rozen-
703 daal, D. M. A., Ruschel, A. R., Sakschewski, B., Salgado-Negret, B., Schietti, J., Simões, M.,
704 Sinclair, F. L., Souza, P. F., Souza, F. C., Stropp, J., ter Steege, H., Swenson, N. G., Thon-
705 icke, K., Toledo, M., Uriarte, M., van der Hout, P., Walker, P., Zamora, N. and Peña-Claros, M.
706 (2015), ‘Diversity enhances carbon storage in tropical forests’, *Global Ecology and Biogeography*
707 **24**, 1314–1328.
- 708 Poorter, L., van der Sande, M. T., Arets, E. J. M. M., Ascarrunz, N., Enquist, B. J., Finegan,
709 B., Licona, J. C., Martínez-Ramos, M., Mazzei, L., Meave, J. A., Muñoz, R., Nytch, C. J., de
710 Oliveira, A. A., Pérez-García, E. A., Prado-Junior, J., Rodríguez-Velázquez, J., Ruschel, A. R.,
711 Salgado-Negret, B., Schiavini, I., Swenson, N. G., Tenorio, E. A., Thompson, J., Toledo, M.,
712 Uriarte, M., van der Hout, P., Zimmerman, J. K. and Peña-Claros, M. (2017), ‘Biodiversity
713 and climate determine the functioning of neotropical forests’, *Global Ecology and Biogeography*
714 **26**, 1423–1434.
- 715 Prado-Junior, J. A., Schiavini, I., Vale, V. S., Arantes, C. S., van der Sande, M. T., Lohbeck, M.
716 and Poorter, L. (2016), ‘Conservative species drive biomass productivity in tropical dry forests’,
717 *Journal of Ecology* **104**, 817–827.
- 718 R Core Team (2019), *R: A Language and Environment for Statistical Computing*, R Foundation
719 for Statistical Computing, Vienna, Austria.
- 720 Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Al-
721 lan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C. C.,
722 Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Češko, E.,
723 Dawud, S. M., de Wandeler, H., Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A.,
724 Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B.,
725 Joly, F., Kambach, S., Kolb, S., Koricheva, J., Liebersgesell, M., Milligan, H., Müller, S., Muys,
726 B., Nguyen, D., Nock, C., Pollastrini, M., Purschke, O., Radoglou, K., Raulund-Rasmussen,
727 K., Roger, F., Ruiz-Benito, P., Seidl, R., Selvi, F., Seiferling, I., Stenlid, J., Valladares, F., Ves-
728 terdal, L. and Baeten, L. (2017), ‘Biodiversity and ecosystem functioning relations in European
729 forests depend on environmental context’, *Ecology Letters* **20**, 1414–1426.
- 730 Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. A., Archibald, S., Lehmann, C. E. R.,
731 Anderson, M. T., Higgins, S. I. and Sankaran, M. (2011), ‘When is a ‘forest’ a savanna, and why
732 does it matter?’, *Global Ecology and Biogeography* **20**, 653–660.

- 733 Roberts, D. W. (2019), *labdsv: Ordination and Multivariate Analysis for Ecology*. R package ver-
734 sion 2.0-1.
- 735 Roques, K. G., O'Connor, T. G. and Watkinson, A. R. (2001), 'Dynamics of shrub encroachment
736 in an African savanna: relative influences of fire, herbivory, rainfall and density dependence',
737 *Journal of Applied Ecology* **38**, 268–280.
- 738 Rosseel, Y. (2012), 'lavaan: An R package for structural equation modeling', *Journal of Statistical*
739 *Software* **48**(2), 1–36.
- 740 Ryan, C. M., Pritchard, R., McNicol, I., Owen, M., Fisher, J. A. and Lehmann, C. (2016),
741 'Ecosystem services from southern African woodlands and their future under global change',
742 *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**(1703), 1–16.
- 743 Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux,
744 J., Higgins, S. I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Cay-
745 lor, K. K., Coughenour, M. B., Diouf, A., Ekaya, W., Feral, C. J., February, E. C., Frost, P.
746 G. H., Hiernaux, P., Hrabar, H., Metzger, K. L., Prins, H. H. T., Ringrose, S., Sea, W., Tews,
747 J., Worden, J. and Zambatis, N. (2005), 'Determinants of woody cover in African savannas', *Na-*
748 *ture* **438**(8), 846–849.
- 749 Sankaran, M., Ratnam, J. and Hanan, N. (2008), 'Woody cover in african savannas: the role of
750 resources, fire and herbivory', *Global Ecology and Biogeography* **17**(2), 236–245.
- 751 Seidel, D., Ehbrecht, M., Dorji, Y., Jambay, J., Ammer, C. and Annighöfer, P. (2019), 'Identifying
752 architectural characteristics that determine tree structural complexity', *Trees* **33**(3), 911–919.
- 753 Selaya, N. G. and Anten, P. R. (2008), 'Differences in biomass allocation, light interception and
754 mechanical stability between lianas and trees in early secondary tropical forest', *Functional*
755 *Ecology* **22**, 30–39.
- 756 SEOSAW (2019), 'SEOSAW: A Socio-Ecological Observatory for Southern African Woodlands'.
757 [Online; 15-January-2019].
- 758 Shapiro, A. (1983), 'Asymptotic distribution theory in the analysis of covariance structures (a uni-
759 fied approach)', *South African Statistical Journal* **17**, 33–81.
- 760 Shirima, D. D., Pfeifer, M., Platts, P. J., Totland, Ø. and Moe, S. R. (2015), 'Interactions between
761 canopy structure and herbaceous biomass along environmental gradients in moist forest and dry
762 miombo woodland of tanzania', *PLoS ONE* **10**(11), 1–15.
- 763 Smith, B. and Wilson, J. B. (1996), 'A consumer's guide to evenness indices', *Oikos* **76**(1), 70–82.
- 764 Solbrig, O. T., Medina, E. and Silva, J. F. (1996), *Biodiversity and Savanna Ecosystem Processes*,
765 Springer-Verlag, Berlin, Germany.
- 766 Spasojevic, M. J., Grace, J. B., Harrison, S. and Damschen, E. I. (2014), 'Functional diversity sup-
767 ports the physiological tolerance hypothesis for plant species richness along climatic gradients',
768 *Journal of Ecology* **102**, 447–455.
- 769 Stark, S. C., Leitold, V., Wu, J. L., Hunter, M. O., de Castilho, C. V., Costa, F. R. C., McMa-
770 hon, S. M., Parker, G. G., Shimabukuro, M. T., Lefsky, M. A., Keller, M., Alves, L. F., Schietti,
771 J., Shimabukuro, Y. E., Brandão, D. O., Woodcock, T. K., Higuchi, N., de Camargo, P. B., de
772 Oliveira, R. C. and Saleska, S. R. (2012), 'Amazon forest carbon dynamics predicted by profiles
773 of canopy leaf area and light environment', *Ecology Letters* **15**, 1406–1414.
- 774 Staver, A. C., Bond, W. J., Stock, W. D., van Rensburg, S. J. and Waldram, M. S. (2009),
775 'Browsing and fire interact to suppress tree density in an African savanna', *Ecological Applica-*
776 *tions* **19**(7), 1909–1919.

777 Stegen, J. C., Swenson, N. G., Enquist, B. J., White, E. P., Phillips, O. L., Jørgensen, P. M.,
778 Weiser, M. D., Mendoza, A. M. and Vargas, P. N. (2011), ‘Variation in above-ground forest
779 biomass across broad climatic gradients’, *Global Ecology and Biogeography* **20**, 744–754.

780 Tilman, D. and Downing, J. A. (1994), ‘Biodiversity and stability in grasslands’, *Nature* **367**, 363–
781 365.

782 Tilman, D., Isbell, F. and Cowles, J. M. (2014), ‘Biodiversity and ecosystem functioning’, *Annual*
783 *Review of Ecology, Evolution, and Systematics* **45**, 471–493.

784 Timberlake, J., Chidumayo, E. and Sawadogo, L. (2010), Distribution and characteristics of
785 African dry forests and woodlands, in ‘The Dry Forests and Woodlands of Africa: Managing
786 for Products and Services’, EarthScan, London, United Kingdom, pp. 11–42.

787 Tobner, C. M., Paquette, A., Gravel, D., Reich, P. B., Williams, L. J. and Messier, C. (2016),
788 ‘Functional identity is the main driver of diversity effects in young tree communities’, *Ecology*
789 *Letters* **19**, 638–647.

790 van der Sande, M. T., Poorter, L., Kooistra, L., Balvanera, P., Thonicke, K., Thompson, J., Arets,
791 E. J. M. M., Alaniz, N. G., Jones, L., Mora, F., Mwampamba, T. H., Parr, T. and Peña-Claros,
792 M. (2017), ‘Biodiversity in species, traits, and structure determines carbon stocks and uptake in
793 tropical forests’, *Biotropica* **49**(5), 593–603.

794 Vilà, M., Inchausti, P., Vayreda, J., Barrantes, O., Gracia, C., Ibàñez, J. J. and Mata, T. (2005),
795 ‘Confounding factors in the observational productivity-diversity relationship in forests’, *Ecologi-*
796 *cal Studies* **176**, 65–86.

797 Wildi, O. (2017), *dave: Functions for "Data Analysis in Vegetation Ecology"*. R package version
798 2.0.

799 Wright, A. J., Wardle, W. D. A., Callaway, W. R. and Gaxiola, A. (2017), ‘The overlooked role of
800 facilitation in biodiversity experiments’, *Trends in Ecology and Evolution* **32**(5), 383–390.

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

804 Data accessibility statement

805 Tables

806 Figure legends and embedded figures

807 Appendix 1 - Data cleaning process

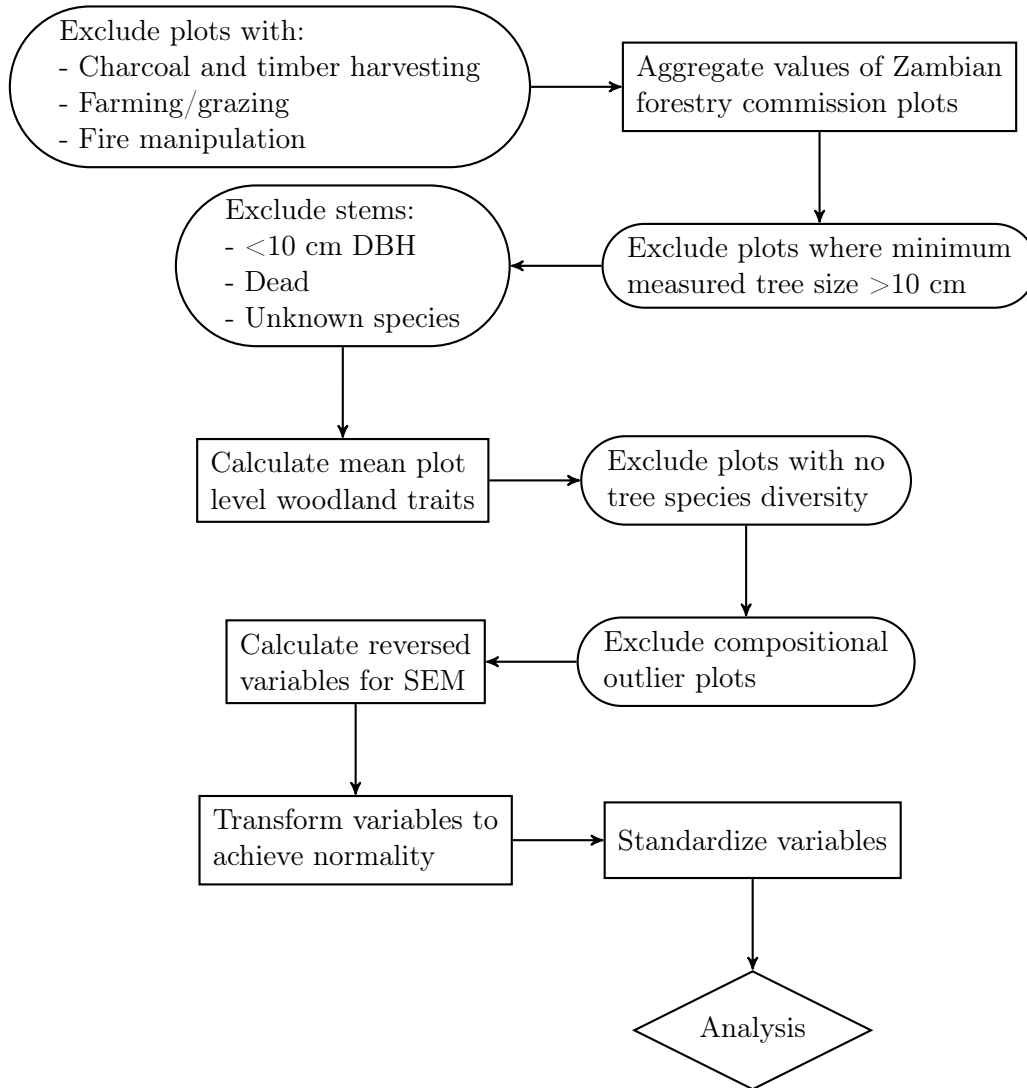


Figure 8: Flow diagram of the data filtering and cleaning process prior to analysis. Rounded boxes indicate filtering events while regular boxes indicate calculation events.

808 Appendix 2 - Estimation of DBH via tree taper

```
809 ##' @title Stem diameter Point Of Measurement (POM) adjustment  
810 ##' @description Function to estimate stem diameter at 1.3 given measurements  
811 ##'   at other POMs.  
812 ##' @author Casey M. Ryan  
813 ##' @return d130, the estimated diameter at a POM of 1.3 m (in cm).  
814 ##' @param d_in the diameter measured at the POM (in cm)  
815 ##' @param POM the height of the POM (in m)  
816 ##' @details The adjustment is based on a tree taper model developed as part of  
817
```



```

8189 ##' the ACES project (Abrupt Changes in Ecosystem Services
8190 ##' https://miomboaces.wordpress.com/), using data from the miombo of Niassa.
8201 ##' The model is a cubic polynomial, with three equations for different sized
8212 ##' stems.
8223 ##' @section Warning: The model should not be used for POMs above 1.7 m.
8234 ##' Extrapolating beyond the training data will give nonsense.
8245 ##' Thus, POMs >1.7 m are not adjusted.
8256 ##' @examples
8267 ##' POMadj(10, 0.3)
8278 ##' POMadj(1, 0.3) # d130 is negative, i.e. the stem probably wasn't 1.3 m tall
8289 ##' POMadj(50, 1.9) # generates warning, as outside calibration data range
8290 ##' \dontrun{
8301 ##' POMadj(50, 0) # zero or -ve POM is outside range, or nonsense
8312 ##' }
8323 POMadj <- function(d_in, POM) {
8334   stopifnot(is.numeric(d_in),
8345             is.numeric(POM),
8356             POM >= 0,
8367             sum(is.na(POM))==0,
8378             length(POM) == length(d_in))
8389   if (any(POM > 1.7))
8390     warning("POMs >1.7 m are outside the calibration data, no correction applied")
8401
8412   NAS <- is.na(d_in)
8423   d_in_clean <- d_in[!NAS]
8434   POM_clean <- POM[!NAS]
8445   # define the size class edges:
8456   edges <- c(5.0, 15.8, 26.6, 37.4)
8467   sm <- d_in_clean < edges[2]
8478   med <- d_in_clean >= edges[2] & d_in_clean < edges[3]
8489   lg <- d_in_clean >= edges[3]
8490
8501   # compute apredictions for delta_d, for all size classes
8512   delta_d <- data.frame(
8523     # if small:
8534     small = 3.4678+-5.2428 *
8545       POM_clean + 2.9401 *
8556       POM_clean^2+-0.7141 *
8567       POM_clean^3,
8578     # if med
8589     med = 4.918+-8.819 *
8590       POM_clean + 6.367 *
8601       POM_clean^2+-1.871 *
8612       POM_clean^3,
8623     # if large
8634     large = 9.474+-18.257 *
8645       POM_clean + 12.873 *
8656       POM_clean^2+-3.325 *
8667       POM_clean^3
8678   )
8689   # index into the right size class
8690   dd <- NA_real_
8701   dd[sm] <- delta_d$small[sm]
8712   dd[med] <- delta_d$med[med]
8723   dd[lg] <- delta_d$large[lg]
8734   dd[POM_clean > 1.7] <- 0 # to avoid extrapolation mess
8745
8756   # add NAs back in
8767   d130 <- NA
8778   d130[NAS] <- NA
8789   d130[!NAS] <- d_in_clean - dd
8790
8801   if (any(d130[!NAS] < 0))
8812     warning("Negative d130 estimated, repaced with NA")
8823   d130[d130 <= 0 & !is.na(d130)] <- NA

```

```

8834 return(d130)
8845 }
885

```

886 Appendix 3 - Frequency distribution of observed variables

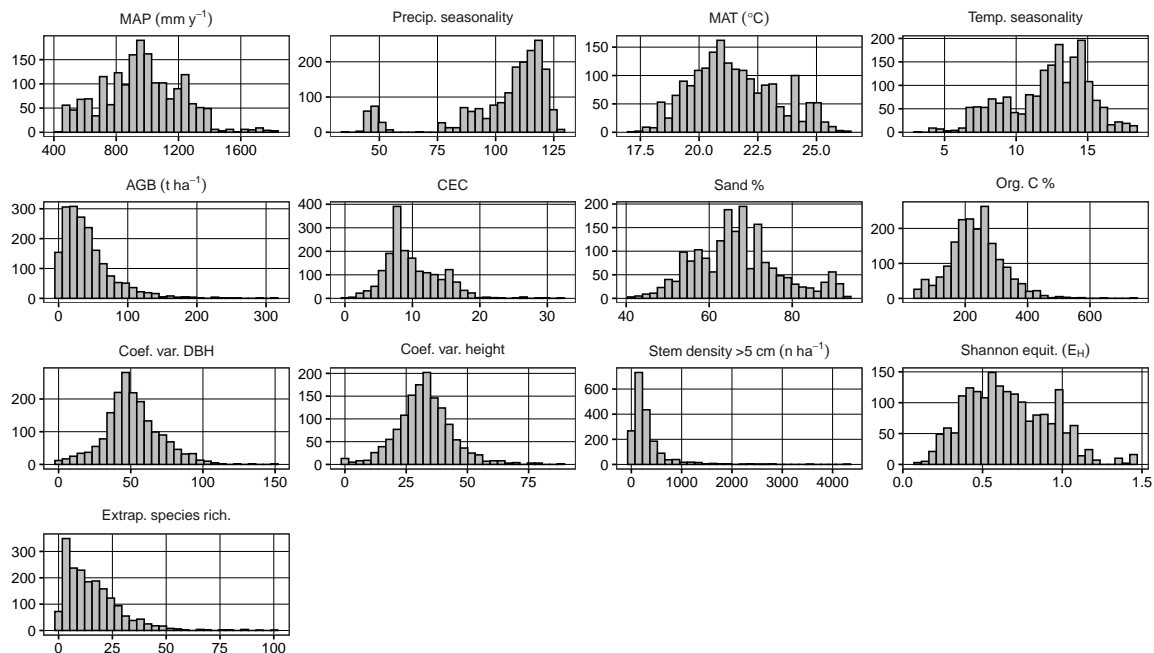


Figure 9: Histograms of raw untransformed observed variables used in final analyses.

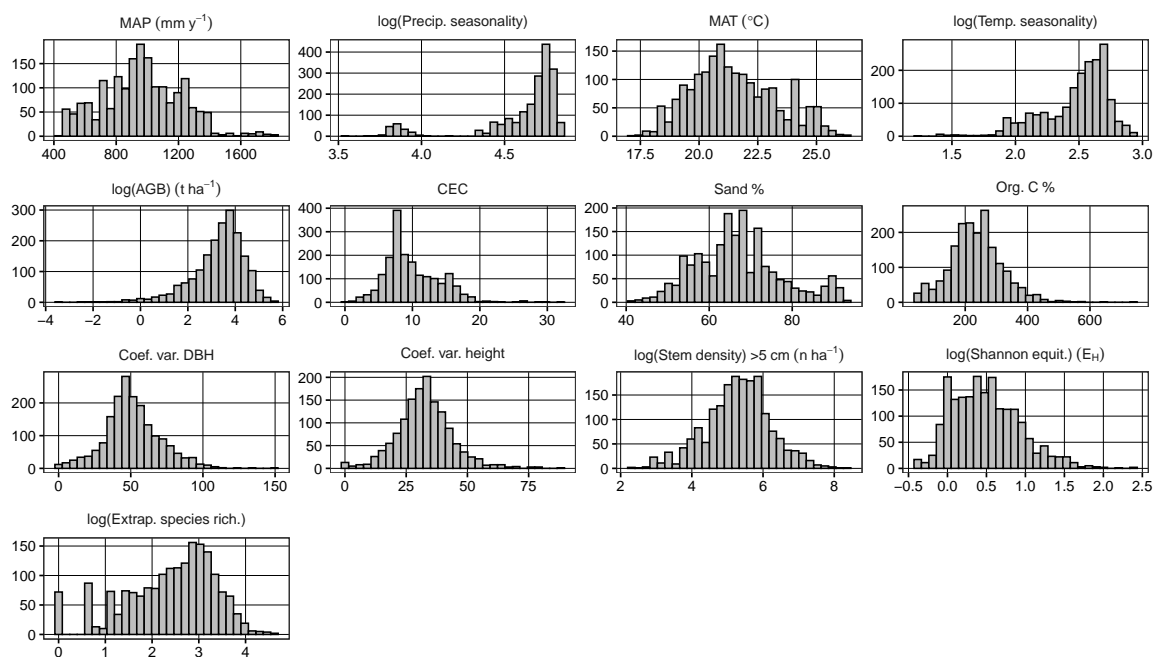


Figure 10: Histograms of observed variables transformed to achieve a normal frequency distribution.

Table 3: Table of correlation fit statistics for each pairwise Pearson correlation test of observed variables used in Structural Equation Models.

| X | Y | r | lower 95% CI | upper 95% CI | n | Prob. |
|----------|----------------|--------|--------------|--------------|------|----------|
| Sand % | Org. C % | -0.510 | -0.540 | -0.470 | 1767 | p < 0.01 |
| Sand % | CEC | -0.560 | -0.600 | -0.530 | 1767 | p < 0.01 |
| Sand % | MAP | -0.500 | -0.530 | -0.460 | 1767 | p < 0.01 |
| Sand % | PS | 0.320 | 0.280 | 0.360 | 1767 | p < 0.01 |
| Sand % | MAT | 0.290 | 0.240 | 0.330 | 1767 | p < 0.01 |
| Sand % | TS | 0.230 | 0.180 | 0.270 | 1767 | p < 0.01 |
| Sand % | Sp. rich. | -0.350 | -0.390 | -0.300 | 1767 | p < 0.01 |
| Sand % | Shannon equit. | -0.240 | -0.280 | -0.190 | 1767 | p < 0.01 |
| Sand % | Tree height CV | -0.200 | -0.250 | -0.150 | 1324 | p < 0.01 |
| Sand % | DBH CV | -0.160 | -0.200 | -0.110 | 1742 | p < 0.01 |
| Sand % | Stems ha | -0.270 | -0.310 | -0.220 | 1767 | p < 0.01 |
| Sand % | AGB | -0.270 | -0.310 | -0.220 | 1767 | p < 0.01 |
| Org. C % | CEC | 0.300 | 0.250 | 0.340 | 1767 | p < 0.01 |
| Org. C % | MAP | 0.450 | 0.410 | 0.490 | 1767 | p < 0.01 |
| Org. C % | PS | -0.300 | -0.340 | -0.260 | 1767 | p < 0.01 |
| Org. C % | MAT | -0.310 | -0.350 | -0.270 | 1767 | p < 0.01 |
| Org. C % | TS | -0.150 | -0.190 | -0.100 | 1767 | p < 0.01 |
| Org. C % | Sp. rich. | 0.240 | 0.190 | 0.280 | 1767 | p < 0.01 |
| Org. C % | Shannon equit. | 0.210 | 0.170 | 0.260 | 1767 | p < 0.01 |
| Org. C % | Tree height CV | 0.110 | 0.060 | 0.160 | 1324 | p < 0.01 |
| Org. C % | DBH CV | 0.100 | 0.050 | 0.140 | 1742 | p < 0.01 |
| Org. C % | Stems ha | 0.200 | 0.160 | 0.250 | 1767 | p < 0.01 |
| Org. C % | AGB | 0.250 | 0.210 | 0.290 | 1767 | p < 0.01 |
| CEC | MAP | 0 | -0.040 | 0.050 | 1767 | p = 0.85 |
| CEC | PS | -0.510 | -0.540 | -0.470 | 1767 | p < 0.01 |
| CEC | MAT | 0.190 | 0.150 | 0.240 | 1767 | p < 0.01 |
| CEC | TS | 0.020 | -0.020 | 0.070 | 1767 | p = 0.35 |
| CEC | Sp. rich. | -0.070 | -0.110 | -0.020 | 1767 | p < 0.01 |
| CEC | Shannon equit. | 0.090 | 0.040 | 0.130 | 1767 | p < 0.01 |
| CEC | Tree height CV | 0.070 | 0.020 | 0.130 | 1324 | p < 0.01 |
| CEC | DBH CV | 0.110 | 0.070 | 0.160 | 1742 | p < 0.01 |
| CEC | Stems ha | 0.060 | 0.020 | 0.110 | 1767 | p < 0.01 |
| CEC | AGB | 0.060 | 0.020 | 0.110 | 1767 | p < 0.01 |
| MAP | PS | -0.120 | -0.170 | -0.080 | 1767 | p < 0.01 |
| MAP | MAT | -0.100 | -0.150 | -0.060 | 1767 | p < 0.01 |
| MAP | TS | -0.690 | -0.720 | -0.670 | 1767 | p < 0.01 |
| MAP | Sp. rich. | 0.390 | 0.350 | 0.430 | 1767 | p < 0.01 |
| MAP | Shannon equit. | 0.100 | 0.050 | 0.150 | 1767 | p < 0.01 |
| MAP | Tree height CV | 0.210 | 0.160 | 0.260 | 1324 | p < 0.01 |
| MAP | DBH CV | 0.110 | 0.060 | 0.160 | 1742 | p < 0.01 |
| MAP | Stems ha | 0.090 | 0.050 | 0.140 | 1767 | p < 0.01 |
| MAP | AGB | 0.220 | 0.180 | 0.270 | 1767 | p < 0.01 |
| PS | MAT | -0.170 | -0.210 | -0.120 | 1767 | p < 0.01 |
| PS | TS | 0.070 | 0.020 | 0.110 | 1767 | p < 0.01 |
| PS | Sp. rich. | 0.080 | 0.030 | 0.120 | 1767 | p < 0.01 |
| PS | Shannon equit. | -0.050 | -0.100 | -0.010 | 1767 | p < 0.05 |
| PS | Tree height CV | -0.030 | -0.090 | 0.020 | 1324 | p = 0.25 |

| | | | | | | |
|----------------|----------------|--------|--------|--------|------|----------|
| PS | DBH CV | -0.070 | -0.120 | -0.020 | 1742 | p < 0.01 |
| PS | Stems ha | -0.030 | -0.080 | 0.020 | 1767 | p = 0.2 |
| PS | AGB | -0.110 | -0.160 | -0.070 | 1767 | p < 0.01 |
| MAT | TS | -0.320 | -0.360 | -0.280 | 1767 | p < 0.01 |
| MAT | Sp. rich. | -0.220 | -0.260 | -0.180 | 1767 | p < 0.01 |
| MAT | Shannon equit. | -0.110 | -0.150 | -0.060 | 1767 | p < 0.01 |
| MAT | Tree height CV | 0 | -0.050 | 0.050 | 1324 | p = 1 |
| MAT | DBH CV | 0.090 | 0.040 | 0.130 | 1742 | p < 0.01 |
| MAT | Stems ha | -0.120 | -0.160 | -0.070 | 1767 | p < 0.01 |
| MAT | AGB | -0.090 | -0.130 | -0.040 | 1767 | p < 0.01 |
| TS | Sp. rich. | -0.300 | -0.350 | -0.260 | 1767 | p < 0.01 |
| TS | Shannon equit. | -0.090 | -0.130 | -0.040 | 1767 | p < 0.01 |
| TS | Tree height CV | -0.180 | -0.230 | -0.130 | 1324 | p < 0.01 |
| TS | DBH CV | -0.110 | -0.160 | -0.070 | 1742 | p < 0.01 |
| TS | Stems ha | -0.090 | -0.140 | -0.050 | 1767 | p < 0.01 |
| TS | AGB | -0.140 | -0.180 | -0.090 | 1767 | p < 0.01 |
| Sp. rich. | Shannon equit. | 0.540 | 0.500 | 0.570 | 1767 | p < 0.01 |
| Sp. rich. | Tree height CV | 0.310 | 0.260 | 0.360 | 1324 | p < 0.01 |
| Sp. rich. | DBH CV | 0.300 | 0.260 | 0.340 | 1742 | p < 0.01 |
| Sp. rich. | Stems ha | 0.570 | 0.540 | 0.600 | 1767 | p < 0.01 |
| Sp. rich. | AGB | 0.500 | 0.460 | 0.530 | 1767 | p < 0.01 |
| Shannon equit. | Tree height CV | 0.180 | 0.130 | 0.230 | 1324 | p < 0.01 |
| Shannon equit. | DBH CV | 0.210 | 0.170 | 0.260 | 1742 | p < 0.01 |
| Shannon equit. | Stems ha | 0.480 | 0.440 | 0.520 | 1767 | p < 0.01 |
| Shannon equit. | AGB | 0.390 | 0.350 | 0.420 | 1767 | p < 0.01 |
| Tree height CV | DBH CV | 0.510 | 0.470 | 0.550 | 1324 | p < 0.01 |
| Tree height CV | Stems ha | 0.190 | 0.140 | 0.250 | 1324 | p < 0.01 |
| Tree height CV | AGB | 0.330 | 0.280 | 0.370 | 1324 | p < 0.01 |
| DBH CV | Stems ha | 0.240 | 0.200 | 0.280 | 1742 | p < 0.01 |
| DBH CV | AGB | 0.490 | 0.460 | 0.530 | 1742 | p < 0.01 |
| Stems ha | AGB | 0.770 | 0.750 | 0.790 | 1767 | p < 0.01 |
