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Research article

Precipitation gradients drive high tree species turnover in the woodlands of eastern and southern Africa

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Savannas cover one-fifth of the Earth's surface, harbour substantial biodiversity, and provide a broad range of ecosystem services to hundreds of millions of people. The community composition of trees in tropical moist forests varies with climate, but whether the same processes structure communities in disturbance-driven savannas remains relatively unknown. We investigate how biodiversity is structured over large environmental and disturbance gradients in woodlands of eastern and southern Africa. We use tree inventory data from the Socio-Ecological Observatory for Studying African Woodlands (SEOSAW) network, covering 755 ha in a total of 6780 plots across nine countries of eastern and southern Africa, to investigate how alpha, beta, and phylogenetic diversity varies across environmental and disturbance gradients. We find strong climate-richness patterns, with precipitation playing a primary role in determining patterns of tree richness and high turnover across these savannas. Savannas with greater rainfall contain more tree species, suggesting that low water availability places distributional limits on species, creating the observed climate-richness patterns. Both fire and herbivory have minimal effects on tree diversity, despite their role in determining savanna distribution and structure. High turnover of tree species, genera, and families is similar to turnover in seasonally dry tropical forests of the Americas, suggesting this is a feature of semiarid tree floras. The greater richness and phylogenetic diversity of wetter plots shows that broad-scale ecological patterns apply to disturbance-driven savanna systems. High taxonomic turnover suggests that savannas from across the regional rainfall gradient should be protected if we are to maximise the conservation of unique tree communities.

Keywords: beta diversity, climate-richness, environmental gradients, miombo, phylogenetic diversity, savanna

Introduction

Savannas cover one-fifth of the Earth's surface and are responsible for up to 30% of terrestrial primary productivity (Scholes and Archer 1997). The distribution of savannas is limited by fire and precipitation regimes globally (Lehmann et al. 2011), and more locally by soil properties and herbivory (Oliveras and Malhi 2016). Savannas are characterised by the co-existence of trees and grasses that supports substantial biodiversity (Scholes and Archer 1997), and the livelihoods of 150 million people alone in the savanna woodlands of eastern and southern Africa (Ryan et al. 2016). Despite harbouring high biodiversity (Byers 2001) and being globally important carbon sinks (McNicol et al. 2018) – a function underpinned by their tree diversity (Godlee et al. 2021) – the processes that structure the biodiversity of savanna woodlands remain understudied. The bulk of research focusing on patterns of plant species composition in the tropics is based on tropical moist forests (Parr et al. 2014), but whether these same patterns are replicated in disturbance-driven savannas is unresolved.

Tropical tree community composition is strongly structured over environmental gradients, with the co-variation of climate and taxonomic diversity being one of the most widely observed, broad-scale patterns in ecology (Currie et al. 2004). Within the well-studied moist lowland tropical forests, species richness increases with precipitation at large scales (ter Steege et al. 2003). Rainfall seasonality and water deficit during the dry season are also important in determining community structure in moist forests (Engelbrecht et al. 2007) with tree species richness in western South America increasing with declining water deficit (Esquivel-Muelbert et al. 2017), and dry season length predicting Amazonian tree alpha diversity (ter Steege et al. 2003) and the beta diversity of trees in the Western Ghats (Davidar et al. 2007). Additionally, tolerance to freezing (Segovia et al. 2020) and gradients of soil nutrient availability (Aleman et al. 2020) are important determinants of diversity at both broad and fine spatial scales. However, there are fundamental differences between the ecology of moist tropical forests and that of savannas (Frost 1996), and there is a lack of regional- to continental-scale studies that use plot-level data to investigate these patterns in disturbance-driven savannas.

Precipitation and disturbance, such as fire and herbivory, are important determinants of the physiognomy and distribution of savannas (Sankaran et al. 2005, Lehmann et al. 2011). Rainfall determines tree cover globally, but at intermediate rainfall tree cover is bimodal with fire differentiating between forest and savanna (Staver et al. 2011). The species richness of southern African woody flora increases linearly with precipitation (O'Brien et al. 1998), whilst wet miombo woodland (>1000 mm mean annual precipitation) contains greater floristic richness than dry miombo (< 1000 mm; Frost 1996). In northern Australian savannas, woody plant species richness increases with increasing rainfall and decreasing soil clay content (Williams et al. 1996).

Fire regimes strongly influence woody vegetation structure (Smit et al. 2010), but in savanna fire experiments, show little effect on both tree richness (Makumbe et al. 2020) and grass composition (Andersen et al. 2005). Browsing herbivores change woody plant composition in Kruger national park, South Africa, by preferentially eating species with high leaf nitrogen, decreasing their abundance outside of exclosures (Wigley et al. 2014), whilst also promoting tree beta-diversity in East African savannas (Pringle et al. 2016). Additionally, the number of woody stems per ha – a possible indication of disturbance by fire and herbivory (Sankaran et al. 2008) – is positively correlated with tree species diversity in southern African woodlands (Godlee et al. 2021). However, the impacts of fire and herbivory on savanna woody plant composition are largely observed in experimental settings. Assessing how these factors influence diversity at broad scales is important for understanding biogeography and to inform effective conservation and restoration action (DRYFLOR 2016).

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It is expected that species resilient to climate extremes will be widely distributed, whilst those with narrow tolerances will have restricted distributions (Esquivel-Muelbert et al. 2017). This could produce two outcomes for the structure of β-diversity: communities in less-diverse areas are subsets of the species found in the most-diverse areas (nestedness), or species are replaced by better-adapted species as environmental conditions change (turnover; Socolar et al. 2016). Contrasting evidence for these two outcomes has been observed in tropical forests. Trees in Panama exhibit compositional and functional turnover across rainfall and phosphorous gradients (Umaña et al. 2021), whereas trees of western South America exhibit compositional nestedness over water availability gradients (Esquivel-Muelbert et al. 2017) albeit over a much greater geographical area and with very little coverage of dry tropical forests. Patterns of turnover could provide further evidence of discontinuous floristic boundaries previously identified across southern African woodlands (Fayolle et al. 2019).

The phylogenetic composition of communities is also structured over environmental gradients due to the different survival and life history tradeoffs that have evolved in lineages in response to environmental filters (Neves et al. 2020). Phylogenetic diversity peaks at intermediate precipitation in lowland South American forests and savannas (Neves et al. 2020), with semideciduous forests containing specialised lineages from both extremes, whilst the phylogenetic beta-diversity of Colombian plant assemblages increases with temperature but remains unaffected by differences in precipitation (González-Caro et al. 2014). Climate is a strong predictor of both taxonomic and phylogenetic turnover of tree species in Amazonia, but overall phylogenetic turnover is low (Andino et al. 2021). Patterns of phylogenetic alpha- and beta-diversity over environmental gradients remain largely unstudied in savannas. Given the positive effects of maintaining phylogenetic diversity on ecosystem function and service provision (Cadotte 2013), deciphering the effect of environmental gradients on evolutionary diversity is of great importance to conservation efforts and management.

Here, we assess how species richness and community composition of savanna trees are structured over environmental gradients. We do this by focussing on the world's largest savanna – the woodlands of eastern and southern Africa (White 1983). We use an extensive network of 6780 plots (SEOSAW 2021), covering a wide range of climatic conditions from across the region, to investigate whether patterns of savanna tree diversity follow those found in the moist tropics. We do this by asking three key questions:

1) What are the effects of environmental and disturbance gradients on tree species richness?
2) How is tree β-diversity structured across environmental and disturbance gradients, and in turn, is there a difference between the tree species composition of wet and dry miombo woodlands?
3) What are the effects of environmental and disturbance gradients on tree phylogenetic α- and β-diversity?

Material and methods

Study area

Our study covers several savanna types from across eastern and southern Africa – a conservation priority area that supports high levels of diversity and endemism (Byers 2001). We focus on savannas with a substantial woody component, sampling from mopane woodlands, mixed woodlands, *Acacia* sensu lato savannas, and miombo woodlands (sensu White 1983). The latter is the most extensive tropical woodland type of Africa – covering an area of 1.9 million km^2 (Ribeiro et al. 2020) which are dominated by trees from the genera *Brachystegia*, *Julbernardia* and *Isoberlina* (Frost 1996). We used tree inventory data from 6780 plots from the Socio-Ecological Observatory for Studying African Woodlands (SEOSAW) database (SEOSAW 2021), spanning nine countries across eastern and southern Africa (Supporting information). Plots were sampled between 2002 and 2019, with the vast majority of plots (97%; 6583/6780 plots) sampled from 2012. We sample over a mean annual precipitation (MAP) gradient of 367 mm to 1968 mm (Supporting information) and mean annual temperature (MAT) of 17.2–26.3°C (Fick and Hijmans 2017).

Data collection

We selected plots from the SEOSAW database that were designated as woodland under White's vegetation map of Africa (White 1983). We used plots between 0.1 and 1 ha, representing a tradeoff between coverage within our target region and sampling homogeneity. While larger plots are likely to have more species (as per the species–area relationship; Dengler 2009), the inclusion of plots of differing size was

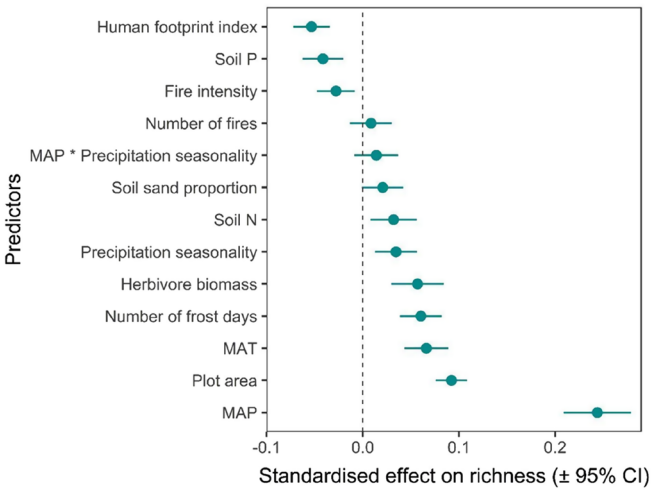

Figure 1. Determinants of tree species richness in the woodlands of eastern and southern Africa. Standardised effect sizes are shown for each variable included in the negative binomial regression model. Points and lines show the mean and 95% credible intervals (CI) respectively. Points to the left of the dashed line had a negative effect on species richness, whilst those to the right had a positive effect.

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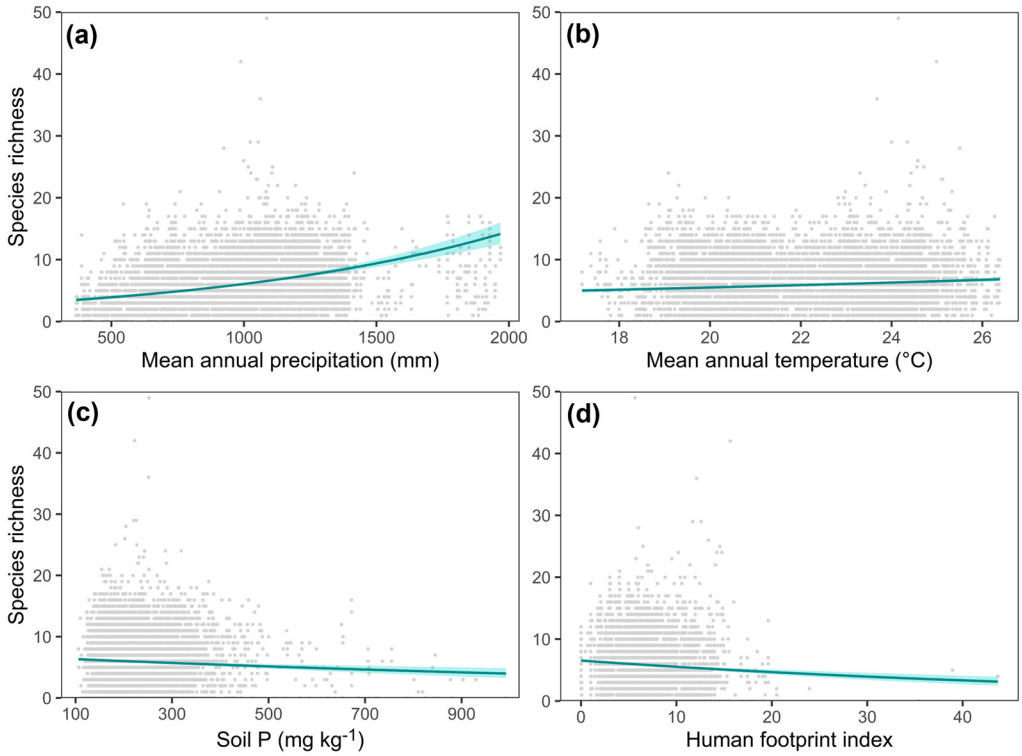

Figure 2. Conditional effect plots of tree species richness as a function of (a) mean annual precipitation, (b) mean annual temperature, (c) soil phosphorous content and (d) human footprint index.

appropriate because we: 1) included plot size as a model predictor, enabling us to analyse how species richness responds to other environmental and disturbance variables whilst controlling for plot area; 2) checked for correlations between the predictor variables included in our models prior to modelling (Supporting information), this showed that plot area was not correlated with any of the other variables included in our model so it is unlikely to be masking or confounding the effects we see from the other model variables and 3) ran individual univariate models for each predictor, and found similar effects to when all variables were tested in the same model (Supporting information).

We included only living stems > 10 cm diameter at breast height (DBH, 1.3 m) in our counts of species richness. Where possible we used tree-level species richness as many trees were comprised of multiple stems at breast height. Trees were then identified to the species-level where possible (91% of trees were identified to species-level, 95% identified to genus), individuals not identified to the species-level were included in analyses as morpho species and counted as unique species.

We extracted climatic data from the WorldClim ver. 2.1 database (Fick and Hijmans 2017). Mean annual precipitation (MAP; BIO12) and mean annual temperature (MAT; BIO1) were taken as the mean value between 1970 and 2000 at 30 arc seconds resolution, with precipitation seasonality (BIO15) calculated as the mean of the coefficient of variation of monthly mean precipitation. Soil nitrogen and phosphorous content (g kg^{-1}), and soil sand proportion data were extracted from the ISRIC SoilGrids data product at 250 m resolution (Hengl et al. 2017). Fire count data was extracted from the MODIS burned area product (Giglio et al. 2015) and taken as the number of times a pixel was recorded as burned between 2001–2018 at a resolution of 1 km. Fire intensity data was extracted from the MODIS active fire product (MODIS Collection 6 NRT Hotspot/Active Fire Detections MCD14ML) measured as the mean fire intensity, again at a 1 km resolution. Present day herbivore biomass was taken from maps created by Hempson et al. (2017) at 0.5° resolution. The number of frost days was taken as the mean annual number of frost days from 1990–2019 at 0.5° resolution from the Climate Research Unit gridded Time Series climate dataset (Harris et al. 2020). We assessed human pressure on our plots using maps of human footprint at a resolution of 1 km (Venter et al. 2016). We initially included more variables in our models but collinearity between variables prevented their inclusion (Supporting information).

Phylogenetic tree and diversity

We used the 'V.PhyloMaker' package to create a phylogenetic tree for all of our species based off a backbone provided by Open Tree of Life (Jin and Qian 2019), with names standardised according to The Plant List (2010). Species that were not present in the backbone, or that were not identified to the species level, were placed into the phylogeny at the lowest-level taxonomic clade possible using the default scenario 3 method (details in Jin and Qian 2019). A very small number of species were not present in the phylogenetic

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tree (7/799 of species; 8121/160 970 trees) and were dropped from this analysis. Using this phylogeny, we calculated phylogenetic diversity (PD; Faith 1992) and the standardised effect size of phylogenetic diversity (sesPD), as phylogenetic diversity is positively correlated with species richness and we aimed to test for phylogenetic patterns independent of species richness (Swenson 2014). Standardised effect sizes for each plot were calculated by comparing the observed phylogenetic indices of communities to those of 999 null communities using the 'taxa.labels' algorithm. Positive values of sesPD indicate that a plot has higher PD than expected by chance, with negative values suggesting the opposite. These analyses were performed in the 'picante' R package (www.r-project.org, Kembel et al. 2010).

Statistical analysis

Species richness and phylogenetic diversity

To assess the effect of environmental gradients on species richness and phylogenetic diversity, we used Bayesian linear models fit using the 'brms' package (Bürkner 2017). We fit the following models for species richness, PD, and sesPD to assess the effects of environmental gradients on biodiversity:

$$\text{Species richness} \sim \text{Negative binomial}(\alpha, \beta)$$

$$\text{PD} \sim \text{Gamma hurdle}(\alpha, \beta)$$

$$\text{sesPD} \sim \text{Gaussian}(\mu, \sigma)$$

For the species richness model, we applied a negative binomial likelihood with a log link as we used over-dispersed count data. The PD model was fit using a gamma-hurdle likelihood with an exponential link as this allowed us to first model the probability of a plot containing any PD (i.e. plots with > 0 species) using a Bernoulli distribution before passing those results with a positive outcome to a truncated gamma distribution. sesPD was modelled using a gaussian likelihood as the model residuals followed a normal distribution. For each of the three models we included the following predictors:

$$= \alpha + \text{plot area} + \text{MAP} + \text{MAT} + \text{precipitation seasonality} + \text{frost days} + \text{soil nitrogen} + \text{soil phosphorous} + \text{soil sand proportion} + \text{fire count} + \text{fire intensity} + \text{herbivore biomass} + \text{MAP} \times \text{precipitation seasonality} + \text{human footprint index}$$

We included plot area as a predictor to account for sampling effort differences between different sized plots as larger plots often contain more species (Dengler 2009). We included the interaction term to assess whether seasonality had a differential effect on woodland diversity along the precipitation gradient. Herbivore biomass included both browsers and grazers as both are likely to influence tree composition – browsers through direct herbivory on trees and grazers through grazer–grass-fire interactions which may reduce fire intensity and grass competition with trees (Staver and Bond 2014). All predictors were standardized to zero mean and one standard deviation, prior to model fitting. We were unable to compute sesPD values for plots with one species as it is not possible to create null communities with only one species in the pool, therefore these plots were dropped from the sesPD analysis (598/6780; 8.8%). We repeated these analyses at the genus-level because if the results between species and genus richness differed this could provide evidence for effects of recent diversification.

Models were fit using weakly informative, non-flat priors (Supporting information), with four chains run for 1000 warmup and 3000 post-warmup samples. Checks of chain convergence and posterior predictive ability were performed on all models. Spatial autocorrelation between plot residuals was tested using Moran's I through the 'spdep' package (Bivand et al. 2013). All statistical analyses were carried out in R (www.r-project.org).

β-diversity and phylogenetic β-diversity analysis

We assessed whether compositional changes between plots were a result of patterns of turnover or nestedness using multi-site Sørensen dissimilarity at the species, genus, and family level. Sørensen dissimilarity (β_{sor}) gives total β-diversity and is comprised of two components: species turnover (β_{sim}) and nestedness (β_{nes}) (Baselga et al. 2010). Beta-diversity metrics were calculated using the 'betapart' R package (www.r-project.org, Baselga and Orme 2012). This process was also performed for phylogenetic β-diversity.

We used generalized dissimilarity modelling (GDM; Ferrier et al. 2007) to identify which environmental predictors best explain observed β-diversity and phylogenetic β-diversity patterns. GDM is an extension of matrix regression, allowing non-linear relationships between compositional turnover and environmental gradients, whilst also depicting the rate of turnover at different points along an environmental gradient. This is achieved through I-spline functions that are fit for each predictor, with the maximum height of an individual I-spline representing the size of a predictor's effect on β-diversity (Ferrier et al. 2007).

Using the 'gdm' R package (www.r-project.org, Fitzpatrick et al. 2021), we first fitted full GDMs that contained all the predictors from our species richness and PD models, excluding plot area, in addition to the pairwise geographical distance between plots. We did this for both taxonomic (Sørensen dissimilarity) and phylogenetic

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β-diversity. After fitting full models, we removed predictors that had no effect on dissimilarity to maximise explained variance and minimise the number of predictors included in the model (Ferrier et al. 2007). Maps of predicted taxonomic turnover were created by projecting our final GDMs back onto rasters of the most influential predictor variables (Ferrier et al. 2007).

Comparing community composition of wet and dry miombo

To test previous assertions that wet and dry miombo are floristically different (Frost 1996), we compared species composition between wet (> 1000 mm MAP; White 1983) and dry (< 1000 mm MAP) miombo plots using permutational multivariate analysis of variance (PERMANOVA). We first filtered plots to only include those from the miombo (White 1983), giving 1663 plots in dry miombo and 3049 plots in wet miombo. We then computed the community composition distances between all pairs of communities using Sørensen dissimilarity, before testing for differences in composition between plots designated as wet or dry miombo using the *adonis2* function from the 'vegan' package (Oksanen et al. 2013).

Results

The effect of environmental gradients on savanna woodland tree species richness

Mean annual precipitation (MAP) had by far the greatest effect on species richness, with richness increasing with rainfall (β_{MAP} = 0.24; 95% credible interval (CI) = 0.20–0.27; model $R^2 = 0.12 \pm 0.01$; Fig. 1, 2a). Species richness also increased with plot area, mean annual temperature, the number of frost days, herbivore biomass, precipitation seasonality, and soil nitrogen content (Fig. 1, 2b, c), although the size of these effects were much smaller than for MAP. Conversely, species richness decreased slightly with increasing human footprint index, soil phosphorous content, and fire intensity (Fig. 1, 2d). The model was highly confident of the direction of these effects, with 0 lying outside of the 95% CI of the posterior for all predictors (Fig. 1). There was no effect of the remaining variables on species richness (Fig. 1), with the 95% credible interval of the posterior overlapping 0 in each case. Our results were similar when we analysed at genus level (Supporting information) and the model residuals showed no evidence of spatial autocorrelation (Moran's I = 0.006; $p < 0.001$).

β-diversity of savanna woodland tree communities over environmental gradients

Changes in community composition across our sampled plots overwhelmingly showed patterns of turnover ($\beta_{SIM} \sim 1$) as opposed to nestedness ($\beta_{NEST} < 0.01$) at the species, genus, and family levels. Turnover between communities increased as the difference in the environmental conditions between communities increased (Fig. 3a). The GDM predicted a clear turnover in species composition over rainfall gradients (Fig. 3a).

Precipitation seasonality (Fig. 3b) and MAP (Fig. 3c) are the most important predictors of community dissimilarity, as judged by the I-spline heights. Their influence was most evident in communities with low seasonality of precipitation and in communities with up to ~ 800 mm MAP (Fig. 3b, c). Geographic distance has the third highest I-spline, with its influence increasing with pairwise distance (Fig. 3d). MAT (Fig. 3e) and herbivore biomass had a greater influence on predicting community dissimilarity as temperatures and herbivore biomass increased, although the overall amplitude of their effects was smaller than that of precipitation seasonality, MAP, and geographic distance. Human footprint index, and fire count and intensity had a small but consistent effect on dissimilarity. Soil P and soil sand proportion had a small effect on dissimilarity at the extreme of their ranges. Soil nitrogen content and number of frost days were not included in the final GDM as they had no influence on community dissimilarity.

Comparing community composition of wet and dry miombo

Species composition differed significantly between wet and dry miombo plots (MANOVA: $r^2 = 0.006$, df = 1, p = 0.001). However, the model had a very low R^2, suggesting that splitting the plots by wet (> 1000 mm MAP) and dry (< 1000 mm) miombo explained very little compositional variation. There was considerable overlap in composition between wet and dry plots (Supporting information). Both MAT ($r^2 = 0.02$, df = 1, p = 0.001) and the number of frost days ($r^2 = 0.01$, df = 1, p = 0.001) explained more of the variation in plot composition than did the split between wet and dry miombo.

Savanna woodland tree phylogenetic α- and β-diversity over environmental gradients

Patterns of phylogenetic diversity (PD) closely mirrored those of species richness. PD increased with MAP (β_{MAP} = 0.13; CI = 0.11–0.15; model $R^2 = 0.09 \pm 0.007$; Fig. 4) and plot area ($\beta_{PLOT\ AREA}$ = 0.05; CI = 0.04–0.06). PD also increased with the number of frost days, MAT, herbivore biomass, and precipitation seasonality but the size of these effects was much less than that of MAP (Fig. 4). Greater fire intensity was associated with a decrease in phylogenetic diversity ($\beta_{FIRE\ INTENSITY}$ = −0.02; CI = −0.03 to 0.01). For the remaining variables the posterior distribution of the parameter estimates overlapped zero, meaning the model was not confident of a directional effect of these (Fig. 4).

In contrast to PD, the standard effect size of PD decreased with MAP (β_{MAP} = −0.2; CI = −0.26 to 0.14; Fig. 4) and plot area ($\beta_{PLOT\ AREA}$ = −0.12; CI = −0.15 to 0.09), and also decreased with greater precipitation seasonality (β_{PRECIP} = −0.12; CI = −0.16 to 0.09). Similarly to PD, sesPD

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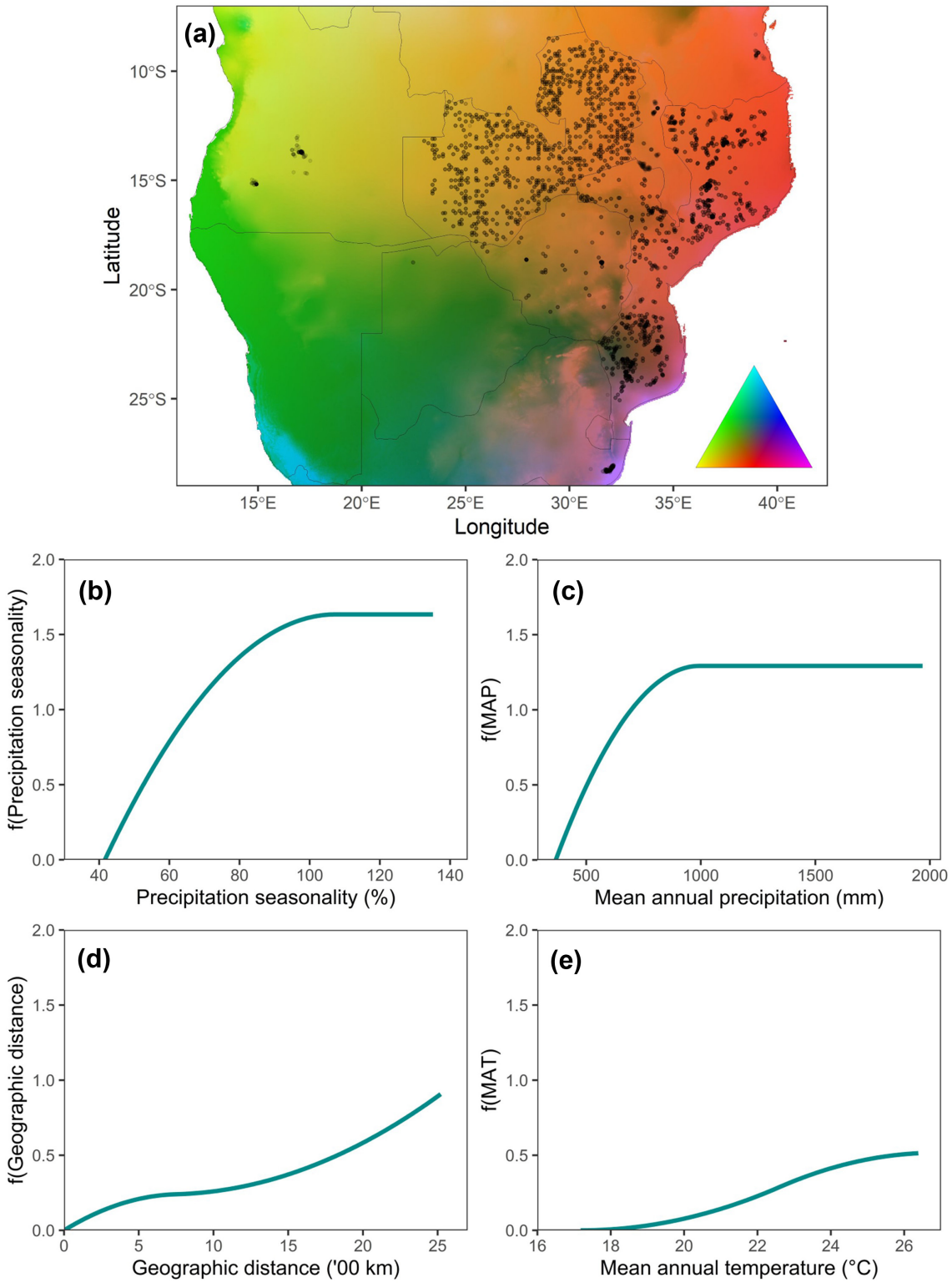

Figure 3. (a) Differences in predicted community composition based on principal component analysis (PCA) of the most important generalized dissimilarity modelling (GDM)-transformed environmental predictors, where more similar colours indicate more similar expected composition (Mokany et al. 2022), black dots indicate plot locations, and inlaid is a triangular colour key showing the range of possible colours. Individual I-splines from final GDM showing the influence of (b) precipitation seasonality, (c) mean annual precipitation, (d) geographic distance and (e) mean annual temperature in predicting community dissimilarity. The maximum height of an I-spline shows the size of a predictor's effect on driving β-diversity patterns whilst the slope of the I-spline shows the rate of change at that point along the predictor's gradient. Higher and steeper I-splines show a greater and more rapid effect on β-diversity, respectively.

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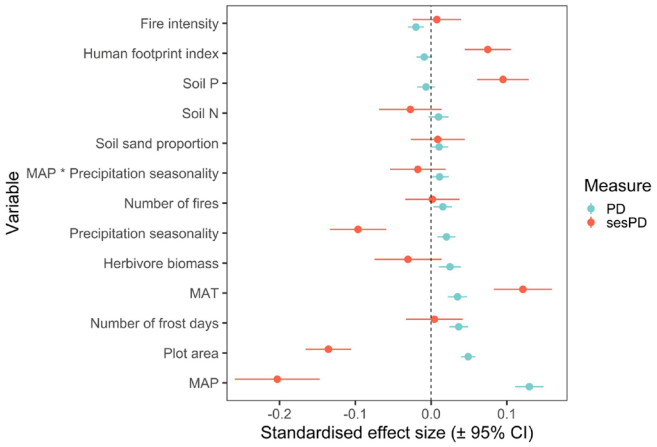

Figure 4. Determinants of tree phylogenetic diversity. Standardised effect sizes are shown for each variable in the regression models. Points and lines show the mean and 95% credible intervals respectively. Points to the left of the dashed line had a negative effect on species richness, whilst those to the right had a positive effect.

increased with MAT, but also increased with soil P content and human footprint index (Fig. 4). The model was highly confident of the direction of these effects, with 0 lying outside of the 95% CI of the posterior for each of these variables (Fig. 4). All other variables had no directional effect on sesPD, with the 95% CI of the posterior of its coefficient overlapping 0 (Fig. 4).

Phylogenetic β-diversity was mostly characterised by patterns of turnover ($\beta_{PHYLO\ SIM} = 0.35$) but, in contrast to species richness, also showed signs of nestedness ($\beta_{PHYLO\ NEST} = 0.15$). Again, precipitation seasonality was the most important predictor of phylogenetic community dissimilarity as judged by its I-spline height (Fig. 5a). Fire count and MAT were then the most important predictors of phylogenetic dissimilarity (Fig. 5b, c), with the effect of both becoming greater towards their upper limits. MAP, soil sand proportion, geographic distance, herbivory, soil phosphorous content and human footprint index all had a minor influence on phylogenetic dissimilarity (Fig. 5d–f). Soil nitrogen content, number of frost days, and fire intensity had no effect on phylogenetic dissimilarity and so were not included in the final GDM.

Discussion

Using plot-level data, we tackled the key knowledge gap of how environmental gradients structure tree biodiversity within disturbance-driven savannas. Focusing on the eastern and southern African woodlands – the world's largest savanna – we find clear climate effects on all aspects of tree diversity with second order effects of soil, human use, and other disturbance agents. Precipitation gradients are particularly strong drivers of tree richness and community assembly in savanna woodlands, with wetter savannas containing more tree species than drier savannas, and high community turnover across the region largely driven by precipitation regimes. Patterns of phylogenetic diversity closely follow those of species richness. Phylogenetic turnover was lower than taxonomic turnover but more pronounced than phylogenetic nestedness, with these patterns again largely driven by precipitation regimes.

Climate–richness relationships in savanna

Species richness was positively related to precipitation volume, similar to observations from moist tropical forests (ter Steege et al. 2003) and previous studies of southern African woodlands (O'Brien et al. 1998, Godlee et al. 2021). Several hypotheses have been proposed to explain the mechanisms that drive this relationship, which is widely observed across taxa and biomes (Gaston 2000, Currie et al. 2004). Previously, positive relationships between rainfall and species richness in southern Africa have been used as evidence in support of the energy-richness hypothesis (O'Brien et al. 1998). The energy-richness hypothesis suggests that greater energy availability leads to more individuals and consequently more species, but evidence for this is conflicting (Keil and Chase 2019). Our finding that species richness increases with both MAP and MAT, proxies for energy, could support the energy-richness hypothesis in savannas. Alternatively, high turnover across the region and the greater PD of wetter plots could provide evidence in support for the physiological tolerance hypothesis determining climate-richness patterns in savanna. Functional tradeoffs to survive extremes may inhibit the ability of species found in the wettest plots of our study region from occurring in the driest plots (Vinya et al. 2013). A trait-based study could more explicitly test this, assessing whether wetter environments allow a greater range of functional strategies and therefore drive our observed climate–richness relationship (Spasojevic et al. 2014).

Tree species richness was also weakly positively related to soil nitrogen content, MAT, herbivore biomass, and the number of frost days, and weakly negatively related to soil phosphorous content. The positive effect of soil nitrogen content is unsurprising given its role in determining miombo canopy structure (Shirima et al. 2015), whilst the negative effect of soil P on richness may be the result of a greater number of ectomycorrhizal species in nutrient-limited soils (Frost 1996). Temperature and the lack of frost is a strong determinant of savanna phenology and productivity (Frost 1996, Chidumayo 2001), potentially explaining its positive relationship with species richness (Godlee et al. 2021).

Increasing species richness with herbivore biomass may result from suppression of dominant competitive plants through grazing and browsing (Pringle et al. 2016) or reduction of fire fuel resulting in less death by fire – potentially evidenced by our result of increasing fire intensity having a negative effect on species richness. Despite its importance in determining the distribution of savannas (Lehmann et al. 2011), fire frequency had no effect on the tree species

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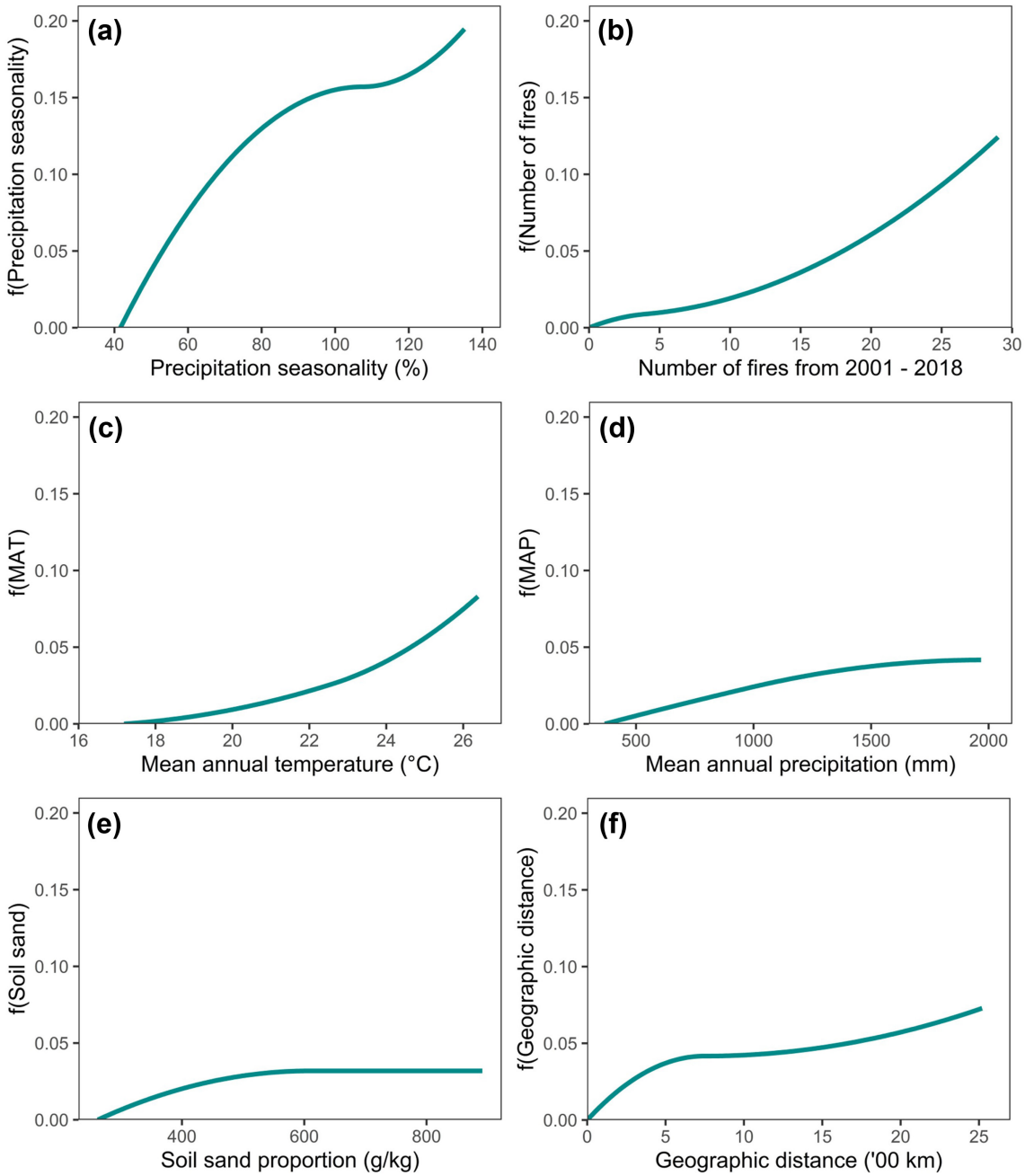

Figure 5. Individual I-splines from phylogenetic GDM showing the influence of (a) precipitation seasonality, (b) fire count, (c) MAT, (d) MAP, (e) soil sand proportion and (f) geographic distance in predicting phylogenetic community dissimilarity of trees across the woodlands of eastern and southern Africa.

richness of woodlands, repeating patterns observed after prescribed fires in the dry miombo (Furley et al. 2008). However, this could result from the coarse nature of available fire and herbivory data, which may not accurately capture the disturbance experienced by these systems as these drivers may operate on smaller spatial scales. Species richness declined with increasing human footprint index, potentially due to widespread utilisation of savannas by local people (Ryan et al. 2016) which can reduce tree diversity (Tripathi et al. 2019, 2021).

Savanna tree β- and phylogenetic-diversity responses to environmental gradients

Our results show widespread turnover in tree community composition across savanna woodlands of eastern and southern African, driven largely by precipitation patterns. High turnover is surprising given the dominance of miombo woodlands by the same genera across their range (Frost 1996). Turnover suggests that interspecific responses to environmental filters are important in structuring

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communities, which is consistent with previous work highlighting strong associations between species and precipitation regimes (Engelbrecht et al. 2007). Our results mirror high taxonomic turnover observed in Panama (Umaña et al. 2021), but contradict patterns of nestedness from the Western Amazon (Esquivel-Muelbert et al. 2017). Turnover might be a characteristic of semiarid tree floras, as similar results have been found in dry forests of the Americas (DRYFLOR 2016), and a result of our study investigating community structure over lower precipitation gradients (< 2000 mm compared to up to 3500 mm in Esquivel-Muelbert et al. 2017).

Precipitation seasonality was the primary driver of compositional turnover, showing a similar pattern to tropical forests in the Western Ghats, India (Davidar et al. 2007). The strong influence of precipitation seasonality is consistent with the role of seasonal water availability in determining miombo species' distributions (Vinya et al. 2013). MAP plays an important role in structuring community dissimilarity between 360 and ~ 800 mm of rainfall, suggesting that at large scales, composition of drier savanna woodland is structured by climate as opposed to disturbance regimes, in a similar way to woody cover (Sankaran et al. 2005). Fire, MAT, and soil nitrogen content played a limited role in determining β-diversity patterns. Fire determines savanna distributions (Lehmann et al. 2011) whilst temperature range is an important determinant of productivity in the miombo (Chidumayo 2001), so their limited effects on community structure are surprising.

Our study provides further evidence of high, almost complete, turnover in the bistable region (700–1900 mm MAP) – the climatic area in which both savannas and forests are widespread – previously identified by Aleman et al. (2020). High turnover reflects the greater floristic heterogeneity of eastern and southern African savannas compared to those in the north and west (Fayolle et al. 2019). Initial classification of miombo drew a clear distinction between wet (> 1000 mm MAP) and dry (< 1000 mm) woodland (White 1983), and whilst we did find a difference in the species composition of wet and dry miombo, there was considerable overlap in communities. However, this may result from our focus on trees, which give rise to different biogeographic divisions than analysis including herbs and shrubs (Droissart et al. 2018).

Evolutionary diversity peaks at around 1500 mm of MAP in South America (Neves et al. 2020), but we did not find such a peak. PD increased with MAP, but this pattern was reversed when accounting for species richness. This suggests that there is both an increase in species richness but also replacement of dry-adapted species with phylogenetically clustered species adapted to wetter conditions. The sesPD of wetter plots was more negative than drier plots, suggesting greater levels of phylogenetic redundancy. This redundancy could protect the long-term functioning of these plots as losses of species are less likely to lead to losses of unique evolutionary diversity (Yachi and Loreau 1999). However, these patterns could also be explained by the negative correlation of sesPD and species richness (Sandel 2018). As the regional species pool increases in size, absolute index values of communities increase making it difficult to compare the magnitude of environmental-biotic filtering between communities with different numbers of species (Sandel 2018). We found very little effect of humans on PD, in contrast to patterns observed in central African rainforests where undisturbed, semi-deciduous and transition forests have greater evolutionary diversity than evergreen forests (Réjou-Méchain et al. 2021).

Caveats

One caveat to our study is that the processes that shape species' evolution and diversification in these woodlands are likely to have acted on a timescale outside of the period which our predictors cover. However, contemporary patterns of biodiversity are a result of both evolutionary processes acting on geological timescales (Mittelbach et al. 2007) and more recent climatic conditions (Currie et al. 2004). Whilst the long abiotic and evolutionary history of these woodlands is likely to have shaped their current diversity and composition, more recent climatic conditions are also strong determinants of community assembly (Field et al. 2009) and reflect measurable processes given the lack of very long-term geological and climatic data. Following this, an additional caveat is that our study only uses climatic data from 1970–2000 as this is the data freely available from WorldClim (Fick and Hijmans 2017). Furthermore, this is the time period during which many of these trees (>10 cm DBH) established. However, given that precipitation is a key driver of tree community composition in these woodlands, understanding how communities are responding to current, and will respond to future rainfall, offers an interesting avenue for future research.

Conclusions

We use plot-level data to show strong climate–richness relationships in savannas. Precipitation patterns play a primary role in determining savanna woodland community composition, similar to patterns observed across the moist tropics. Tree species richness and evolutionary diversity increase with rainfall, while precipitation seasonality and amount are important drivers of β-diversity patterns. Disturbance from herbivory and fire plays an important role in determining savanna physiognomy and distribution globally, but disturbance appears to play a minor role in influencing community composition and diversity in eastern and southern African woodlands. High turnover across eastern and southern African woodlands at multiple taxonomic levels suggest that protecting woodlands across environmental gradients is necessary to maximise conservation outcomes.

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Author contributions

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k98sf7mcb (Davies et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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